TITLE: SPECIATION IN THE NORTH AMERICAN GENUS *DIONDA* (TELEOSTEI: CYPRINIFORMES)

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INTRODUCTION

Cyp Fishes of the genus *Dionda* are common inhabitants of ~~many~~ streams and springs in arid and semi-tropical regions of southwestern North America. Most species occur in tributaries of the Gulf of Mexico from the Colorado River, Texas, to the Río Misantla, Veracruz, Mexico. Two species are now known to occur on the Pacific versant in the upper Río Mezquital, Durango and Zacatecas, Mexico. The genus was previously reviewed by Hubbs and Miller (1977), as well as Hubbs and Brown (1956), and consisted of eight species. Since then, two new species were discovered in the Río del Tunal (Río Mezquital) (R. R. Miller, Pers. Comm.) and *Dionda episcopa* has remained a complex of forms.

Most intriguing about the members of this genus, from an evolutionary perspective, has been the distributions of individual species, their morphological similarities, and their heretofore unknown evolutionary relationships. Unique to these species among North American rs of species have sympatric distributions, and each pair is distributed allopatrically with respect to all other paired members. Morphological similarities of sympatric forms, as well as their predilection for particular habitats and geological provinces has prompted a nomenclature of "species pairs" within the genus (Hubbs and Miller, 1977).

One hypothesis obvious from the patterns of diversity and overall similarity within *Dionda* is that the distinctive, sympatric species pairs are the result of multiple occurrences of sympatric speciation, wherein sympatric members represent closest genealogical relatives. If corroborated with appropriate patterns of descent, these species would represent a significant occurrence among vertebrate organisms. Sympatric speciation, as a general mechanism for diversity, is extremely rare among vertebrates, perhaps accounting for only about 6% of the speciation events in clades where patterns of relationship and distributions are well known

Alternatively, species pairs within *Dionda* may have resulted from multiple, congruent speciation events involving two or more separate and independent ancestral lineages evolving

nch (1989). Thus oecu es paia Dionda uould represent a NM, yet

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in sympatry, and responding to similar geographic isolating mechanisms. In other words, this latter hypothesis involves a vicariant explanation with largely allopatric speciation, wherein two or more ancestral species, occupying the same geographic ranges together, underwent a similar pattern of isolation and divergence to produce the paired species observed today. Simply from a statistical perspective, this latter hypothesis is more likely in that about 70% of investigated speciation events in vertebrates involve strict allopatric speciation (Lynch, 1989).

Evaluation of hypotheses such as these in evolutionary biology and biogeography requires knowledge of genealogical descent among the organisms in question. Support for a general hypothesis of sympatric speciation requires that sympatric taxa be sister species. For the general hypothesis of large-scale vicariant patterns, members of a given species pair should have sister species located in the same region. All too frequently, however, these data are not available in discussions identifying differing modes of speciation. The same is true for members of the genus *Dionda.* Although displaying intriguing evolutionary patterns of diversity and adaptation, fruitful for studies in evolutionary biology, patterns of descent are virtually unknown.

[illegible] Herein we investigate the evolutionary relationships of the species of *Dionda* using allozyme electrophoresis. These relationships are then employed in the evaluation of alternative hypothesis for modes of speciation and biogeographic history ~~of members of this intriguing North American fish genus.~~ [illegible]

MATERIALS AND METHODS

Specimens were captured by seine, placed in liquid nitrogen upon capture, and stored at -70°C until dissected for electrophoretic examination. All species of *Dionda* were examined, except *D. rasconis.* Attempts to collect this species were unsuccessful. Voucher materials representing most sampled localities are deposited in the University of Alabama Ichthyological Collection (UAIC) and listed below. Other vouchers are under the ~~the property~~ of Klaus D. Kallman (KDK), New York Aquarium. Samples are arranged by species and by drainage; the number of specimens of each examined electrophoretically is enclosed in parentheses.

Dionda catostomops Las Cascadas and Río Tamasopo near town of Tamasopo, San Luis Potosi, Mexico, UAIC 7898.01 (109). *D. dichroma*: Spring at Puerta del Río, 20 km SE of Cerritos, San Luis Potosi, Mexico, UAIC 7903.02 (20); spring-fed marsh (La Media Luna System) 10 km S Rio Verde, San Luis Potosi, Mexico, UAIC 7899.01 (30). *D. diaboli:* Devils River at Bakds Crossing, Hwy 163, Val Verde Co., TX, UAIC 8354.04 (20). *D. erimyzonops:* Río Axtla on Hwy 20, 0.8 km W jct 120 and 85, San Luis Potosi, Mexico, UAIC 7900.00 (20). *D. ipni:* Rio Tamesi Dr.: Río Guayalejo at Llera, Tamaulipas, Mexico, UAIC 9148.01 (20). Río Pánuco Dr.: Río Matlapa, 2 km N Matlapa at Chalchitepetl, San Luis Potosi, Mexico UAIC 9153.01 (7). Arroyo Palitla at Palitla, 3 km N Tamazunchale, San Luis Potosi, Mexico, UAIC 9152.01 (7). Río Calnali at Calnali, Hidalgo, Mexico KDK88-21 (9). Río Tuititlan at San Felipe de Orizatlan, Hidalgo, Mexico, KDK88-11 (15). *D.* sp. cf. *ipni*: Río Axtla on Hwy 120, 0.8 km W jct 120 and 85, San Luis Potosi, Mexico, UAIC 7900.05 (13). *D. mandibularis*: Spring at Puerta del Río, 20 km SE of Cerritos, San Luis Potosi, Mexico, UAIC 7903.01 (9). Spring-fed marsh (La Media Luna System) 10 km S Rio Verde, San Luis Potosi, Mexico, UAIC 7899.02 (20). *D.* sp. cf. *episcopa* (Ojo de Agua): Ojo de Agua de San Juan, 1 km N of Los Berros, Durango, Mexico, UAIC 7893.01 (20). *D.* sp. cf. *episcopa* (El Vergel): El Vergel spring near Gualterio, Zacatecas, Mexico, UAIC 7894.01 (19). *D. episcopa:* Lost River at Bitter Lake, Chavie. Co., NM (20). Pecos River at Pandale, Val Verde Co., TX (20). Creek at Hwy 17, 11 km S Fort Davis, Jeff Davis Co., TX (15). Limpia Cr. at Fort Davis, Jeff Davis Co., TX (15). *D. argentosa*: Devil's R. at Baker Crossing, Val Verde Co., TX, UAIC 8354.03 (20). San Felipe Spring, Val Verde Co., TX, UAIC 8351.03 (20). *D. serena:* Río Frio Dr.: Río Frio at Hwy 127, Uvalde Co., TX (9). Cedar Cr. at RR336, Uvalde Co., TX (18). Can Creek at Lost Maples State Park, Bandera Co., TX UAIC 8348.02 (20). *Nueces R. Dr.:* Nueces R. at Hwy 55, S of Barksdale, Real Co., TX (20). Nueces R. at Hwy 335, Edwards Co., TX (10). Campwood Creek at RR 337, Real Co., TX (12). *D.* sp. cf. *episcopa* (Guadalupe/Colorado R.): Fesenden Spring at Heart of Hills Texas Park and Wildlife Station, Kerr Co., TX, UAIC 8350.01 (20). Creek at Heart of Hills Texas Park and Wildlife

Station, Kerr Co., TX (10). Bailey Cr., 19 km SW Junction on Hwy 337, Kimble Co., TX, UAIC 8347.10 (20). ***D.** couchi:* Rio San Juan at Castillos, Nuevo Leon, Mexico, UAIC 0000.00 (20). ***D.*** sp. cf. *episcopa* (Conchos R.): tributary, **Río** San Juan, 26 km S Canutillo on Hwy 45, Durango, Mexico, UAIC 7904.01 (20). *Hybognathus regius:* Turkey Cr., Hwy 97, 17 km NW Chester, Chester Co., SC, UAIC 7930.01 (4). ***H.** placitus:* South Canadian R., Hwy 99, Seminole-Pontotoc Co. line, OK, UAIC 8005.02 (10). *Campostoma oligolepis:* Gurley Cr. at Gurley on Co. Rd. east of Hwy 75, Blount Co., AL, UAIC 3023.02 (10). *C. ornatum*: **Río** San Pedro at **Meoquí,** Chihuahua, Mexico, UAIC 7909.02 (10). *Nocomis micropogon:* Red Bird R., unmarked rd. 5 km from Hwy 80, near jct 66, Clay Co., KY, UAIC 7972.05 (6). *Cyprinella camura:* Buffalo R., 2.4 mi NW Hwy 24, Wilkinson Co., MS.

Skeletal muscle and eye/brain were dissected from each individual, mechanically homogenized, and centrifuged at 16,000 g at 4°C for 10 min to obtain the separate supernatant fraction. Extracts were subjected to horizontal starch gel electrophoresis at 5°C using 12% gels (Connaught Laboratories, Toronto). The products of 35 presumptive structural gene loci were resolved using standard histochemical staining methods and electrophoretic conditions (Table 1). Locus designations follow vertebrate homology, except where homology is uncertain and then they are numbered. Allelic products were lettered (lower case) to reflect differing mobilities within a locus and are relative to this study only.

Presumed individual genotypes were analyzed using BIOSYS-1 (Swofford and Selander, 1981) and FREQPARS (Swofford and Berlocher, 1987). BIOSYS-1 algorithm was used to compute allelic frequencies, mean heterozygosity per locus, mean number of alleles per locus, percent polymorphic loci, and genetic distances (Cavalli-Sforza and Edwards, Rogers, Prevosti). Distance coefficients were clustered using the distance Wagner algorithm, multiple addition criterion, and outgroup rooting. FREQPARS (IBM mainframe version) was used to calculate the shortest evolutionary tree using allelic frequencies from polymorphic loci and maximum parsimony. Character/state coding was not employed. The initial FREQPARS tree was compared with user input trees with topologies derived from distance routines, as well as alternative solutions of the initial FREQPARS tree modified in branch swapping manipulations. The single minimum length phylogenetic tree derived from FREQPARS (length = 388.730) was used to infer history of speciation in *Dionda* and is supported by the presence or absence of synapomorphic electromorphs (alleles) and not only changes in gene frequencies. Outgroup taxa used for *Dionda* relationships included *Hybognathus regius, H. placitus, Campostoma oligolepis, C. omatum, Nocomis micropogon,* and *Cyprinella camura.* Most of these taxa *(Hybognathus* and *Campostoma)* represent nearest genealogical relatives *to Dionda* (Mayden, 1989). Genotypic arrays and distance trees are available from RLM.

Distribution of Species

Traditionally, *D. episcopa* has been considered a single, polytypic species ranging from the Colorado River, Texas, west into the Río Grande System and south to the Río Conchos. Girard (1854), Hubbs and Brown (1956), and others have noted that the roundnose minnow is a complex of forms. Results from the present investigation support previous findings based strictly on morphological data. *Dionda episcopa* Girard is restricted to the Río Grande and tributaries ~~above~~ the Devils River ~~and probably isolated streams west of the Río Grande in the Big Bend region~~ (Fig. 1). *Dionda serena* Girard and an undescribed form are endemic to the Nueces/Frio and Colorado/Guadelupe rivers drainages, respectively, east of the Río Grande. Knapp (1953) included both drainages for *D. serena,* but Hubbs and Brown (1956) noted morphological traits distinguishing minnows from these drainages and suggested that such a taxonomy was not warranted. *Dionda couchi* Girard, another species previously aligned with *D. episcopa,* is known to inhabit the Río San Juan in the lower Río Grande. This species is presumably the form also found in the Río Salado and perhaps the distinctive form in the Cuatro Cienegas Basin (Minckley, 1969; Rosen and Kallman, 1969), although we have not sampled specimens from either basin. *Dionda argentosa* and at least one undescribed species from the Río Conchos System represent the remaining species removed from the traditional *D. episcopa* complex. Populations from the Devils River and San Felipe Spring include *D. argentosa.* Populations from the upper Rio Conchos represent a distinct species, possibly distinct from populations in the lower reaches of the river. Results from this analysis and observations by Hubbs and Brown (1956) indicate the Río Conchos may contain more than one species. It is likely that samples from the lower Conchos may be more closely related to or the same as *D. episcopa,* rather than the upper Conchos species.

The Devils River minnow, *D. diaboli,* is known only from the Devil River and San Felipe, Sycamore, and Las Moras creeks in Texas, and two locations in Mexico (Fig. 1) (Smith and Miller, 1986). This species is known (or was known, prior to extirpation) to occur sympatrically with *D. argentosa* in Texas. Significantly disjunct from any populations of the *D. episcopa* complex is an isolated record of *D. episcopa* from the endorheic Parras Basin (Smith and Miller, 1986) (Fig. 2) and two undescribed species from Río del Tunal, Durango and Zacatecas (Fig. 1). Because we do not know to what the Parras Basin form is related, or conspecific with, we have not aligned this population with any known species and refer to it as *D.* sp. (Parras) at present.

At least seven species of *Dionda* inhabit rivers draining the Gulf Slope, south of the Río Grande. Distributional details of six of these forms are provided by Hubbs and Miller (1977). *Dionda ipni* is the only species from this compliment known to inhabit Coastal Plain rivers outside the Rio Pánuco Basin. This species ranges from the Río Tamesí to Rio Misantla (Figs. 1, 2). Sympatric throughout-Paeg of the range of *D. ipni* within the Pánuco Basin is *D. erimyzonops* (Fig. 1). *Dionda mandibularis* and *D. dichoma* are sympatric throughout most of their ranges within the Rio Verde System (Figs. 1, 2), although the latter species is more widespread. The species pair *D. catostomops* and *D. rasconis* is restricted to the Río Gallinas System, particularly Río Tamasopo (Hubbs and Miller, 1977) (Figs. 1, 2). The remaining species is an undescribed form detected in this analysis, previously thought to be *D. ipni* from Río Axtla, a tributary to Río Moctezuma (Figs. 1, 2). This species possesses 14 gene products distinct from *D. ipni* and is more closely related to species in the *D. episcopa* complex than to any species presently known to inhabit the Pánuco Basin.

Allozyme Variation

Presumptive gene products for Cbp-2, Gp-1, and M-Icdh-A were monoallelic for all species and populations of Dionda and outgroup taxa. The remaining 32 loci were polymorphic for two (Ald-A, Cbp-1, Ck-B) to seven (Acp-1, Gpi-A, Gpi-B, Mpi-A) allelic products in these taxa (Table 2). Within Dionda, the number of alleles per locus ranged from two at Cbp-1, Ck-B, S-Icdh-A, Ldh-A, and a-Man to seven at Gpi-A, Gpi-B, and Mpi-A (Table 2). For most populations Cbp-1, Ldh-A, and a-Man were monoallelic except for a rare allele observed at Cbp-1 in Pecos River D. episcopa and a-Man in La Media Luna D. mandibularis, and an alternative allele fixed for Ldh-A i *D.* s from the Río Axtla.

As a relative measure of variability, based upon the entire array of polymorphic loci, the mean number of alleles averaged 1.15 per locus and ranged from 1.0 in D. mandibularis, D. ipni, D. sp (Ojo de Agua), D. *episcopa*, D. sp (Guadalupe-Colorado), and *Hybognathus* regius, to 1.4 ± 0.1 (mean + SE) in both samples of D. argentosa (Table 3). The mean number of alleles across all loci within Dionda was 1.16. The percentage of loci polymorphic (100% criterion) averaged 12.0 and ranged from 0 in some samples of D. mandibularis, D. ipni, and D. episcopa, to 28.1% in D. erimyzonops and one Nueces River sample of D. serena (Table 3). Proportions of heterozygosity observed in samples averaged 0.019 and ranged from 0 in some samples of D. mandibularis, D. ipni, and D. episcopa, to 0.062 in the San Felipe Spring population of D. argentosa (Table 3). These populations also possessed the extremes in expected mean levels of heterozygosity, ranging from 0 in populations of the former three species to 0.099 in D. argentosa (Table 3).

Monophyly and Relationships of Dionda

Phylogenetic relationships of species of Dionda have never before been examined. Monophyly of the genus and its relationships to other cyprinids was discussed previously by Mayden (1989). In that study, *Dionda* was considered monophyletic and concluded to be part of a clade involving Nocomis, Campostoma, and Hybognathus. Dionda and Campostoma were found to share a derived modification of the ascending process of the premwdllary, and these genera, plus *Nocomis*, shared a derived closure of the typically open posterior myodome, not shared with *Hybognathus*. *Dionda*, *Campostoma*, and *Hybognathus*, however, also shared a derived morphology of the pharyngeal pad, supporting intimate relationships of these three genera. All five genera shared a coiled intestine, occurring only occasionally outside of this clade in other North American minnows (Mayden, 1989).

Using products from 32 gene loci and the shortest tree generated by FREQPARS (length = 388.730), the monophyly and relationships of *Dionda* were unambiguously resolved (Fig. 3). In the shortest tree, *Dionda* and *Hybognathus* formed sister groups, sister to *Campostoma*. Using *Cyprinella* as a distant outgroup for *Dionda* (Mayden, 1989), the genus *Nocomis* formed the sister group to the *Dionda-Hybognathus-Campostoma* clade.

Monophyly of *Dionda* is supported by the presence of four derived electromorphs (characters) (gene frequency changes not interpreted as synapomorphic characters). These include derived Cbp-1 (allele b), M-Me(b), G6pdh-A(b), and G6pdh-A(c) (Table 4). The sister group relationship between *Dionda* and *Hybognathus* was supported by M-Aat-A(b), Ada(b), and Ldh-B(a). Six characters support the monophyly of the *Campostoma*, *Hybognathus*, and *Dionda* clade. These include Acp-1(b), G3pdh-A(b), S-Icdh-A(a), S-Mdh-A(b), M-Me(c), and Gpi-A(a). The monophyly of *Hybognathus* is supported by 10 allozyme characters, including Ck-A(d), Est-2(a), G3pdh-A(e), S-Icdh-A(c), a-Man(c), S-Sod(e), Tpi-B(a), Tpi-B(e), Gpi-B(a), and the loss of Gpi-A(a). Monophyly of the genus *Campostoma* is also well corroborated with six derived allozyme characters, including Ald-A(b), M-Mdh-A(c), S-Me(c), Pgm-A(a), Pk-A(b), and M-Aat-A(a) (Table 3).

Species **Relationships within** Dionda

Patterns of allozymic evolution within *Dionda* are inconsistent with the present classification employed for the genus 4, 5). Two species, *D. ipni* and *D. episcopa*, do not form natural "species" in that not all populations presently allocated to either ~~of these species~~ form a monophyletic group. For both, some populations are more closely related to other taxonomically recognized species than to other members presently included within each.

Within *D. ipni*, all populations form a monophyletic group, except those from the Río Axtla, which form the sister group to the *D. episcopa* complex (Fig. 4). Among other populations of *D. ipni,* a Río Tamesí and Río Pánuco dichotomy is not supported. All populations examined within *D. ipni* from the Pánuco Basin (excluding Rio Axtla), however, possessed synapomorphic alleles and are distinctive, but only some dichotomous relationships between these samples is evident (Fig. 4; Table 4).

Within the presently recognized *D. episcopa*, *not* all populations form a monophyletic group (Fig. 5). Some samples are more closely related to *D. diaboli* and the two undescribed species from the Río del Tunal. In addition to *D. diaboli* and the two Río del Tunal forms, recognizable monophyletic groups, referable to distinct and diagnosable species within the *D. episcopa* complex, include *D. argentosa* Girard, *D. couchi* Girard, *D. episcopa* Girard, *D.* sp. (Rio Conchos), and *D.* sp. (Guadelupe/Colorado R.). Among these taxa the two Río del Tunal species form a monophyletic group, sister to the Devil's River *D. diaboli* (other populations of *D. diaboli* were not examined). In descending order within the phylogeny, relationships of these three species to others within the complex are nested with the following sister groups: *D.* sp. (Conchos), *D. couchi*, *D. argentosa*, *D. episcopa*, *D. serena,* and *D.* sp. (Guadelupe/Colorado) (Fig. 5; Table 4). All of these species are diagnosable on the basis of allozyme characteristics (Table 4), where multiple populations exist for the species they form monophyletic groups, and some have known diagnostic morphological features (Hubbs and Brown, 1956) further supporting the separation of *D. episcopa* into several species.

Dionda species examined from the Río Pánuco Basin do not form a monophyletic assemblage (Fig. 4). Except for *D. ipni* as a whole (including Río Axtla), however, all other species within the Pánuco Basin possess unique allozyme characters, aut~~o~~apomorphies, supporting their identity and/or monophyly. Between the two identifiable forms of *D. ipni,* the Río Axtla species forms the sister group to the *D. episcopa* complex, while *D. ipni* is sister to this clade. The two populations of *D. dichroma* are monophyletic and form the sister group to the *D. ipni*-*D. episcopa* clade. The three remaining Río Pánuco Basin *Dionda, D.*

catostomops, D. erimyzonops, and *D. mandibularis,* together form a monophyletic group, sister to all other species of *Dionda.* Within the former clade, *D. erimyzonops* and *D. mandibularis* are sister species, sister to *D. catostomops* (Fig. 4; Table 4). Thus, the Pánuco Basin members form a paraphyletic group, relative to *D. ipni* and the *D. episcopa* complexes.

Apparent from the above patterns of descent is that in only one case of the multiple sympatric species pairs present within *Dionda* are two sympatric species sister taxa. Only in the species pair involving the two undescribed forms from the Río del Tunal is a sister species relationship observed. For all other *Dionda* species, sister species are distributed allopatrically.

Alternative Hypotheses of Relationship

In addition to the species relationships described above, additional hypotheses generated from distance Wagner procedures or produced through branch swapping of user-defined trees were evaluated using FREQPARS. Although impossible to evaluate all trees, in all cases the overall length of each alternative tree exceeded the maximally parsimonious tree described above.

Tree length for the hypothesis that *Hybognathus* and *Campostoma* were sister taxa and sister to *Dionda,* with species relationships within *Dionda* as described above, was 395.032. Resolutions examined with *Campostoma* sister to *Dionda* ranged from 391.452 to 391.994. With *Hybognathus* sister to *Dionda,* tree length ranged from 392.086 to 397.679 if Río Pánuco Basin *Dionda* were considered monophyletic. Imposed monophyly of *D. ipni* and *D. episcopa* increased the overall tree length from 399.821 to 409.172 and 389.728, respectively. Tree length supporting the monophyly of *D. ipni* and *D. episcopa* together, with other species relationships within *Dionda* as described in the shortest tree, was 396.052. Relationships of *Dionda* species consistent with the hypothesis that sympatric species represent sister species *(D. mandibularis-D. dichroma, D. ipni-D. erimyzonops, D. episcopa-D. diaboli, D.* sp. Ojo de Agua-D. sp. El Vergel) increased tree length to 400.680.

Although not presented here, none of the generated distance Wagner trees duplicated the tree topology in the shortest tree from FREQPARS. Evaluation of the shortest four or five dendrograms from each of the genetic distances indicate that all of the phylogenies for *Dionda* produced with this method had lengths in excess of the phylogeny employed herein (Table 5). FREQPARS trees derived from Prevosti distance ranged in length from 394.180 to 397.534; those from Rogers trees ranged from 394.110 to 397.530; and from Cavalli-Sforza and Edwards trees ranged from 395.378 to 402.967. Species relationships derived by distance measures varied mostly in the placement of Rio Pánuco *Dionda, Hybognathus, Campostoma,* and *Nocomis.* In some trees, the Río Pánuco *Dionda,* except for the Rio Axtla species, formed a monophyletic group, sister to *Hybognathus.* Some trees resolved *Campostoma* as paraphyletic with respect to *Nocomis* and offered differing relationships within Río Pánuco *Dionda* and the *D. episcopa* complex. In no topologies, however, was *D. ipni* or *D. episcopa* resolved as a monophyletic species. *Dionda episcopa* was paraphyletic with respect to *D. diaboli, D.* sp. (Ojo de Agua), or *D.* sp. (El Vergel), and the placement of the Río Axtla species was basally, but always outside of *D. ipni.* In all resolutions, however, the monophyly of individual species within the *D. episcopa* complex (*D. episcopa, D. argentosa, D. couchi, D.* sp. (Ojo de Agua), *D.* sp. (El Vergel), *D.* sp. Conchos, *D.* sp. Guadalupe-Colorado) was substantiated. Each of these forms was recognized as distinct and monophyletic entities in distance trees, although relationships of these species to one another did vary. In fact, the next shortest phylogenies, relative to the shortest tree employed herein, all varied from this tree only in alternative placements of *D. diaboli, D.* sp. Conchos, and *D. couchi* relative to *D.* sp. (Ojo de Agua) and *D.* sp (El Vergel) (389.73-390.01) or in a possible sister group relationship between the upper Pecos RA. *episcopa* and *D.* sp. Guadalupe-Colorado (391.79).

Relationships of species from the Río Pánuco Basin based on distance measures were incongruent with the shortest FREQPARS tree. In all Rogers and Prevosti trees sympatric species *D. erimyzonops* and *D. ipni* were identified as sister taxa. Sister to these two species was *D. dichroma.* This clade, together with *D. mandibularis* and *D. catostomops* had unresolved relationships. Trees generated with the Cavalli-Sforza and Edwards arc distance were of three types, none of which supported sympatric taxa as sister species. In all three tree types *D. ipni* (excluding Rio Axtla) formed the sister group to other Pánuco Basin members. For two of the tree types *D. mandibularis* formed the sister to the remaining three species, which in one case *D. dichroma* was sister to *D. erimyzonops* and these species sister together were sister to ***D.catostomops.*** The alternative tree displayed *D. dichroma* as sister to *D. catostomops,* with these species sister to *D. erimyzonops.* In the third tree, *D. catostomops* formed the sister group to *D. dichroma* and this clade had unresolved relationships with *D. erimyzonops* and *D. mandibularis.*

Conversion of distance Wagner trees, using three distance measures, into user-defined tree topologies in FREQPARS provided an opportunity to evaluate the relative success of distance techniques in deriving maximally parsimonious trees. Further, these comparisons also provided for an evaluation of the statistical measures typically used in tree comparisons. For the 14 shortest trees generated using distance Wagner procedures (Table 5) no apparent relationship was found to exist between the length of the tree generated by FREQPARS (FPL) and the length of the distance tree (L), the Farris (1972) "f", the Prager and Wilson "F", or the cophenetic correlation (CC). For all three distance measures, tree statistics associated with each resolution before and after optimization were very poor predictors of a "best" or more parsimonious tree, as judged by overall tree length derived from FREQPARS.

Speciation and Biogeography

Integral to any discussion of the evolutionary history of many freshwater fish groups is knowledge of historic drainage patterns, as well as geological and ecological regimes of the past. This is particularly true for fishes exhibiting limited tolerance for a broad spectrum of environmental conditions and those generally restricted to headwater streams and springs, like many species of *Dionda.* Much of the geology and paleohydrology of the southwest in the Río Grande Basin and Range and Central Mexico has been described by Smith and Miller 1986 , Miller and Smith 1986 , and Conner and Suttkus 1986 . Portions of these discussions are summarized here, where relevant to speciation in *Dionda*.

see back (A)

Paleohydrology

The Río Grande system has experienced great change over the last 65 my. The pre-Pleistocene drainage did not include its upper reaches above an area between El Paso, Texas and Las Cruces, New Mexico (Fig. 2 . Prior to this time, in ~~the~~ Miocene to mid-Pleistocene, the upper Río Grande was an endorheic basin draining at times into a series of bolsons, including the extensive Plio-Pleistocene Lake Cabeza deVaca of the Guzmán Basin (Miller, 1981: fig. 4 . Permanent connection between the upper and lower Río Grande occurred in the middle Pleistocene.

see back (C

The Pecos River before ~~the~~ Pliocene was a relatively small tributary to the Río Grande, extending only to the ~~Sacramento~~ Mountains of west Texas. Portions of the upper reaches of the present-day Pecos flowed eastward into the Red and Canadian Rivers, while the middle Pecos flowed eastward into headwaters of rivers of the southwestern Gulf of Mexico Echelle, et al., 1984 . Not until the late Pliocene-early Pleistocene did the ~~headwaters of the~~ early Pecos River ~~begin to~~ erode northward to capture these east-flowing ~~Gulf Coast~~ headwater streams.

Past and present major tributaries of the Río Grande in north-central Mexico include the Ríos Conchos, Aguanaval, Nazas, del Tunal, streams of the Laguna de las Palomas, and the Parras Basin, as well as many other smaller endorheic systems in Chihuahua, Coahuila, Durango, and Zacatecas (Fig. 2 . Of these, only the Río Conchos is presently connected to the Rio Grande system. The other ~~rivers~~, with the exception of Rio del Tunal, flow without exit into the alluvial plains of the Bolsón de Mapimi (Fig. 2 . Ríos Aguanaval and Nazas have their headwaters on the eastern slopes of the Sierra Madre Occidental and flow

7

[illegible] flow

[illegible] hotly [illegible]
[illegible] from southern CO & N [illegible]
[illegible] S by [illegible]

[illegible] too much!

[illegible] Lake [illegible] Pliocene
How can [illegible] ? The [illegible] time [illegible] area
[illegible] suggested

Lake [illegible]
[illegible] began
about 2.7 my [illegible] and swept westward [illegible] and 7.44 ya in
[illegible] suggested [illegible]

eastward across a relatively flat 'alluvial fan. The **Río** Nams has historically migrated within the **bolsón** and emptied at one time into Lake **Tlahualilo** (Tamayo, **1949)** together with rivers of the Laguna de Las Palomas (Fig. 2), between the ~~headwaters of the~~ Conchos and Nazas. Presently, the **Río** Nazas flows into Lake **Mayrán,** together with the small, west-flowing **(now** dry) Parras Basin (Tamayo and West, 1964). The **Río** Aguanaval presently empties into Lake Viesca, which was historically connected to Lake **Mayrán** (Conant, 1963). The curiously situated **Río** del Tunal discharges presently into the **Río** Mezquital **(Río** San Pedro), but was historically part of the Nazas-Aguanaval complex.

Available information regarding drainage patterns of the southern Rio Grande tributaries suggests that a pattern of endorheic basins and expansive **bolsóns** has been a characteristic of the Quaternary period. The bulk of the **Río** Conchos has continued to flow to the north into the **Río** Grande near its present mouth. **Ríos** Aguanaval, Nazas, del Tunal, and those of the Palomas and Parras **basins,** however, have had drainages ~~patterns~~ independent of the **Río** Conchos. Prior to late Pliocene these rivers formed the Old **Río** Nazas flowing northeast and emptying into the **Río** Grande downstream from the Conchos. Three outlets have been proposed for this pre-Pleistocene river system (Fig. 2). Meek (1904) proposed an ancestral outlet into the **Río** Grande near the border of Chihuahua and Coahuila. Arellano (1951) suggested a more likely outlet would have been to the east near Saltillo **(Río** San Juan Dr.) or through a northeastern pass near the Cuatro Cienegas Basin **(Río** Salado Dr.). The latter hypotheses were **questioned** by Minckley (1969) on the basis of geological formations but thought the former of these two would have been more likely.

Stream piracy and isolation **been ~~a~~ common** occurrences in the **history** of ffiettref the southern Rio Grande tributaries. In addition to ~~drainage~~ alterations resulting from rivers shifting course over the relatively low alluvial relief of the **Mexican Plateau,** several headwater transfers appear ~~occurre~~ ~~during the Pleistocene~~ along ~~the~~ eastern slopes of the Sierra Madre Occidental between the Nazas, Aguanavaltnd Palomas, Conchos, and between these rivers and those of the Pacific Slope. Most notably was ~~the~~ capture of the Río del Tunal from the Nazas-Aguanaval by the Río Mezquital during the middle Pleistocene (Fig. 2) (Albritton, 1958).

The lower rios Río Grande has maintained its present location since the Tertiary and flows over a gently sloping Coastal Plain. Along its course, numerous springs and spring-fed creeks flow directly into the river. The two major tributaries containing Dionda species are Río Salado and Río San Juan. The former has its headwaters in northwestern Coahuila, serves as an outlet for Cuatro Ciénegas, and flows southeast to join the Río Grande just south of Nuevo Laredo. Río San Juan drains the bulk of central Nuevo Leon and has its headwaters west of Monterrey. This river ~~was previously connected with the Parras Basin of the interior and~~ empties into the Río Grande downstream from the Río Salado, between the mouth of the latter and that of the Río Grande. Historical drainage m [redacted]d these two rivers are poorly known (Minckley, 1969), except for the hypothesized outlet of the Old Río Nazas through one or both ~~basins.~~

Drainages of the western Gulf Coast containing Dionda have also experienced some drainage modifications, aside from the previously addressed Pliocene early [illegible] headwater capture by the Pecos River (Fig. 2). Headwaters of the Colorado, Guadelupe, and Nueces/Frío rivers all occur above the Balcones Escarpment and drain portions of the Edwards Plateau. Although the lower reaches of these rivers traverse ~~through~~ Coastal Plain sediments and empty independently into the Gulf today, during Pleistocene th base level fluctuated as much as 120 m. With the lowered sea level, drainages now separate were interconnected on the continental shelf, providing the potential for fish dispersal from one ~~river~~ to another. Lower river connection is known to have occurred between the Colorado and Brazos ~~rivers~~, and likely ~~provided connections for~~ between the Guadelupe and Nueces/Frio rivers. However, Rio Grande sediments have obscured the outlets of the last ~~tter~~ two deltas (Conner and Suttkus, 1986).

The paleohydrology of rivers draining the eastern slopes of Mexico, south of the Río Grande, the smaller are not well known. Those containing species of D[illegible] include the major, Pánuco Basin, and lower south Ríos Tuxpán, Cazones, Nautla, and Misantl The last ~~latter~~ four and most of the Río Tamesí, northerdbutary to the Pánuco ~~Basin~~, are ~~primari~~ly entrenched mostly in low relief Coastal Plain sediments derived from the eastern slopes of the Sierra Madre Oriental. The headwaters of the Río Pánuco, however, are intermontane ~~and extend~~ pents in into ~~the~~ highlands of the Sierra Madre Oriental and farther west onto the Mesa Central (Fig. 2 . The origin of this ~~eastern~~ mountain range, forming the eastern border of the Mesa Central (Fig. 2 , dates to ~~the~~ early Eocene during the Hidalgoan Orogeny (de Cserna, 1975 . ~~Following the Eocene orogeny~~, drainage connections between the eastern slopes and central Mexico were terminated with and rivers along the Gulf Slope began to erode into the highland ~~th their drainage advantage~~. Since then, rivers of the Pánuco Basin have incised channels through the mountains and captured some e ~~ern~~ -flowing rivers ~~and~~ associated faunas, previously part of the Río Lerma Basin on the Mesa Central. The Río Moctezuma has its headwaters on the Mesa Central and dos San Juan del Rio, Santa Maria, and Verde'. all been previous tributaries to the Río Lerma ~~Basin~~ (Fig. 2 .

Speciation

Patterns of evolution within D[illegible], derived from allozyme variation, are largely incongruous with the hypothesis of widespread sympatric speciation between species pairs (Figs. 3-5 . In every instance, except perhaps for the species in the Río del Tunal (Fig, all speciation events were allopatric and the recent, descendant species exist in allopatry. Even with the two Río del Tunal species allopatric or perhaps parapatric speciation would be the most likely mode. Presently, both forms are endemic to single springs in the upper Río Mezquital system. However, the form from El Vergel is believed to have been an inhabitant of the river ~~and~~ is found today only in the spring (R. R. Miller, pers. comm.). It is possible that both were sympatric ~~at a previous time~~ before alterations of the river. However, given their present distributions and some knowledge of ~~previous~~ habitats of both forms, allopatric divergence is most parsimonious.

The ancestral species to *Dionda* also presumably evolved in allopatry from its sister species, the then ancestor to *Hybognathus* (Fig.3). Today, sympatry between these two genera occurs only in the Río Grande and Pecos River proper. *Hybognathus amarus* occurs only in the Río Grande drainage probably as a result of dispersa y a Great Plains ancestor (sp. cf. *H. placitus)* when headwaters of Plains streams were captured by the upper Río Grandand Pecos River before ~~the~~ Pliocene Pleistocene (see above). drawn Additional support for this hypothesis is the observation that ***Hybognathus*** is endemic to rivers east of the Río Grande, except the Nueces, Frio, Guadelupe, and Colorado rivers, which are inhabited by species of ***Dionda.*** Thus, the ancestral *Dionda* species presumably inhabited a series of rivers ~~occupying~~ Mexíco, perhaps as far south as the Río Lerma Basin, north to the ancestral Río Grande/Pecos and east along the Gulf Slope to the Old Colorado River. The ancestral *Hybognathus* would have represented ~~the~~ its eastern counterpart. Speciation events leading to the origins of both ~~of~~ these ancestors ~~must have~~ postdated the Cretaceous, and probably Paleocene, ~~because~~ ice much of the Río Grande ~~Basin~~ and other rivers basins inhabited by be *Dionda* and *Hybognathus* were at shore in undated by shallow seas (Thornbury, 1965; Chapin and Seager, 1975; Curtis, 1975).

Some geological events altering a historical pattern of rivers once containing the ancestor to *Dionda* can be identified. In the east, formation of the Sierra Madre Oriental during ~~the~~ Eocene represents one of the earliest events altering the environment between Pánuco Basin and interior drainages (Fig. 2) that contain~~ing~~ the widespread ancestor. This orogeny is correlated with the speciation event separating the Coastal Plain *D. erimyzonops* from its intecmontane sister species, *D. mandibularis.* Another likely correlate with this event includes members of *Dionda* sympatric with these taxa, the Coastal Plain *D. ipni,* or *D. ipni*-like form, and the ~~inter~~montane *D. dichroma.* In both cases the ~~inter~~montane taxon is more

using "inter"

restricted in distribution and found in upland streams, isolated by significant falls from the predominantly Coastal Plain form. The occurrence of *D. dichroma* in a few locations below falls (Hubbs and Miller, 1977) is probably a result of downstream movement.

Interesting in this scenario is that significant evidence supports a paraphyletic *"D. ipni* complex" to the north and west (Fig. 4; *D. ipni, D.* sp., plus *D. episcopa* complex). The widespread distribution of the "*D. ipni* complex" along the Gulf Slope, outside athe Pánuco Basin, suggests that these inferred relationships may not be unusual if a *D. ipni-like* species was ancestral to the *D. episcopa* complex, and was widespread ~~during and shortly after the Eocene~~ in the lower Río Grand&System and interior drainages of Mexico (Fig. 2). This species would have approximated the ancestral *Dionda* species in distribution and in ecology, since many species of *Hybognathus* inhabit Coastal Plains or lowland-type habitats, very much like *"D. ipni"* (Hubbs and Miller, 1977). Because our data for *D. ipni* are restricted to populations of the Pánuco Basin and not inclusive of other Coastal Plain streams inhabited by this form, we cannot immediately address this hypothesis. However, if with further analysis *D. ipni* along the Gulf is not supported as a monophyletic entity and some are found to be more closely related to the *D. episcopa* complex, then this hypothesis may be further corroborated, and a *D. ipni-like* species could have been ancestral to the *D. episcopa* complex. Additional support for this hypothesis is discussed below.

The time of origin for *D. catostomops*, the ancestor to *D. dichroma,"D. ipni"* and the *D. episcopa* complex, and the missing species *D. rasconis* (see Figs. 3-5) remains unresolved. It should be noted, however, that *D. catostomops* and *D. rasconis* have limited, sympatric distributions in the upper Río Gallinas System (trib. to Río Santa Maria) and are isolated from other *Dionda* by a 300 m long series of cascades providing a formidable barrier of isolation. The age of these cascades are unknown but resulted during the Hidalgoan Orogeny and may well be responsible for the divergence of these two species. If so, the relationship of *D. rasconis* may be sister to the *dichroma-ipni-episcopa* clade, congruent with the *D. catostomops* and *D. erimyzonops-D. mandibularis* clade. If both species had their origins in headwater tributaries of the Rio Gallinas then this location in the phylogeny is expected.

Early evolution within the *D. episcopa* complex is marked first by the divergence of the Guadalupe-Colorado species, and then by the separation of *D. serena* from a more southern and western ancestor in the Old Rio Grande System (Figs. 2, 5). Events accounting for these relationships are unknown, but relationships of these species imply a sequence of isolation of the Colorado-Guadelupe rivers and then the Nueces-Frio rivers from the Río Grande System.

The remaining representatives within the *D. episcopa* complex together are found in the ancestral Río Grande System (Figs. 1, 2, 5). The earliest diversification within this complex includes those species north of the river proper (Fig. 1). Although actual dates for the events are unknown, *Dionda episcopa* presumably evolved in the ancestral Pecos River, prior to its capture of headwaters of rivers in the Plains, and *D. aigentosa* likewise became isolated in the Devil's River System. A similar pattern occurs in *Etheostoma lepidum* and *E. grahami* (Echelle et al., 1984). The absence of either *Dionda* species in the upper Río Grande is the result of isolation of this river from the lower section until Pleistocene. A capture of upper Colorado River populations of a *Dionda* species into the Pecos River during the enlargement of the Pecos River in the Pliocene-Pleistocene, and the evolution of either one from a single common ancestor, is not supported. The middle Pecos (Lost River) sample is more closely related to other Pecos samples than to any other populations, including those from the Colorado, Guadelupe, Nueces, and Frio (Fig. 1, 2, 5). There are, however, some cases of homoplasy of alleles shared between the Lost River sample and Gulf Slope drainages that may, in fact, support a previous~~ drainage~~ interchange in ~~the~~ Pleistocene between t1 wo species that had already diverged. ~~However,~~ an exchange leading to speciation via isolation from this event is not supported. Between some or all rivers of the

Nueces-Frio system and the Lost River alleles S-Aat-A(a), Acp(c), Ada(c), and S-Icdh(b) are shared at some frequency (Table 4). The only allele shared between the Pecos and Colorado ~~River~~ ers is S-Icdh(b) in Bailey Creek. The observed expression of these putative homologous alleles may lend support for a the previous transfer and swamping of populations in these two Gulf Slope *Dionda* or may be the result of an expression of shared-primitive electromorphs.

Speciation in the southern component of the *D. episcopa* complex involved an ancestral species largely restricted to an extensive Old Río Nazas system,inclusive-of the Ríos ~~Tunal, Aguanaval;and Nazas~~, the Parras Basin, the-Laguna de las Palomas, portions of the headwaters of the Rio Conchos, some tributaries of the lower Río Grande, and perhaps the Río Lerma of the Mesa Central. Most of this master river system has been supported by geological data, while other components (portions of ríos Conchos and Lerma) are not refuted by geological data, but are suggested on the basis of species distributions and their evolutionary relationships. Outlet of the Old Rio Nazas through the lower Rio Grande, as suggested by Arellano (1951) is supported by the sister group relationship of the Río San Juan *D. couchi* (perhaps the same species from the Rio Salado) to the western members of this clade (Figs. 1, 2, 5). This speciation event could be associated with a separation of the Río San Juan from the Old Río Nazas System, with divergence of *D. couchi* in the San Juan and its subsequent dispersal to the Rio Salado, if the San Juan and Salado *Dionda* represent the same species. The latter remains to be seen. Alternatively, the Old Río Nazas may have flowed northward and connected with the Río Grande between the outlet of the Río Conchos and Pecos, as suggested by Meek (1904) and ~~discussed~~ by Minckley (1969). If so, the isolation of *D. couchi* in the Rios San Juan and Salado, downstream of the mouth of the Old Nazas would account for this speciation event and eliminate the explanation of dispersal of *D. couchi* between the two former rivers. Whatever the case, relationships of the southern members of the *D. episcopa* complex support a lower Río Grande connection and further investigation into the pre-Pleistocene outlets of this river is warranted

Two of the next three speciation events involve exchanges in western headwater tributaries to the Old Rio Nazas. The origin of *D.* sp (Ojo de Agua) and *D.* sp. (El Vergel) in the Río del Tunal is well corroborated by the mid-Pleistocene capture of the Tunal from the Río Nazas System. However, the placement of the upper Río Conchos species with the Old Río Nazas and not with *D. episcopa* and *D. argentosa* of the middle Río Grande ~~is~~ was unexpected considering the ancient history of the Rio Conchos. Presumably this river was not part of the Old Nazas, but was ~~has-~~been in place and emptying into the middle Río Grande well before the Pleistocene, a history which at first appears to be incongruous with dates of speciation hypothesized for the southern *episcopa* complex clade. However, this pattern is put into perspective if one considers the location of the Conchos population and the history of the presently endorheic rivers of the interior.

Prior to the Quaternary desiccation of teinterior rivers previously flowing to the east, either through the Old Nazas or into the BolsOn de Mapimi, the Old Nazas undoubtedly contained at least one form of *Dionda* ~~that was probably throughout the~~ ríos Nazas-and Aguanaval, rivers of the Laguna de las PalomAs, and the Parras Basin (Figs. 1 and 2; also see below). This is supported by relationships of the extant forms of *Dionda* in north central Mexico(as well as the ~~actual~~ occurrence of *D. episcopa* from the Parras Basin within historic time (Smith and Miller, 1984 Given the Río Conchos sample used in this study is from the upper-most headwaters of this river, as well as the documented meanderings and exchanges between rivers on the eastern slopes of the Sierra Madre Occidental and the central alluvial plains (Smith and Miller, 1986), it is not unlikely that the upper Río Conchos *Dionda* sp. represents a relative of a form that previously inhabited the interior basins, but ~~has~~ subsequently became extinct, and exists today in the Conchos as a result of stream capture. Thus, the Río Conchos probably contains more than one species of *Dionda* and the sister group relationship of the upper Río Conchos form with *D. diaboli* plus the del Tunal species has resulted from a peripheral isolation, allopatric event correlated with a headwater transfer to the Conchos early in the Pleistocene. That the Río Conchos *D. episcopa* represents more than one form is further supported by observations of Hubbs and Brown (1956) in their morphological analysis of the *D. episcopa* complex and *D. diaboli*, as well as morphological evidence (pers. obs.). The absence of any *Dionda* from the central interior basins in Mexico excluding the Parras, prof asbeen the result of large scale extinction from desiccation, affecting other taxa as well as *Dionda* (Smith and Miller, 1986).

The sister group relationship between *D. diaboli* and the two Río del Tunal species (Fig. 5) probably resulted from a sequence of events beginning with the closure of the outlet of the Old Río Nazas into the lower Río Grande in the Pleistocene (Arelleno, 1951) and the extinction of *Dionda* species from the interior basins (Fig. 2). The separation of the central basins from the lower Río Grande, either through desiccation or orogenic events ~~in the northern Sierra Madres,~~ would have isolated populations of an ancestor to *D. diaboli* to diverge in direct and free-flowing streams in the middle Río Grande (Fig. 2). The observed broadly allopatric distributions of these sister clades resulted from the desiccation of intervening rivers between *D. diaboli* and the Río del Tunal forms and the extinction of *Dionda* from these interior basins as discussed above. Given this scenario, one might expect, ~~however,~~ that the Río Conchos form would then be more closely related to species of the Río del Tunal. This would not be the case, however, if the isolation and divergence of the Conchos form occurred as a result of stream capture before the termination of the Rio Grande outlet, via peripheral isolation. One might predict, however, that the *Dionda* from the Parras Basin, if available, would be most closely related to the upper Conchos and Río del Tunal

The Río Lerma (Fig. 2) is hypothesized to be the southern-most river system involved in the evolution of *Dionda*. Although no species of *Dionda* ..re known to inhabit this system today, there is some evidence that this drainage ~~was~~ were previously connected to the Old Río Nazas system and with the Río Pánuco, and is known to contain a northern ichthyofaunal component. This river probably contained at one time one or more species of *Dionda*,

[illegible]

similar to the Rio Axtla species. The distributions of four fish species or clades confirm a previous connection between the Río Lerma and more northern or eastern drainages (Miller and Smith, 1986). *Moxostoma austrinum, M. congestum,* and *M. mascotae* together form a track in the Lerma, Mezquital, Conchos, and Río Grande system (Fig. 2). *Hybopsis calientis, H. audidion,* and *H. amecae* form a clade and are distributed in the Ríos Pánuco, Lerma, Mezquital, and Ameca (Chernoff and Miller, 1986; Mayden, 1989). *Chirostoma jordani* is distributed in the Lerma, Pánuco, Mezquital, and Laguna de Santiaguillo (Fig. 2) (Barbour, 1973a) and *Aztecula sallei* occurs in the Lerma, Pánuco, and Balsas rivers (Fig. 2) (Chernoff and Miller, 1981). The Río Lerma also contains *Micropterus relictus,* a fossil centrarchid related to northern species (Smith et al., 1975).

Distributions of the *Moxostoma* are nearly identical to present-day distributions of members in the *D. episcopa* complex, except a Río Lerma basin representative of the ~~latter~~ last clade is absent. The separation and isolation of many interior basins of the Mesa Central is of noted antiquity, dating to at least the Miocene (Barbour, 1973b; Miller and Smith, 1986). Thus, isolation of a member of the *Dionda episcopa* complex in this watershed may have postdated the Hidalgoan Orogeny, yet predated the numerous Pleistocene episodes and the Pliocene entrenchment of the Pecos River, discussed above, and exchange of their faunas. The Hidalgoan Orogeny is correlated with *Dionda* speciation in the Pánuco Basin and the Pliocene-Pleistocene events are associated with divergence within the *episcopa* complex. Temporally between these two correlated events, within the framework of speciation, is the evolution of the Río Axtla *Dionda* sp. (Fig. 4). Although this species is now only known from the Río Axtla, our sampling has been limited and the species is predicted to occur more widely in the Río Axtla/Moctezuma systems.

The Río Axtla species is morphologically similar to *D. ipni,* as is predicted on the basis of the probable distribution of the ancestor to the *D. episcopa* complex and its early divergence from the *D. episcopa* clade. Further, the Río Moctezuma (containing Río Axtla) is known to have captured a significant portion of the Old Rio Lerma as well as other rivers on the Mesa Central (West, 1964; Tamayo and West, 1964). Thus, the highly distinctive and ancient *D.* sp. (Fig. 4) discovered from the Río Axtla is hypothesized to have evolved in an Old Río Lerma Basin, after the isolation of this interior basin from the Old Río Nazas-Río Grande Basin, probably in the Miocene. Subsequently, this species or a relative was transferred to and found refuge in the Río Pánuco Basin, along with other taxa (Miller and Smith, 1986), by the entrenchment of Gulf Slope headwater streams into the Plateau. In addition to significant volcanic disruption, the Lerma system underwent extensive desiccation in the Quaternary, similar to those rivers of the Bolsón de Mapimí (Miller and Smith, 1986). The extinction of a *Dionda* in the Río Lerma system was undoubtedly associated with extremely harsh environmental conditions and represents another example of the fish diversity lost in many interior basins of Mexico (Smith and Miller, 1986; Miller and Smith, 1986).

The above discussion of speciation in *Dionda* is consistent with the phylogenetic, or evolutionary, relationships of the species. For several river systems of the southwest we have only cursory information concerning their previous flow patterns and thus events leading to the divergence of some members are speculative. However, other fish clades are known to inhabit many similar drainages and are appropriate tests of hypotheses proposed herein. Future investigations into populational/species relationships of the *Cyprinella lutrensis* complex, *Cyprinella ornata, Moxostoma austrimum, M. congestum,* and *M. mascotae, Etheostoma pottsi, E. grahami, E. lepidum,* and *E. australe,* as well as other fish group and aquatic organisms will provide a valuable insight into the evolution of the southwestern North American ichthyofauna.

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Paleohydrology

The Rio Grande Rift, south from Colorado through New well into northern Mexico, began to form about 27 mya (Chapin and Seager, 1975; Cape et al., 1983), and was likely occupied by a south-flowing ancestor of the upper Rio Grande shortlv thereafter (Mincklev et al., 1986). This developing system ~~likel~~ flowed east, until deflected south by late Miocene uplift of the Sangre de Cristo Me • (Chapin and Seager, 1975). Drainage to the south in Miocene to middle Pleistocene ~~was lil~~ ~~ly into~~ ended in closed basins, including in Plio-Pleistocene the extensive Lake Cabeza de Vaca of the Guzman Basin (Miller, 1981: Fig. 4) (= Pluvial Lake Palomas of Miller and Smith, 1986). AN a cestral lower Rio Grande, flowing to the Gulf of Mexico from the Big Bend region of Texas or slightly farther west (Fig. 2), was not permanently connected through fb reach between El Paso, Texas, and Las Cruces, New Mexico, until middle Pleistocene.

Before Pleistocene, the Pecos River was a small tributary to the Old (lowermost) Rio Grande, extending north to the Davis Mountains of Texas. Portions of the present-day upper Pecos system flowed east to the Plains (Red and Canadian rivers), while the middle part formed headwaters for streams draining to the southwestern Gulf of Mexico (Echelle, et al., 1987). Not until late Pliocene-early Pleistocene did the ~~early~~ Old Pecos erode north to capture east-flowing streams and become integrated into its present state.

Based in large oart on their faunas (Meek, 1904; Smith and Miller, 1986), past and present major tributaries o the Rio Grande in north-central Mexico include(d) the rios Conchos, Aguanaval, Nazas, del

well as the Parras b
spread
including

Tunal, streams of the lagunas de las Palomas (separate and south of Pluvial Lake Palomas; Fig. 2) and Parras basins, as well as a number of other, smaller systems in Chihuahua, Coahuila, Durango, and Zacatecas (Fig. 2). Of these, only the Rio Conchos is presently connected to the Rio Grande. The others, with exception of Rio del Tunal flow east-northeast from the Sierra Madre Occidental through a narrow zone of basin and range topography onto alluvial floors of a series of endorheic basins. This region is collectively called the Bolson de Mapimi (Tamayo and West, 1964), which forms much of the vast Mesa del Norte of Mexico (West, 1964). The Rio Nazas (together with streams of the Laguna de los Palomas basin (Fig. 2) ~~hat lies~~ between the Conchos and Nazas watersheds,) historically migrated over the flat alluvial surfaces to empty at one time into Lake Tlahualilo (Tamayo, 1949). Presently, the Rio Nazas ends in Lago de Mayran, which persisted as an extensive lake as late as the 16th Century, only desiccate because of artificial control of the stream. The Rio Aguanaval now empties into Laguna Viesca (also dry), which was historically connected to Lago de Mayran (Conant, 1963). The curiously located Rio del Tunal, historically part of the Nazas-Aguanaval complex, presently discharges into the Rio Mezquital (Rio San Pedro) to flow west through the Sierra Madre Occidental to the Pacific Ocean.

Available information indicates a pattern of expansive, sometimes interconnected bolsones and interspered mountains has characterized this region from Miocene to pre ent. The wave of basin and range faulting and extension began with the Rio Grande Rift (27 mya) and passed west to end in Baja California about 7.0 mya. The bulk of the Rio Conchos basin may have drained north into the Rio Grande through much of this period, largely in its present course as marked by deeply incised canyons alternating with reaches crossing all uviated basin floors. Rios Nazas, Aguanaval, del Tunal, and lesser ~~dr~~ ~~nages~~, however, must have had drainages variously independent of the Rio Conchos. Prior to Pleistocene they are thought to have formed an Old Rio Nazas that emptied into the Rio Grande downstream from the Rio Conchos. Three outlets have been proposed for this system (Fig. 2): 1) Meek (1904) proposed an ancestral outlet to the Rio Grande near the border of Chihuahua and Coahuila; 2) Arellano (1951) suggested a more likely path would have been to the east, near Saltillo (thus to the present Rio San Juan drainage); or perhaps 3) draining northeast toward or through the Cuatro Ciénegas area (Río Salado drainage) (see Conant, 1963). The second alternative was considered most probable by Minckley (1969).

Stream piracy and isolation must have been common occurrences in the history of these southern Rio Grande connectives. In addition to alterations resulting from lower parts of rivers shifting their courses over relatively low alluvial relief, several headwater transfers are evident on maps of stream patterns along eastern slopes of the Sierra Madre Occidental between the Nazas, Aguanaval, (Palomas) and Conchos basins, and between these rivers and the Pacific slope. Especially notable was capture of the Rio del Tunal from the Nazas-Aguanaval by the Rio Mezquital during middle Pleistocene (Fig. 2) (Albritton, 1958).

The lowermost Rio Grande has maintained its present course ~~wh~~ ~~it~~ ~~was~~ over the gently sloping Gulf Coastal Plain since the Tertiary. The three major tributaries containing <u>DiondA</u> species are Devil's River, Texas, and Rio Salado and Rio San Juan in northern Mexico. Permanent flow in the Devil's River originates in a large spring and passes a few 10s of kilometers of channel to enter the Rio Grande just upstream from Del Rio. Rio Salado has its source in northwest Coahuila, serves as an outlet for the Cuatro Ciénegas basin, then flows southeast to join the Rio Grande just south of Nuevo Laredo. Rio San Juan drains most of central Nuevo Leon from its headwaters west of Monterrey, to empty into the Rio Grande between the mouth of the Rio Salado. Their historical drainage relations are poorly known (Minckley, 1969), except for the hypothesized outlet of the Old Rio Nazas through one or both of them.

Drainage of the western Gulf Coast containing <u>Dionda</u> have also experienced drainage modifications aside from the previously-addressed, Pliocene-Early Pleistocene headwater captures by the Pecos River (Fig. 2). Headwaters of the Colorado, Guadalupe, and Nueces/Frio rivers all occur above the Balcones Escarpment and drain portions of the Edwards Plateau of Texas. Although the lower reaches of these rivers traverse Coastal Plain **sediments** and today empty independently into the Gulf of Mexico, their base level fluctuated as much as 120 m during episodic climatic oscillations of Plio-Pleistocene. With lowered sea level, drainages now separated were interconnected on the Continental shelf, providing the potential for fish dispersal from one to another. Lower river connection is known to have occurred between the Colorado and Brazos, and likely between the Guadalupe and Nueces/Frio rivers. However, Rio Grande sediments have obscured outlets and deltas of the last two (Conner and Suttkus, 1986).

The paleohydrology of rivers draining the eastern slopes of Mexico, south of the Rio Grande, are less well known. Those containing species of <u>Dionda</u> include the major Rio Panuco basin, and the smaller rios Tuxpan, Cazones, Nautla, and Misantla to the south. The last four and most of the Rio Tamesi, northernmost tributary to Rio Panuco, are entrenched in low-relief Coastal Plain sediments derived from eastern slopes of the Sierra Madre Oriental. The origin of this mountain range, forming the eastern boundary of the Mesa Central, dates to early Eocene, during the Hidalgoan Orogeny (de Cserna, 1975). Drainage connections between the eastern slopes and central Mexico were disrupted with this uplift, and rivers along the Gulf Slope began to erode into the Sierra [illegible] highlands. The southern, well-watered headwaters of the Rio Panuco penetrated even farther, onto the Mesa Central, to capture some west-flowing rivers and associated faunas that were previously part of the Rio Lerma basin. The Rio Moctezuma has its headwaters on the Mesa Central, and the rios San Juan del Rio, Santa Maria, and Verde all may have been earlier tributaries to the Rio Lerma system (Fig. 2).

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TABLE 1: ENZYME SYSTEMS EXAMINED AND ELECTROPHORETIC CONDITIONS

Enzyme (EC Number)	Locus	Tissue	Electrophoretic Conditions*
Acid phosphatase (EC 3.1.3.2)	Acp-A	Brain	D
Adenosine deaminase (EC 3.5.4.4)	Ada-A	Muscle	A
Adenylate kinase (EC 2.7.4.3)	Ak-A	Muscle	A
Aspertate aminatransferase (EC 2.6.1.1)	M-Aat-A	Muscle	B
	S-Aat-A	Muscle	B
Calcium-binding proteins (non-specific)	Cbp-1	Muscle	C
	Cbp-2	Muscle	C
Creatine kinase (EC 2.73.2)	Ck-A	Muscle	C
	Ck-B	Brain	F
Cytosol aminopeptidase (EC 3.4.11.1)	S-Ap-A	Muscle	C
Dipeptidase (EC 3.4.13.11)	Pep-A	Muscle	E
Esterase (non-specific)	Est-1	Brain	E
	Est-2	Brain	E
Fructose-bisphospate aldolase (EC 4.1.2.13)	Ald-A	Muscle	D
General protein (non-specific)	Gp-1	Muscle	C
Glucose-6-phosphate dehydrogenase (EC 1.1.1.49)	G-6pdh-A	Brain	D
Glucose-6-phosphate isomerase (EC 53.1.9)	Gpi-B	Brain	E
	Gpi-A	Muscle	E
Glycerol-3-phosphate dehydrogenase (EC 1.1.1.8)	G3pdh-A	Muscle	D
Isocitrate dehydrogenase (EC 1.1.1.42)	M-Icdh-A	Brain	D
	S-Icdh-A	Brain	D

Table 1. Continued.

Enzyme (EC Number)	Locus	Tissue	Electrophoretic Conditions*
L-Lactate dehydrogenase (EC 1.1.1.27)	Ldh-A	Brain	A
	Ldh-B	Brain	A
Malate dehydrogenase (EC 1.1.1.37)	M-Mdh-A	Brain	D
	S-Mdh-A	Brain	C
	S-Mdh-B	Muscle	C
Malic enzyme (EC 1.1.1.40)	M-Me-A	Muscle	D
	S-Me-A	Muscle	D
Mannose-6-phosphate isomerase (EC 5.3.1.88)	Mpi-A	Brain	C
a-Mannosidase (EC 3.2.1.24)	a-Man	Muscle	E
Phosphoglucomutase (EC 5.4.2.2)	Pgm-A	Muscle	C
Pyruvate kinase (EC 2.7.1.40)	Pk-A	Muscle	D
Superoxide dismutase (EC 1.15.1.1)	S-Sod-A	Brain	A
Triosephosphate isomerase (EC 5.3.1.1)	Tpi-A	Brain	A
	Tpi-B	Brain	A

* A: Tris-citrate pH 8.0 (Selander, et al., 1971); B: Phosphate-citrate pH 8.0 (Selander, et al., 1971); C: Histidine-HCI, pH 8.0 (Brewer, 1970); D: Tris-citrate pH 7.0 (Whitt, 1970); E: "Poulik" system (Selander, et al. 1971); F: EBT system of Page and Whitt (1973).

Table 2. ALLELIC FREQUENCIES FOR SPECIES OF DIONDA, OUTGROUPS AND HYPOTHETICAL ANCESTORS DERIVED FROM FREQPARS.

Node	M-Aat	S-Aat	Acp-1	Ada-A	Ak-A	Ald-A	S-Ap-A	Cbp-1	Ck-A	Ck-B	Est-1
Dionda catostomops	B:1.000	8:1.000	B:1.000	B:1.000	B:0.980 D:0.020	A:1.000	C:1.000	B:1.000	B:1.000	A:1.000	8:1.000
D. dichroma Puerta del Río	B:1.000	B:1.000	B:1.000	B:0.050 C:0.525 D:0.425	B:0.950 C:0.050	A:1.000	C:1.000	8:1.000	8:1.000	A:1.000	B:1.000
La Media Luna	B:1.000	8:1.000	B:1.000	B:0.125 C:0.725 D:0.150	B:1.000	A:1.000	C:1.000	B:1.000	8:1.000	A:1.000	B:1.000
D. mandibularis Puerta del Río	8:1.000	B:1.000	A:1.000	8:1.000	8:1.000	A:1.000	C:1.000	8:1.000	B:1.000	A:1.000	B:1.000
La Media Luna	B:0.950 C:0.050	B:1.000	A:1.000	B:1.000	8:1.000	A:1.000	C:1.000	B:1.000	8:1.000	A:1.000	8:1.000
D. ipni Río Matlapa	B:0.050 C:0.950	8:0.950 C:0.050	C:1.000	C:0.800 D:0.200	B:1.000	8:1.000	C:1.000	B:1.000	C:1.000	A:1.000	B:1.000
Río Axtla	8:1.000	B:1.000	B:1.000	A:1.000	8:1.000	A:1.000	D:1.000	B:1.000	8:1.000	A:1.000	A:1.000
Río Canali	B:1.000	B:1.000	C:1.000	D:1.000	B:1.000	B:1.000	B:1.000	8:1.000	C:1.000	A:1.000	B:1.000
Río Tuititlan	B:1.000	B:1.000	C:1.000	A:0.292 C:0.542 D:0.167	B:1.000	A:1.000	B:1.000	B:1.000	C:1.000	A:1.000	B:1.000
Arroyo Palitla	C:1.000	B:1.000	C:1.000	C:1.000	B:1.000	B:1.000	8:1.000	B:1.000	C:1.000	A:1.000	8:1.000
Río Guayalejo	C:1.000	B:1.000	C:1.000	C:0.286 D:0.607 E:0.107	8:1.000	A:1.000	B:1.000	8:1.000	C:1.000	A:1.000	B:1.000
D. erimyzonops	8:0.950 C:0.050	B:1.000	A:1.000	B:1.000	B:1.000	A:1.000	B:1.000	8:1.000	B:1.000	A:1.000	A:1.000
D. sp. (Ojo de Agua)	A:1.000	B:1.000	D:1.000	A:1.000	B:1.000	A:1.000	B:1.000	8:1.000	B:1.000	A:1.000	B:1.000
D. sp. (El Vergel)	A:1.000	B:0.579 D0.421	A:1.000	A:1.000	B:1.000	A:1.000	B:1.000	B:1.000	B:1.000	A:1.000	A:1.000
D. diaboli	A:1.000	B:1.000	D:1.000	F:1.000	B:1.000	A:1.000	B:1.000	8:1.000	B:1.000	A:1.000	D:1.000

Node	M-Aat	S-Aat	Acp-1	Ada-A	Ak-A	**Ald-A**	S-Ap-A	Cbp-1	Ck-A	Ck-B	Est-1
D. couchi	A:1.000	B:1.000	A:1.000	**A:1.000**	**B:1.000**	A:1.000	A:1.000	B:1.000	A:0.025 8:0.975	A:1.000	**C:1.000**
D. sp. (Conchos)	C:1.000	B:0.975 C:0.025	A:0.184 **D:0.816**	F:1.000	**B:1.000**	A:1.000	8:1.000	8:1.000	8:1.000	A:1.000	E:1.000
D. argentosa **Devils** River	A:1.000	**A:0.275** 8:0.675 C:0.025 E:0.025	A:1.000	C:1.000	B:1.000	A:1.000	B:1.000	B:1.000	B:1.000	A:1.000	E:1.000
San **Felipe** Spring	A:0.944 8:0.056	A:0.182 B:0.682 C:0.136	A:1.000	C:1.000	**B:1.000**	A:1.000	8:1.000	8:1.000	**B:1.000**	A:1.000	E:1.000
D. serena Rio Frio	A:1.000	A:0.278 **B:0.722**	**B:1.000**	8:1.000	**B:1.000**	A:1.000	C:1.000	8:1.000	8:1.000	**B:1.000**	B:1.000
Cedar Creek	A:1.000	A:0.059 B:0.941	**A:0.188** B:0.813	B:1.000	**B:1.000**	A:1.000	C:1.000	8:1.000	**B:1.000**	**B:1.000**	8:1.000
Can Creek	A:1.000	A:0.125 B:0.875	**B:1.000**	B:1.000	B:1.000	A:1.000	C:1.000	**B:1.000**	**B:1.000**	A:1.000	B:1.000
Nueces River (Hwy 55)	A:1.000	A:0.025 **B:0.975**	A:0.750 **B:0.075** **C:0.175**	8:0.075 C:0.900 **D:0.025**	B:1.000	A:1.000	C:1.000	**B:1.000**	B:1.000	A:0.950 **B:0.050**	**B:1.000**
Nueces River (Hwy 335)	A:1.000	8:1.000	**A:0.444** **B:0.111** C:0.444	C:1.000	**B:1.000**	A:1.000	C:1.000	**B:1.000**	8:1.000	A:1.000	B:1.000
Campwood Creek	A:1.000	A:0.042 B:0.958	A:0.250 B:0.667 C:0.083	C:1.000	B:1.000	A:1.000	C:1.000	**B:1.000**	**B:1.000**	A:1.000	B:1.000
D. sp. **(Guadelupe-** **Colorado)** Heart of **Hills**	A:1.000	B:1.000	B:1.000	F:1.000	B:1.000	A:1.000	B:1.000	8:1.000	C:1.000	A:1.000	A:1.000
Fesenden Spring	A:1.000	**B:0.925** C:0.075	8:1.000	F:1.000	**B:1.000**	A:1.000	8:1.000	8:1.000	**C:1.000**	A:1.000	A:1.000

Node	M-Aat	S-Aat	Acp-1	Ada-A	Ak-A	**Ald-A**	S-Ap-A	Cbp-1	Ck-A	Ck-B	Est-1
Bailey Creek	A:1.000	8:1.000	**B:1.000**	F:1.000	**B:1.000**	A:1.000	B:1.000	B:1.000	C:1.000	A:1.000	A:1.000
D. episcopa Pecos River	A:1.000	**B:0.150** C:0.850	8:1.000	A:1.000	**B:1.000**	A:1.000	8:1.000	A:0.550 B:0.450	**B:1.000**	A:1.000	E:1.000
Lost River	A:1.000	A:0.025 8:0.975	8:1.000	C:1.000	A:0.025 8:0.975	A:1.000	C:1.000	**B:1.000**	B:1.000	A:1.000	E:1.000
Ft. Davis	B:1.000	**B:1.000**	**B:1.000**	A:1.000	B:1.000	A:1.000	C:1.000	**B:1.000**	B:1.000	A:1.000	E:1.000
Limpia Creek	8:1.000	8:1.000	8:1.000	A:1.000	8:1.000	A:1.000	C:1.000	8:1.000	B:1.000	A:1.000	E:1.000
Campostoma ornatum	A:1.000	B:1.000	**B:1.000**	C:1.000	8:1.000	**B:1.000**	C:1.000	A:1.000	B:0.950 C:0.050	A:1.000	8:1.000
C. **oligolepis**	A:1.000	F:1.000	F:1.000	A:1.000	**B:1.000**	B:1.000	C:1.000	A:1.000	8:1.000	A:1:000	**B:1.000**
Nocomis micropogon	A:1.000	8:1.000	E:1.000	C:1.000	**B:1.000**	A:1.000	C:1.000	A:1.000	B:1.000	A:1.000	**B:1.000**
Hybognathus regius	B:1.000	B:1.000	B:1.000	D:1.000	**B:1.000**	A:1.000	C:1.000	A:1.000	D:1.000	A:1.000	8:1.000
H. placidus	8:1.000	B:1.000	8:0.813 C:0.188	A:0.100 B:0.900	B:1.000	A:1.000	C:1.000	A:1.000	A:1.000	A:1.000	8:1.000
Cyprinella camura	A:1.000	**B:0.050** F:0.950	F:1.000	A:1.000	A:1.000	A:1.000	C:1.000	A:1.000	A:1.000	A:1.000	A:1.000
39	A:1.000	8:1.000	D:1.000	A:1.000	**B:1.000**	A:1.000	8:1.000	**B:1.000**	8:1.000	A:1.000	B:1.000
40	A:1.000	B:1.000	D:1.000	F:1.000	**B:1.000**	A:1.000	**B:1.000**	8:1.000	8:1.000	A:1.000	D:1.000
41	A:1.000	**B:1.000**	A:0.184 D:0.816	F:1.000	**B:1.000**	A:1.000	B:1.000	B:1.000	8:1.000	A:1.000	E:1.000
42	A:1.000	**B:1.000**	A:1.000	A:1.000	**B:1.000**	A:1.000	B:1.000	**B:1.000**	8:1.000	A:1.000	E:1.000
43	A:1.000	A:0.182 8:0.682 C:0.136	A:1.000	C:1.000	B:1.000	A:1.000	B:1.000	8:1.000	B:1.000	A:1.000	E:1.000

Node	M-Aat	S-Aat	Aop-1	Ada-A	AN-A	Ald-A	S-Ap-A	Cbp-1	Ck-A	Ck-B	Est-1
44	B:1.000	B:1.000	B:1.000	A:1.000	B:1.000	A:1.000	**E:1000**	B:1.000	B:1.000	A:1.000	E:1.000
45	A:1.000	B:1.000	B:1.000	A:1.000	B:1.000	A:1.000	**E:1000**	**81000**	B:1.000	A:1.000	**E:1000**
46	A:1.000	B:1.000	B:1.000	A:1.000	B:1.000	A:1.000	B:1.000	B:1.000	B 000	A:1.000	E:1.000
47	A:1.000	A:0.059 B:0.941	B:1.000	B:1.000	B:1.000	A:1.000	C:1.000	B:1.000	B:1.000	B:1.000	B:1.000
48	A:1.000	A:0.059 B:0.941	B:1.000	**81000**	B:1.000	A:1.000	C:1.000	B:1.000	**80000**	A:1.000	B:1.000
49	A:1.000	A:0.025 B:0.975	A:0.444 B:0.111 C:0.444	C:1.000	B:1.000	A:1.000	**E:1000**	B:1.000	B:1.000	A:1.000	B:1.000
50	A:1.000	A:0.042 B:0.958	A:0.250 B:0.667 C:0.083	C:1.000	B:1.000	A:1.000	**E:1000**	B:1.000	B:1.000	A:1.000	B:1.000
51	A:1.000	A:0.042 B:0.958	B:1.000	B:1.000	B:1.000	A:1.000	**E1000**	B:1.000	B:1.000	A:1.000	B:1.000
52	A:1.000	B:1.000	B:1.000	F:1.000	B:1.000	A:1.000	B:1.000	**8:1000**	C:1.000	A:1.000	A:1.000
53	A:1.000	B:1.000	B:1.000	F:1.000	B:1.000	**A:1000**	B:1.000	B:1.000	C:1.000	A:1.000	A:1.000
54	A:1.000	B:1.000	A:1.000	A:1.000	B:1.000	A:1.000	B:1.000	B:1.000	B:1.000	A:1.000	E:1.000
55	**A1000**	B:1.000	B:1.000	A:1.000	B:1.000	A:1.000	B:1.000	B:1.000	B:1.000	A:1.000	**E:1000**
56	A:1.000	B:1.000	**81000**	A:1.000	B:1.000	A:1.000	B:1.000	B:1.000	B:1.000	A:1.000	B:1.000
57	A:1.000	**81000**	B:1.000	A:1.000	B:1.000	A:1.000	B:1.000	B:1.000	B:1.000	A:1.000	A:1.000
56	B:0.050 C:0.950	B:1.000	C:1.000	**E:0600**	B:1.000 D:0.200	B:1.000	B:1.000	B:1.000	C:1.000	A:1.000	B:1.000

Node	M-Aat	S-Aat	Acp-1	Ada-A	Ak-A	Ald-A	S-Ap-A	Cbp-1	Ck-A	Ck-B	Est-1
59	B:1.000	B:1.000	C:1.000	A:0.225 C:0.542 D:0.233	B:1.000	8:1.000	B:1.000	8:1.000	C:1.000	A:1.000	B:1.000
60	8:1.000	B:1.000	C:1.000	A:0.225 C:0.542 D:0.233	B:1.000	A:1.000	8:1.000	B:1.000	C:1.000	A:1.000	B:1.000
61	B:1.000	B:1.000	C:1.000	A:0.225 C:0.542 D:0.233	8:1.000	A:1.000	B:1.000	B:1.000	C:1.000	A:1.000	8:1.000
62	B:1.000	B:1.000	8:1.000	A:0.100 B:0.125 C:0.542 D:0.233	B:1.000	A:1.000	C:1.000	B:1.000	B:1.000	A:1.000	B:1.000
63	B:0.950 C:0.050	B:1.000	A:1.000	8:1.000	B:1.000	A:1.000	C:1.000	B:1.000	B:1.000	A:1.000	B:1.000
64	B:0.950 C:0.050	B:1.000	A:1.000	B:1.000	B:1.000	A:1.000	C:1.000	B:1.000	B:1.000	A:1.000	8:1.000
65	8:1.000	B:1.000	B:1.000	B:1.000	B:1.000	A:1.000	C:1.000	B:1.000	8:1.000	A:1.000	B:1.000
66	8:1.000	B:1.000	8:1.000	A:0.100 B:0.900	B:1.000	A:1.000	C:1.000	A:1.000	D:1.000	A:1.000	B:1.000
67	A:1.000	B:1.000	8:1.000	A:1.000	8:1.000	B:1.000	C:1.000	A:1.000	B:1.000	A:1.000	B:1.000
68	8:1.000	B:1.000	8:1.000	A:1.000	8:1.000	A:1.000	B:1.000	8:1.000	8:1.000	A:1.000	A:1.000
69	B:1.000	8:1.000	B:1.000	A:0.225 C:0.542 D:0.233	B:1.000	A:1.000	8:1.000	8:1.000	B:1.000	A:1.000	8:1.000
70	B:1.000	B:1.000	B:1.000	A:0.100 B:0.125 C:0.542 D:0.233	B:1.000	A:1.000	C:1.000	B:1.000	B:1.000	A:1.000	8:1.000

Node	M-Aat	S-Aat	Acp-1	Ada-A	Ak-A	Ald-A	S-Ap-A	Cbp-1	Ck-A	Ck-B	Est-1
71	8:1.000	B:1.000	B:1.000	A:0.100 B:0.900	8:1.000	A:1.000	C:1.000	B:1.000	B:1.000	A:1.000	B:1.000
72	B:1.000	B:1.000	B:1.000	A:0.100 B:0.900	8:1.000	A:1.000	C:1.000	A:1.000	B:1.000	A:1.000	8:1.000
73	A:1.000	B:1.000	B:1.000	A:1.000	B:1.000	A:1.000	C:1.000	A:1.000	B:1.000	A:1.000	B:1.000
74	A:1.000	8:1.000	E:1.000	A:1.000	B:1.000	A:1.000	C:1.000	A:1.000	8:1.000	A:1.000	B:1.000
Locus length	12.3120	8.4360	19.1380	29.8450	2.1900	4.0000	14.0000	3.1000	10.1500	2.100	18.0000

Node	Est-2	G3pdh-A	**G6pdh-A**	Gpi-A	Gpi-B	S-Icdh-A	Ldh-A	Ldh-B	a-Man	M-Mdh-A	S-Mdh-A	**S-Mdh-B**
Dionda catostomops	8:1.000	B:1.000	8:0.989 D:0.011	A:0.010 B:0.990	8:1.000	A:1.000	**B:1.000**	A:1.000	B:1.000	**B:1.000**	B:1.000	B:1.000
D. dichroma Puerta del **Río**	B:1.000	A:0.050 **B:0.900** C:0.050	C:1.000	A:1.000	**B:1.000**	A:1.000	B:1.000	A:1.000	**B:1.000**	B:1.000	A:1.000	B:1.000
La Media Luna	**B:1.000**	8:1.000	C:1.000	A:1.000	A:0.025 B:0.975	A:1.000	**B:1.000**	A:1.000	**B:1.000**	B:1.000	A:1.000	B:1.000
D. mandibularis Puerto del Rio	**B:1.000**	B:1.000	C:1.000	D:1.000	**B:1.000**	A:1.000	B:1.000	A:1.000	B:1.000	C:1.000	B:1.000	**B:1.000**
La Media Luna	**B:1.000**	8:1.000	C:1.000	D:1.000	8:0.900 **C:0.100**	A:1.000	B:1.000	A:1.000	A:0.075 **B:0.925**	C:1.000	**B:1.000**	B:1.000
D. ipni Rio **Matlapa**	**B:1.000**	A:1.000	A:1.000	C:1.000	B:1.000	A:1.000	8:1.000	A:1.000	B:1.000	8:1.000	A:0.950 B:0.050	**B:1.000**
Rio **Axtla**	B:1.000	8:1.000	A:1.000	E:1.000	**B:0.885** C:0.115	A:1.000	A:1.000	B:1.000	**B:1.000**	A:1.000	D:1.000	0:1.000
Rio Canali	B:1.000	**B:1.000**	A:1.000	C:1.000	B:1.000	A:1.000	B:1.000	A:1.000	B:1.000	B:1.000	A:1.000	**B:1.000**
Rio **Tuititlan**	8:1.000	B:1.000	F:1.000	C:1.000	A:0.067 8:0.900 C:0.033	A:1.000	B:1.000	A:1.000	**B:1.000**	8:1.000	A:1.000	**B:1.000**
Arroyo **Palita**	B:1.000	B:1.000	A:1.000	C:1.000	C:1.000	A:1.000	8:1.000	A:1.000	**B:1.000**	**B:1.000**	A:1.000	B:1.000
Rio **Guayalejo**	B:1.000	**B:1.000**	A:1.000	C:0.133 F:0.867	8:1.000	A:1.000	8:1.000	A:1.000	**B:1.000**	B:1.000	A:1.000	8:1.000
D. erimyzonops	8:1.000	**B:1.000**	**B:0.053** C:0.947	**B:0.975** E:0.025	B:1.000	A:1.000	B:1.000	A:1.000	8:1.000	B:0.950 **D:0.050**	**B:0.278** C:0.722	**B:0.550** C:0.450
D. sp. **(Ojo** de Agua)	C:1.000	D:1.000	E:1.000	**B:0.025** F:0.975	A:1.000	A:1.000	**B:1.000**	**B:1.000**	**B:1.000**	E:1.000	E:1.000	A:1.000
D. sp. (El **Vergel)**	D:1.000	D:1.000	B:1.000	F:1.000	A:1.000	A:1.000	B:1.000	8:1.000	8:1.000	E:1.000	E:1.000	A:1.000
D. diaboli	C:1.000	B:1.000	B:1.000	C:1.000	A:0.700 C:0.250 D:0.050	A:1.000	B:1.000	8:1.000	8:1.000	E:1.000	**D:1.000**	E:1.000

Node	Est-2	G3pdh-A	G6pdh-A	Gpi-A	Gpi-8	S-Icdh-A	Ldh-A	Ldh-B	a-Man	M-Mdh-A	S-Mdh-A	S-Mdh-B
D. couchi	D:1.000	B:1.000	8:1.000	B:0.700 C:0.300	A:0.500 8:0.184 C:0.105 D:0.132 E:0.053 F:0.026	A:1.000	B:1.000	C:1.000	B:1.000	E:1.000	D:1.000	E:1.000
D. sp. (Conchos)	D:1.000	A:1.000	B:1.000	C:1.000	A:1.000	A:1.000	B:1.000	B:1.000	B:1.000	E:1.000	D:1.000	E:1.000
D. argentosa Devils River	D:0.800 E:0.200	A:0.025 B:0.975	B:1.000	B:0.175 C:0.825	A:0.900 8:0.050 D:0.025 F:0.025	B:1.000	B:1.000	C:1.000	B:1.000	E:1.000	D:1.000	E:1.000
San Felipe Spring	D:0.600 E:0.400	B:1.000	8:1.000	A:0.200 B:0.050 C:0.750	A:0.675 B:0.025 F:0.300	A:0.553 B:0.447	8:1.000	C:1.000	B:1.000	E:1.000	D:1.000	[0.000
D. serena Rfo Frio	F:1.000	8:1.000	B:1.000	A:0.500 B:0.375 C:0.125	A:0.056 F:0.944	A:1.000	B:1.000	C:1.000	B:1.000	E:1.000	A:0.111 D:0.889	E:1.000
Cedar Creek	F:1.000	B:1.000	B:1.000	A:0.929 C:0.071	C:0.063 D:0.094 F:0.844	A:1.000	B:1.000	C:1.000	8:1.000	E:1.000	A:0.067 D:0.933	E:1.000
Can Creek	F:1.000	B:1.000	B:1.000	A:1.000	F:1.000	A:1.000	B:1.000	C:1.000	B:1.000	E:1.000	D:1.000	E:1.000
Nueces River (Hwy 55)	F:1.000	B:1.000	B:1.000	A:1.000	D:0.025 F:0.975	A:0.925 8:0.075	B:1.000	C:1.000	B:1.000	E:1.000	A:0.050 D:0.950	E:1.000
Nueces River (Hwy 335)	F:1.000	B:1.000	8:0.900 C:0.100	A:1.000	F:1.000	A:1.000	B:1.000	C:1.000	B:1.000	E:1.000	D:1.000	E:1.000
Campwood Creek	F:1.000	B:1.000	8:1.000	A:1.000	F:1.000	A:1.000	B:1.000	C:1.000	B:1.000	E:1.000	A:0.083 D:0.917	E:1.000
D. sp. (Guadelupe- Colorado) Heart of Hills	F:1.000	B:1.000	A:1.000	B:1.000	C:1.000	A:1.000	8:1.000	C:1.000	B:1.000	E:1.000	D:1.000	E:1.000
Fesenden Spring	F:1.000	B:1.000	A:1.000	8:1.000	C:1.000	A:1.000	B:1.000	C:1.000	8:1.000	B:0.075 E:0.925	D:1.000	E:1.000

Node	Est-2	G3pdh-A	G6pdh-A	Gpi-A	Gpi-B	S-Icdh-A	Ldh-A	Ldh-B	a-Man	M-Mdh-A	S-Mdh-A	S-Mdh-B
Bailey Creek	F:1.000	8:1.000	A:0.975 B:0.025	B:1.000	C:1.000	**B:1.000**	8:1.000	C:1.000	B:1.000	**E:1.000**	**D:1.000**	**E:1.000**
D. episcopa Pecos River	F:1.000	**B:1.000**	8:1.000	8:0.375 C:0.575 F:0.050	A:0.425 **B:0.425** F:0.025 G:0.125	A:1.000	B:1.000	C:1.000	8:1.000	B:0.175 E:0.825	**D:1.000**	E:1.000
Lost River	**D:1.000**	B:1.000	B:1.000	A:0.184 8:0.816	A:0.895 8:0.105	**B:1.000**	**B:1.000**	C:1.000	B:1.000	**B:0.175** **E:0.825**	**D:1.000**	E:1.000
Ft. Davis	F:1.000	B:1.000	8:1.000	**B:1.000**	A:1.000	A:1.000	8:1.000	C:1.000	8:1.000	E:1.000	**D:1.000**	E:1.000
Limpia Creek	F:1.000	B:1.000	**B:1.000**	B:1.000	A:1.000	A:1.000	B:1.000	C:1.000	8:1.000	**E:1.000**	**D:1.000**	E:1.000
Campostoma ornatum	B:1.000	**B:1.000**	**D:1.000**	A:0.750 **B:0.250**	B:1.000	A:1.000	**B:1.000**	C:1.000	**B:1.000**	C:1.000	B:1.000	8:1.000
C. oligolepis	8:1.000	B:1.000	C:1.000	A:0.700 **B:0.300**	**B:1.000**	B:1.000	**B:1.000**	C:1.000	A:1.000	A:1.000	A:1.000	A:1.000
Nocomis micropogon	8:1.000	C:1.000	**D:1.000**	B:0.250 C:0.750	A:0.500 B:0.500	**B:1.000**	**B:1.000**	C:1.000	**B:1.000**	B:1.000	**D:1.000**	E:1.000
Hybognathus regius	A:1.000	A:1.000	D:1.000	**D:1.000**	A:1.000	C:1.000	**B:1.000**	A:1.000	C:1.000	B:1.000	8:1.000	**B:1.000**
H. placitus	A:0.875 8:0.125	A:1.000	E:1.000	8:1.000	A:1.000	C:1.000	8:1.000	A:1.000	C:1.000	B:1.000	**B:0.950** C:0.050	8:1.000
Cyprinella camura	B:1.000	C:1.000	C:0.900 **E:0.100**	C:1.000	B:1.000	**D:1.000**	**D:1.000**	A:1.000	C:1.000	8:1.000	**D:1.000**	**B:1.000**
39	C:1.000	D:1.000	**B:1.000**	8:0.025 F:0.975	A:1.000	8:1.000	**B:1.000**	8:1.000	8:1.000	E:1.000	**E:1.000**	A:1.000
40	C:1.000	8:1.000	8:1.000	B:0.025 C:0.975	A:1.000	B:1.000	8:1.000	8:1.000	**B:1.000**	E:1.000	**D:1.000**	**E:1.000**
41	**D:1.000**	**B:1.000**	8:1.000	**B:0.025** C:0.975	A:1.000	B:1.000	**B:1.000**	**B:1.000**	**B:1.000**	**E:1.000**	**D:1.000**	E:1.000
42	0:1.000	B:1.000	**B:1.000**	**B:0.175** C:0.825	A:0.895 B:0.105	B:1.000	B:1.000	C:1.000	B:1.000	E:1.000	**D:1.000**	E:1.000
43	**D:0.800** E:0.200	**B:1.000**	B:1.000	B:0.175 C:0.825	A:0.895 8:0.080 F:0.025	**B:0.553** **C:0.447**	B:1.000	C:1.000	B:1.000	E:1.000	**D:1.000**	E:1.000

Node	Est-2	G3pdh-A	G6pdh-A	Gpi-A	Gpi-B	S-Icdh-A	Ldh-A	Ldh-B	a-Man	M-Mdh-A	S-Mdh-A	S-Mdh-B
44	**F:1.000**	B:1.000	**B:1.000**	B:1.000	A:1.000	**B:1.000**	**B:1.000**	C:1.000	8:1.000	E:1.000	**D:1.000**	E:1.000
45	**F:1.000**	**B:1.000**	8:1.000	A:0.184 B:0.816	A:0.895 **B:0.105**	**B:1.000**	8:1.000	C:1.000	B:1.000	B:0.175	D:1.000 E:0.825	E:1.000
46	**F:1.000**	**B:1.000**	B:1.000	A:0.050 8:0.375 C:0.575	A:0.895 **B:0.105**	B:1.000	**B:1.000**	C:1.000	**B:1.000**	8:0.175 E:0.825	**D:1.000**	E:1.000
47	**F:1.000**	**B:1.000**	8:1.000	A:0.929 C:0.071	A:0.056 F:0.944	8:1.000	**B:1.000**	C:1.000	B:1.000	E:1.000	A:0.067 **D:0.933**	E:1.000
48	**F:1.000**	8:1.000	**B:1.000**	A:1.000	**F:1.000**	B:1.000	B:1.000	C:1.000	**B:1.000**	E:1.000	A:0.050 **D:0.950**	E:1.000
49	**F:1.000**	B:1.000	**B:1.000**	A:1.000	**F:1.000**	8:1.000	**B:1.000**	C:1.000	B:1.000	E:1.000	A:0.050 **D:0.950**	E:1.000
50	**F:1.000**	8:1.000	B:1.000	A:1.000	**F:1.000**	8:1.000	**B:1.000**	C:1.000	8:1.000	E:1.000	A:0.050 **D:0.950**	E:1.000
51	**F:1.000**	8:1.000	**B:1.000**	A:1.000	F:1.000	8:1.000	B:1.000	C:1.000	8:1.000	E:1.000	A:0.050 0:0.950	E:1.000
52	**F:1.000**	**B:1.000**	A:1.000	B:1.000	C:1.000	B:1.000	B:1.000	C:1.000	8:1.000	E:1.000	**D:1.000**	E:1.000
53	**F:1.000**	**B:1.000**	A:0.975 B:0.025	B:1.000	C:1.000	8:1.000	**B:1.000**	C:1.000	**B:1.000**	E:1.000	**D:1.000**	E:1.000
54	**D:1.000**	B:1.000	**B:1.000**	B:0.175 C:0.825	A:0.895 **B:0.105**	**B:1.000**	8:1.000	C:1.000	B:1.000	E:1.000	**D:1.000**	E:1.000
55	**F:1.000**	B:1.000	8:1.000	A:0.050 B:0.375 C:0.575	A:0.895 B:0.105	8:1.000	**B:1.000**	C:1.000	B:1.000	E:1.000	D:1.000	E:1.000
56	F:1.000	**B:1.000**	8:1.000	A:0.050 **B:0.375** C:0.575	A:0.895 B:0.105	B:1.000	**B:1.000**	C:1.000	B:1.000	E:1.000	**D:1.000**	E:1.000
57	F:1.000	B:1.000	A:0.975 8:0.025	A:0.050 **B:0.375** C:0.575	B:0.105 C:0.895	**B:1.000**	**B:1.000**	C:1.000	**B:1.000**	E:1.000	**D:1.000**	E:1.000
58	8:1.000	B:1.000	A:1.000	C:1.000	**B:1.000**	**B:1.000**	B:1.000	A:1.000	B:1.000	8:1.000	A:1.000	8:1.000

Node	Est-2	G3pdh-A	G6pdh-A	Gpi-A	Gpi-B	S-Icdh-A	Ldh-A	Ldh-B	a-Man	M-Mdh-A	S-Mdh-A	S-Mdh-B
59	B:1.000	B:1.000	A:1.000	C:1.000	8:1.000	8:1.000	B:1.000	A:1.000	B:1.000	B:1.000	A:1.000	B:1.000
60	8:1.000	B:1.000	A:1.000	C:1.000	8:1.000	B:1.000	8:1.000	A:1.000	B:1.000	B:1.000	A:1.000	8:1.000
61	8:1.000	B:1.000	A:1.000	C:1.000	B:1.000	B:1.000	B:1.000	A:1.000	B:1.000	8:1.000	A:1.000	B:1.000
62	B:1.000	B:1.000	C:1.000	A:1.000	B:1.000	B:1.000	B:1.000	A:1.000	8:1.000	8:1.000	A:1.000	B:1.000
63	8:1.000	B:1.000	C:1.000	D:1.000	B:1.000	B:1.000	B:1.000	A:1.000	B:1.000	C:1.000	8:1.000	8:1.000
64	B:1.000	B:1.000	B:0.053 C:0.947	B:0.975 E:0.025	B:1.000	8:1.000	8:1.000	A:1.000	8:1.000	B:0.950 D:0.050	B:1.000	B:1.000
65	B:1.000	8:1.000	B:0.053 C:0.947	A:0.010 B:0.990	B:1.000	8:1.000	B:1.000	A:1.000	8:1.000	B:1.000	8:1.000	B:1.000
66	A:0.875 8:0.125	A:1.000	D:1.000	B:1.000	A:1.000	D:1.000	8:1.000	A:1.000	C:1.000	B:1.000	B:1.000	B:1.000
67	B:1.000	8:1.000	0:1.000	A:0.700 B:0.300	8:1.000	B:1.000	B:1.000	C:1.000	B:1.000	C:1.000	B:1.000	8:1.000
68	B:1.000	B:1.000	A:1.000	A:0.050 B:0.375 C:0.575	8:0.885 C:0.115	B:1.000	B:1.000	B:1.000	8:1.000	A:1.000	D:1.000	D:1.000
69	B:1.000	8:1.000	A:1.000	A:0.050 B:0.375 C:0.575	8:1.000	8:1.000	B:1.000	A:1.000	8:1.000	8:1.000	A:1.000	8:1.000
70	B:1.000	B:1.000	C:1.000	A:0.050 B:0.375 C:0.575	8:1.000	B:1.000	B:1.000	A:1.000	B:1.000	8:1.000	A:1.000	B:1.000

Node	Est-2	G3pdh-A	**G6pdh-A**	Gpi-A	Gpi-B	S-Icdh-A	Ldh-A	Ldh-B	a-Man	M-Mdh-A	S-Mdh-A	S-Mdh-B
71	B:1.000	B:1.000	**B:0.053** C:0.947	A:0.010 **B:0.990**	8:1.000	**B:1.000**	B:1.000	A:1.000	8:1.000	B:1.000	**B:1.000**	B:1.000
72	B:1.000	8:1.000	D:1.000	**A:0.010** **B:0.990**	B:1.000	**B:1.000**	B:1.000	A:1.000	**B:1.000**	B:1.000	B:1.000	**B:1.000**
73	8:1.000	8:1.000	D:1.000	A:0.700 B:0.300	**B:1.000**	**B:1.000**	**B:1.000**	C:1.000	B:1.000	B:1.000	**B:1.000**	8:1.000
74	B:1.000	C:1.000	D:1.000	**B:0.250** C:0.750	8:1.000	C:1.000	8:1.000	C:1.000	**B:1.000**	8:1.000	**D:1.000**	8:1.000
Locus **length**	12.800	10.2500	18.3560	25.3820	15.1250	14.15000	4.0000	10.0000	6.1500	10.9500	12.1320	10.9000

Node	S-Me-A	M-Me-A	Mpi-A	Pep-A	Pgm-A	Pk-A	S-Sod	Tpi-A	Tpi-B	Ancestor	BRANCH LENGTH
Dionda catostomops	**B:1.000**	**B:1.000**	A:1.000	**B:1.000**	**B:1.000**	A:1.000	8:1.000	8:1.000	B:1.000	65	3.9340
D. dichroma Puerta del Rio	**B:1.000**	**B:1.000**	**B:0.675** C:0.325	A:1.000	B:0.975 C:0.025	A:1.000	8:1.000	8:1.000	B:1.000	62	0.6840
La Media **Luna**	**B:1.000**	8:1.000	**B:0.675** C:0.325	A:1.000	8:0.975 C:0.025	A:1.000	**B:1.000**	B:0.950 C:0.050	**B:0.900** C:0.100	62	0.7160
D. **mandibularis** Puerta del Rio	B:1.000	8:1.000	E:1.000	6:1.000	**B:1.000**	C:1.000	A:1.000	**B:1.000**	8:1.000	63	0.1000
La Media Luna	8:1.000	**B:1.000**	E:1.000	8:1.000	B:0.900 C:0.100	C:1.000	A:1.000	8:1.000	8:0.950 **C:0.050**	63	0.6500
D. ipni **Río Matlapa**	A:0.050 8:0.950	B:1.000	C:1.000	**B:1.000**	B:1.000	B:1.000	**B:1.000**	**B:1.000**	A:1.000	58	6.3000
Río Axtla	**B:1.000**	B:0.923 D:0.077	**B:1.000**	**B:1.000**	A:1.000	A:1.000	6:1.000	B:1.000	8:1.000	68	8.0000
Rio **Canalí**	**B:1.000**	**B:1.000**	C:1.000	**B:1.000**	**B:1.000**	8:1.000	**B:1.000**	B:1.000	**B:1.000**	59	1.5340
Rio Tuititlan	8:1.000	B:1.000	C:0.867 F:0.133	B:1.000	**B:1.000**	**B:1.000**	B:1.000	B:1.000	**B:1.000**	60	2.5990
Arroyo **Palitla**	B:1.000	B:1.000	C:1.000	8:1.000	**B:1.000**	**B:1.000**	8:1.000	8:1.000	**B:1.000**	58	2.5000
Rio **Guayalejo**	A:0.400 **B:0.600**	B:1.000	C:1.000	8:1.000	**B:1.000**	**B:1.000**	8:1.000	B:1.000	B:1.000	61	5.4960
D. **erimyzonops**	**B:1.000**	A:0.059 B:0.882 E:0.059	C:0.875 F:0.125	A:0.975 **B:0.025**	**B:1.000**	A:1.000	C:1.000	**B:1.000**	8:1.000	64	8.5300
D. sp. (Ojo de Agua)	8:1.000	C:1.000	F:1.000	A:1.000	C:1.000	D:1.000	**B:1.000**	6:1.000	C:1.000	39	3.6320
D. sp. (El **Vergel)**	**B:1.000**	F:1.000	C:1.000	A:0.184 C:0.816	C:1.000	**D:1.000**	**B:1.000**	**B:1.000**	C:1.000	39	10.8920
D. diaboli	A:0.050 **B:0.950**	A:0.050 **B:0.950**	8:1.000	**B:1.000**	C:0.800 D:0.200	**D:1.000**	8:1.000	**B:1.000**	A:0.278 8:0.722	40	1.1500

Node	S-Me-A	**M-Me-A**	Mpi-A	Pep-A	Pgm-A	Pk-A	S-Sod	Tpi-A	Tpi-B	Ancestor	BRANCH LENGTH
D. couchi	B:0.975 **C:0.025**	E:1.000	**B:0.925** **D:0.075**	**B:1.000**	**C:1.000**	**B:1.000**	**B:1.000**	**B:1.000**	B:1.000	42	6.0900
D. sp. (Conchos)	**B:1.000**	E:1.000	8:1.000	8:1.000	C:1.000	**B:1.000**	B:1.000	**B:1.000**	A:0.150 **B:0.850**	41	4.1000
D. argentosa **Devils** River	**B:1.000**	E:1.000	8:1.000	B:0.950 **D:0.050**	**B:0.625** C:0.375	D:1.000	B:0.950 C:0.050	8:1.000	8:1.000	43	3.5520
San **Felipe** Spring	B:1.000	E:1.000	B:1.000	8:1.000	A:0.025 **B:0.875** C:0.100	B:1.000	B:0.650 E:0.350	B:1.000	B:1.000	43	2.7120
D. serena **Río** Frio	8:1.000	**E:1.000**	B:0.889 C:0.111	B:1.000	C:1.000	B:1.000	**B:1.000**	A:0.278 B:0.722	A:0.444 D:0.556	47	2.4760
Cedar Creek	B:1.000	E:1.000	B:0.969 **C:0.031**	**B:1.000**	C:1.000	**B:1.000**	**B:1.000**	A:0.029 8:0.971	A:0.147 D:0.853	47	0.8480
Can Creek	**B:1.000**	E:1.000	8:0.675 C:0.325	8:1.000	C:1.000	B:1.000	**B:1.000**	8:1.000	D:1.000	48	0.6600
Nueces River (Hwy 55)	8:1.000	E:1.000	B:1.000	**B:1.000**	C:1.000	**B:1.000**	B:1.000	B:0.750 C:0.250	C:0.125 **D:0.875**	49	1.2610
Nueces River (Hwy 335)	**B:1.000**	E:1.000	**B:1.000**	**B:1.000**	C:1.000	B:1.000	B:1.000	**B:0.389** C:0.611	C:0.050 D:0.950	49	1.0720
Campwood Creek	**B:1.000**	E:1.000	B:1.000	8:1.000	C:1.000	**B:1.000**	**B:1.000**	**B:0.778** C:0.222	C:0.083 0:0.917	50	0.1320
D. sp. **(Guadelupe-Colorado)** Heart of **Hills**	B:1.000	E:1.000	**B:1.000**	A:0.050 C:0.950	C:1.000	B:1.000	B:1.000	8:1.000	C:0.700 D:0.300	52	0.0000
Fesenden Spring	**B:1.000**	E:1.000	**B:1.000**	**D:1.000**	C:1.000	**B:1.000**	**B:1.000**	**B:1.000**	D:1.000	52	1.8000

Node	S-Me-A	M-Me-A	Mpi-A	Pep-A	Pgm-A	Pk-A	S-Sod	Tpi-A	Tpi-8	Ancestor	BRANCH LENGTH
Bailey Creek	B:1.000	E:1.000	**B:1.000**	**B:1.000**	C:1.000	**B:1.000**	8:1.000	8:1.000	**B:1.000**	53	2.0000
D. episcopa Pecos River	8:1.000	E:1.000	8:1.000	B:1.000	**B:0.895** C:0.105	**B:1.000**	**B:1.000**	**B:1.000**	**B:1.000**	46	4.7480
Lost River	**B:1.000**	E:1.000	A:0.289 8:0.711	**B:1.000**	8:0.441 C:0.559	**B:1.000**	D:1.000	B:1.000	8:1.000	45	6.6780
Ft. Davis	8:1.000	E:1.000	8:1.000	**B:1.000**	C:1.000	**B:1.000**	D:1.000	B:1.000	8:1.000	44	0.0000
Limpia Creek	**B:1.000**	E:1.000	8:1.000	**B:1.000**	C:1.000	**B:1.000**	D:1.000	B:1.000	**B:1.000**	44	0.0000
Campostoma ornatum	C:1.000	C:1.000	A:1.000	D:1.000	A:1.000	8:1.000	B:1.000	C:0.550 0:0.450	C:0.200 E:0.800	67	10.2000
C. **oligolepis**	C:1.000	C:1.000	8:0.550 C:0.450	B:1.000	A:1.000	D:1.000	**B:1.000**	8:1.000	8:1.000	67	**18.0000**
Nocomis micropogon	D:1.000	E:1.000	A:0.917 **B:0.083**	D:1.000	8:1.000	E:1.000	C:1.000	D:1.000	E:1.000	74	18.8340
Hybognathus regius	**B:1.000**	C:1.000	8:1.000	8:0.875 E:0.125	**B:1.000**	A:1.000	E:1.000	B:1.000	**A:1.000**	66	6.6000
H. **placidus**	B:1.000	C:1.000	**B:0.900** C:0.100	B:1.000	**B:0.900** C:0.100	D:1.000	E:1.000	**B:1.000**	A:0.050 **B:0.800** E:0.150	66	6.6750
Cyprinella camura	8:1.000	E:1.000	B:1.000	8:1.000	A:0.750 B:0.250	A:1.000	B:1.000	B:1.000	**B:1.000**	74	22.5500
39	**B:1.000**	C:1.000	F:1.000	A:0.184 C:0.816	C:1.000	D:1.000	**B:1.000**	B:1.000	C:1.000	40	19.9500
40	8:1.000	A:0.050 **B:0.950**	8:1.000	B:1.000	C:1.000	D:1.000	**B:1.000**	A:0.278	8:0.722 8:1.000	41	8.6240
41	**B:1.000**	E:1.000	8:1.000	**B:1.000**	C:1.000	8:1.000	8:1.000	A:0.150	B:0.850 **B:1.000**	42	6.4420
42	8:1.000	E:1.000	B:1.000	B:1.000	C:1.000	8:1.000	**B:1.000**	8:1.000	**B:1.000**	54	0.8820
43	**B:1.000**	E:1.000	**B:1.000**	8:1.000	8:0.625 C:0.375	**B:1.000**	**B:0.950** C:0.050	**B:1.000**	8:1.000	54	4.4480

Node	S-Me-A	M-Me-A	Mpi-A	Pep-A	**Pgm-A**	Pk-A	S-Sod	Tpi-A	Tpi-B	Ancestor	BRANCH LENGTH
44	8:1.000	E:1.000	B:1.000	8:1.000	C:1.000	B:1.000	D:1.000	8:1.000	B:1.000	45	3.8100
45	B:1.000	E:1.000	**B:1.000**	8:1.000	8:0.441 C:0.559	B:1.000	**D:1.000**	8:1.000	**B:1.000**	46	5.1500
46	**B:1.000**	E:1.000	B:1.000	8:1.000	**B:0.441** C:0.559	B:1.000	B:1.000	**B:1.000**	8:1.000	55	0.3500
47	8:1.000	E:1.000	8:0.889 C:0.111	8:1.000	C:1.000	**B:1.000**	B:1.000	A:0.029 8:0.971	A:0.147 D:0.853	48	2.6400
48	8:1.000	E:1.000	**B:0.889** C:0.111	**B:1.000**	C:1.000	B:1.000	8:1.000	B:1.000	**D:1.000**	51	0.3560
49	8:1.000	E:1.000	8:1.000	**B:1.000**	C:1.000	8:1.000	**B:1.000**	B:0.750 C:0.250	C:0.050 D:0.950	50	1.2010
50	**B:1.000**	E:1.000	B:1.000	**B:1.000**	C:1.000	B:1.000	8:1.000	B:0.778 C:0.222	C:0.050 **D:0.950**	51	3.1100
51	B:1.000	E:1.000	B:1.000	8:1.000	C:1.000	B:1.000	**B:1.000**	8:1.000	C:0.050 D:0.950	56	10.0840
52	8:1.000	E:1.000	B:1.000	A:0.050 C:0.950	C:1.000	**B:1.000**	B:1.000	**B:1.000**	C:0.700 **D:0.300**	53	4.0500
53	8:1.000	E:1.000	**B:1.000**	B:1.000	C:1.000	8:1.000	8:1.000	B:1.000	**B:1.000**	57	5.4600
54	**B:1.000**	E:1.000	B:1.000	B:1.000	8:0.441 C:0.559	**B:1.000**	B:1.000	8:1.000	B:1.000	55	4.5000
55	B:1.000	E:1.000	**B:1.000**	B:1.000	**B:0.441** C:0.559	8:1.000	**B:1.000**	B:1.000	B:1.000	56	2.8820
56	8:1.000	E:1.000	B:1.000	8:1.000	C:1.000	**B:1.000**	**B:1.000**	B:1.000	**B:1.000**	57	5.7400
57	B:1.000	E:1.000	**B:1.000**	B:1.000	C:1.000	B:1.000	B:1.000	**B:1.000**	8:1.000	68	15.6100
58	B:1.000	B:1.000	C:1.000	B:1.000	**B:1.000**	8:1.000	B:1.000	8:1.000	B:1.000	59	2.4160

Node	S-Me-A	M-Me-A	Mpi-A	Pep-A	Pgm-A	Pk-A	S-Sod	Tpi-A	Tpi-B	Ancestor	BRANCH LENGTH
59	B:1.000	B:1.000	C:1.000	B:1.000	8:1.000	B:1.000	B:1.000	B:1.000	B:1.000	60	2.0000
60	8:1.000	B:1.000	C:1.000	B:1.000	B:1.000	B:1.000	8:1.000	B:1.000	B:1.000	61	0.0000
61	8:1.000	8:1.000	C:1.000	B:1.000	B:1.000	B:1.000	B:1.000	B:1.000	B:1.000	69	6.2000
62	8:1.000	B:1.000	B:0.675 C:0.325	A:1.000	B:0.975 C:0.025	A:1.000	B:1.000	B:1.000	B:1.000	70	3.9500
63	8:1.000	B:1.000	E:1.000	B:1.000	B:1.000	C:1.000	A:1.000	B:1.000	B:1.000	64	10.1060
64	B:1.000	B:1.000	C:0.875 F:0.125	B:1.000	B:1.000	A:1.000	C:1.000	8:1.000	8:1.000	65	4.2500
65	B:1.000	8:1.000	C:0.875 F:0.125	B:1.000	B:1.000	A:1.000	B:1.000	B:1.000	B:1.000	71	1.5500
66	B:1.000	C:1.000	8:0.900 C:0.100	B:1.000	B:1.000	A:1.000	E:1.000	8:1.000	A:0.050 B:0.800 E:0.150	72	14.6200
67	C:1.000	C:1.000	B:0.550 C:0.450	B:1.000	A:1.000	B:1.000	B:1.000	8:1.000	B:1.000	73	10.2500
68	B:1.000	B:0.923 D:0.077	8:1.000	B:1.000	A:1.000	B:1.000	B:1.000	B:1.000	8:1.000	69	14.5840
69	8:1.000	B:1.000	B:0.675 C:0.325	B:1.000	8:1.000	B:1.000	8:1.000	B:1.000	B:1.000	70	6.2500
70	B:1.000	8:1.000	B:0.675 C:0.325	8:1.000	B:1.000	A:1.000	B:1.000	B:1.000	B:1.000	71	4.8860

Node	S-Me-A	M-Me-A	Mpi-A	Pep-A	Pgm-A	Pk-A	S-Sod	Tpi-A	Tpi-B	Ancestor	BRANCH LENGTH
71	B:1.000	**B:1.000**	**B:0.675** C:0.325	B:1.000	B:1.000	A:1.000	B:1.000	**B:1.000**	8:1.000	72	6.0000
72	**B:1.000**	C:1.000	B:0.675 C:0.325	B:1.000	**B:1.000**	A:1.000	**B:1.000**	B:1.000	**B:1.000**	73	7.1800
73	B:1.000	**C:1.000**	**B:0.675** C:0.325	**B:1.000**	B:1.000	A:1.000	**B:1.000**	B:1.000	B:1.000	74	11.5000
74	B:1.000	E:1.000	**B:0.675** C:0.325	**B:1.000**	8:1.000	A:1.000	8:1.000	B:1.000	8:1.000		
Locus **length**	5.0500	12.3900	18.5380	14.0320	12.8220	18.0000	10.8000	5.8780	17.7600		388.7360

TABLE 3. GENETIC VARIABILITY OF 35 LOCI IN ALL POPULATIONS OF ***DIONDA*** AND OUTGROUP TAXA (± STANDARD ERROR)

Population	Mean no. of alleles per locus	Percentage of loci polymorphic*	Mean heterozygosity	
			Direct-count	HdyWbg expected**
Dionda catostomops	1.0±.1	9.4	.000	.002±.001
D. dichroma				
Puerta del Río	1.2±.1	15.6	.023±.015	.042±.023
La Media Luna	1.2±.1	18.8	.019±.014	.040±.020
D. mandibularis				
Puerta del Río	1.0	.0	.000	.000
La Media Luna	1.2±.1	15.6	.014±.009	.022±.010
D. ipni				
Río Matlapa	1.2±.1	15.6	.016±.013	.022±.011
Río Axtla	1.1	6.3	.007±.007	.011±.008
Río Canalí	1.0	.0	.000	.000
Rio Tuititlan	1.2±.1	9.4	.019±.012	.033±.021
Arroyo Palitla	1.0	.0	.000	.000
Río Guayalejo	1.1±.1	9.4	.028±.020	.040±.024
D. erimyzonops	1.3±.1	28.1	.022±.014	.055±.022
D sp. A	1.0	3.1	.002±.002	.002±.002
D. sp. B	1.1	6.3	.012±.010	.025±.018
D. diaboli	1.2±.1	15.6	.022±.014	.044±.021
D. couchi	1.3±.2	15.6	.029±.015	.043±.026
D. sp. (Conchos)	1.1±.1	9.4	.006±.004	.019±.012
D. argentosa				
Devils River	1.4±.1	25.0	.041±.017	.063±.024
San Felipe Spring	1.4±.1	25.0	.062±.027	.099±.033
D. serena				
Río Frio	1.3±.1	21.9	.039±.016	.079±.031

Table 3. Continued

Population	Mean no. of alleles per locus	Percentage of loci polymorphic*	Mean heterozygosity	
			Direct-count	HdyWbg expected**
Cedar Creek	1.3±.1	25.0	.019±.008	.042±.016
Can Creek	1.1	6.3	.025±.019	.021±.016
Nueces River (Hwy 55)	1.3t.1	28.1	.026±.010	.051±.019
Nueces River (Hwy 335)	1.2±.1	12.5	.020±.013	.044±.025
Campwood Creek	1.2i.1	15.6	.008±.006	.040±.020
D. sp. (Guadelupe-Colorado)				
Heart of Hills	1.1	6.3	.009i.007	.017±.014
Fesenden Spring	1.1	6.3	.003±.002	.009±.006
Bailey Creek	1.0	3.1	.002±.002	.002±.002
D. episcopa				
Pecos River	1.3i.1	18.8	.045±.019	.076±.031
Lost River	1.2±.1	21.9	.043±.018	.057±.024
Ft. Davis	1.0	.0	.000	.000
Limpia Creek	1.0	.0	.000	.000
Campostoma omatum	1.1±.1	12.5	.034±.019	.042±.022
C. oligolepis	1.1	6.3	.034±.024	.030±.021
Nocomis micropogon	1.1±.1	9.4	.021±.012	.035±.021
Hybognathus regius	1.0	3.1	.008±.008	.008±.008
H. placitus	1.3±.1	21.9	.034i.018	.049±.018
Cyprinella camura	1.1±.1	9.4	.013±.010	.021±.014

* A locus is considered polymorphic if more than one allele was detected

** Unbiased estimate (see Nei, 1978)

Table 4. ALLOZYME CHARACTERS SUPPORTING NUMBERED NODES IN PHYLOGENETIC HYPOTHESES PRESENTED IN FIGURES 3, 4, AND 5. ALL ELECTROMORPHS IN HYPOTHESIZED ANCESTORS EITHER IN FIXED OR POLYMORPHIC CONDITION; LOSS OF PARTICULAR ELECTROMORPH INDICATED WITH *.

Node	Character	Node	Character	Node	Character	Node	Character
39	Ada-A(a)	47	Ck-B(b)	57	M-Aat-A(a)	66	Ck-A(d)
	Est-1 (b)		Gpi-A(c)		Est-2(f)		Est-2(a) *
	Gpi-A(g)		Gpi-B(a)		G-6pdh-A(b)		Gpi-A(a)
	G3pdh-A(d)		Tpi-A(a)		Ldh-B(c)		Gpi-B(a)
	S-Mdh-A(e)		Tpi-B(a)		M-Mdh-A(e)		G3pdh-A(a)
	S-Mdh-B(a)				S-Mdh-B(e)		S-Icdh-A(c)
	Mpi-A(g)	48	Mpi-A(c)*		M-Me(e)		a-Man(c)
	Pep-A(a)		Tpi-B(c)		Pgm-A(c)		S-Sod-A(c)
	Pep-A(c)						Tpi-B(a)
	Tpi-B(c)	50	Acp-A(a)	58	M-Aat-A()		Tpi-B(e)
			Acp-A(c)		Ada-A(a)		
40	Acp-A(d)		Ada-A(c)			67	Ald-A(b)
	Est-1(d)		Tpi-A(c)	59	Ald-A(b)		M-Aat-A(a)
	Est-2(c)						M-Mdh-A(c)
	M-Me(a)	51	S-Aat-A(a)	61	Acp-A(c)		S-Me(c)
	M-Me(b)		Ada-A(b)		Ck-A(c) *		Pgm-A(a)
	Pk-A(d)		S-Ap-A(c)*		Gpi-A(a)*		Pk-A(b)
			Gpi-A(b)*		Gpi-A(b) *		
41	Acp-A(d)		Gpi-A(c)		Mpi-A(b)	68	Ada A(c)*
	Ada-A(f) *		Gpi-B(g)				Ada-A(d)
	Ada A(a)*		S-Mdh-A(a)	62	Gpi-A(b)*		Est-1(a)
	Gpi-B(b)		Tpi-B(c)		Pep-A(a)		Gpi-B(c)
	Ldh-B(b)		Tpi-B(d)		Pgm-A(c)		Ldh-B(b)
	Tpi-B(a)						M-Mdh-A(a)
		52	G6pdh-A(b)*	63	G6pdh-A(b)*		S-Mdh-A(d)
42	Pgm-A(b)*		Pep-A(a)		Gpi-A(d) *		S-Mdh-Bid)
			Pep-A(c)		M-Mdh-A(b)*		Mpi-A(c)
43	S-Aat-A(a)		Tpi-B(c)		M-Mdh-A(d)		Pgm-A(a)
	S-Aat-A(c)		Tpi-B(d)		M-Mdh-A(c)		
	Ada-A(c)				Mpi-A(e)	69	Ada-A(b)*
	Est-2	53	Ada-A(f)		Pk-A(c)		S-Ap-A(b)
	Gpi-B(f)		Ck-A(c) *		S-Sod-A(a)		G6pdh-A(a)*
	S-Icdh-A(b)		Gpi-A(a)*				G6pdh-A(c)
	S-Sod-A(c)		Gpi-A(c)	64	M-Aat-A(c)		Gpi-A(c)
			Gpi-B(c)		Acp-A(a)*		Pk-A(b)
44	M-Aat-A(b) *				Gpi-A(a)		
	M-Mdh-A(b)*	54	Acp-A(a)		Gpi-A(e)	70	Ada-A(c)
	Gpi-A(a)*		Est-2(d) *		M-Mdh-A(d)		Ada-A(d) *
	Gpi-B(b) *		Gpi-A(a)		Mpi-A(f)		G6pdh-A(b)
	Pgm-A(b)				S-Sod-A(c)		S-Mdh-A(a)
		55	Est-1(e)				
45	S-Ap-A(c)		Pgm-A(b)	65	Ada-A(a)*	71	Cbp-1 (b)
	Gpi-A(c)				Mpi-A(b)		G6pdh-A(c)
	S-Sod-A(d)	56	Est-1 (b) *				M-Me(b)
			G6pdh-A(a)				
46	M-Mdh-A(b)		Gpi-B(a)				

TABLE 4. CONTINUED.

Node	Character
72	M-Aat-A(b)
	Ada-A(b)
	Ldh-B(a)
73	Acp-A(b)
	Gpi-A(a)*
	Gpi-A(c)
	G3pdh-A(b)
	S-Icdh-A(a)
	S-Mdh-A(b)
	M-Me(c)
74	Acp-A(e)
	Ak-A(b)
	Gpi-A(b)
	Gpi-A(c)
	S-Icdh-A(b)
	Ldh-A(b)
	Ldh-B(c)
	a-Man(b)

TABLE 5. COMPARISONS OF TREE STATISTICS BEFORE OPTIMIZATION FOR THE SHORTEST TREES GENERATED USING DISTANCE WAGNER ALGORITHM AND PREVOSTI, ROGERS, AND CAVALLI-SFORZA AND EDWARDS ARC DISTANCES. L = LENGTH OF TREE BASED UPON SPECIFIC DISTANCE MEASURE, FPL = LENGTH OF TREE BASED UPON FREQPARS, f = FARRIS (1972) 1" MEASURE, F = PRAGER AND WILSON (1976) "F" MEASURE, AND CC = COPHENETIC CORRELATION COEFFICIENT. GOODNESS OF FIT CRITERIA WERE CALCULATED FOR THE DISTANCE WAGNER TREES.

Prevosti

	FPL			
5.542	396.180	72.21	20.06	0.909
5.542	396.122	72.21	20.06	0.909
5.558	396.491	71.95	19.98	0.911
5.558	397.534	71.95	19.98	0.911
5.582	394.180	80.16	22.27	0.905

Rogers

	FPL	f	F	CC
5.462	396.276	71.75	20.20	0.910
5.471	394.176	93.90	26.44	0.840
5.473	397.530	71.40	20.10	0.912
5.486	394.110	73.12	20.58	0.908

Cavalli-Sforza and Edwards

	FPL			CC
8.083	401.345	52.99	11.85	0.934
8.093	401.729	52.85	11.81	0.934
8.094	402.967	56.39	12.61	0.928
8.853	397.928	61.38	12.41	0.925
8.865	395.378	68.44	12.84	0.900

Figure 1. Distributions of species of *Dionda.*

Figure 2. Select drainages and geological formations in southwestern North America. 1. Colorado/Guadelupe R. 2. Nueces/Frio R. 3. Devil R. 4. Old Pecos R. 5. Upper Pecos R. 6. Old Upper Rio Grande. 7. Upper Río Grande. 8. Location of Guzmán Basin and ancestral outlet of Old Upper R. Grande. 9. R. Conchos. 10. Lagunas de las Palomas and location of Lake Tlahualilo. 11. R. Nazas. 12. Parras Basin. 10-12. Area of Bolsón de Mapimí. 13. Probable outlets to the Old R. Nazas drainage. 14. R. Aguanaval. 15. R. del Tunal and area of connection with Old R. Nazas drainage. 16. R. Mezquital. 17. Laguna de Santiaguillo. 18. R. Grande de Santiago. 19. R. Lerma. 20. R. Balsas. 21. R. Misantla. 22. R. Nautla. 23. R. Cazones. 24. R. Tuxpan. 25. R. Moctezuma. 26. R. Santa Maria. 27. R. Verde. 28. R. Guayalejo. 29. R. Pánuco. 30. R. Tamesí. 31. R. San Juan. 32. R. Salado. Dashed line circumcribes Mesa Central.

Figure 3. Phylogenetic relationships of the genus *Dionda* and closely related genera. Tree derived from FREQPARS and supported by characters in Table 4. Numbers at each node refer to hypothetical ancestral species possessing genotypic frequencies identified in Table$\overset{2}{\text{A}}$. Synapomorphic characters possessed by these hypothetical ancestral species represent the presence or absence of specific alleles and not frequency change (Table

Figure 4. Species relationships for the Pánuco Basin *Dionda* and the *D. episcopa* complex based on allozyme variation. See Figure 3 for details concerning support for the tree.

Figure 5. Species and population relationships within the *Dionda episcopa* complex based on allozyme variation. See Figure 3 for details concerning support for the tree.

Fig 1.
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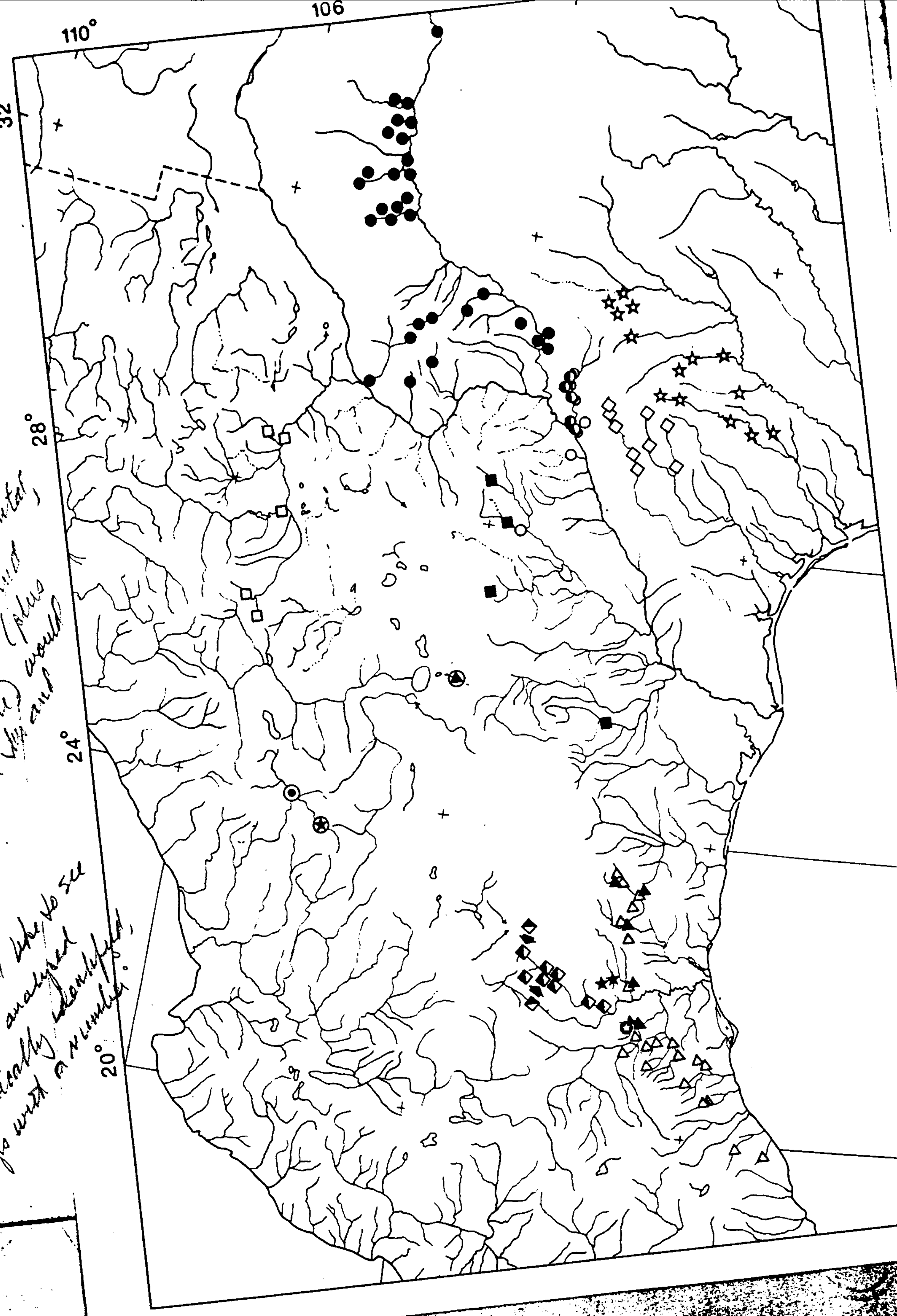


General maps of the Sierra Madre oriental, Mesa del Norte, and Mesa Central (plus continental divide) would be helpful on this and Fig 2

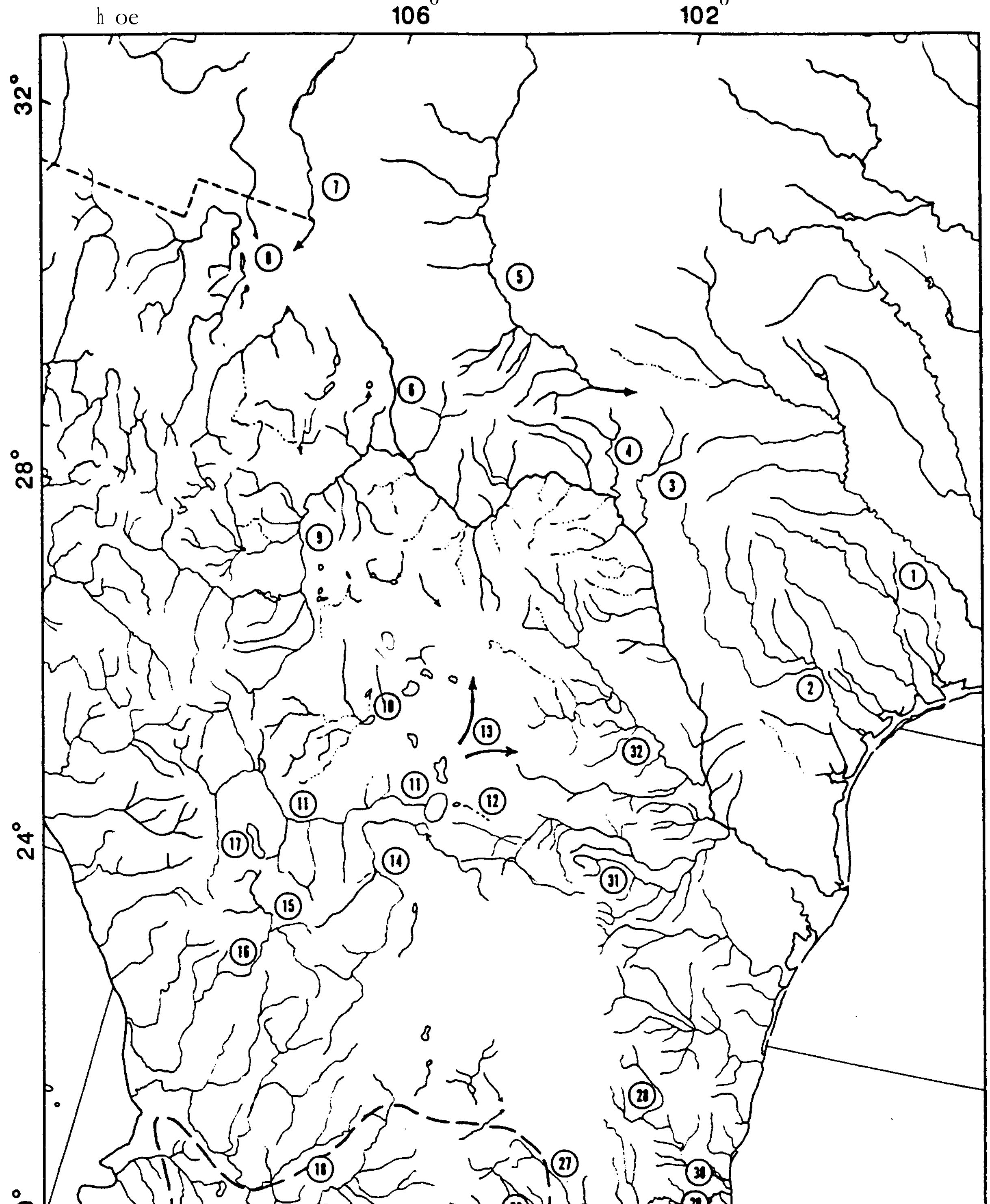
I also would like to see the populations analysed electrophoretically identified, perhaps with a number.

•	*D. episcopa*	*	*D. rasconis*
0	*D. serena*	*	*D. catostomops*
0	*D. argentosa*	△	*D. ipni*
•	*D. couchi*	•	*D. erimyzonops*
0	*D. diaboli*	*	*D. dichroma*
*	*D.* sp. (Guad.-Col. R.)	⬘	*D. mandibularis*
	D. sp. (El Vergel)	0	*D.* sp. (R. Axtla)
®	*D.* sp. (Ojo de Agua)	□	*D.* sp. (R. Conchos)
*	*D.* sp. (Parras)		

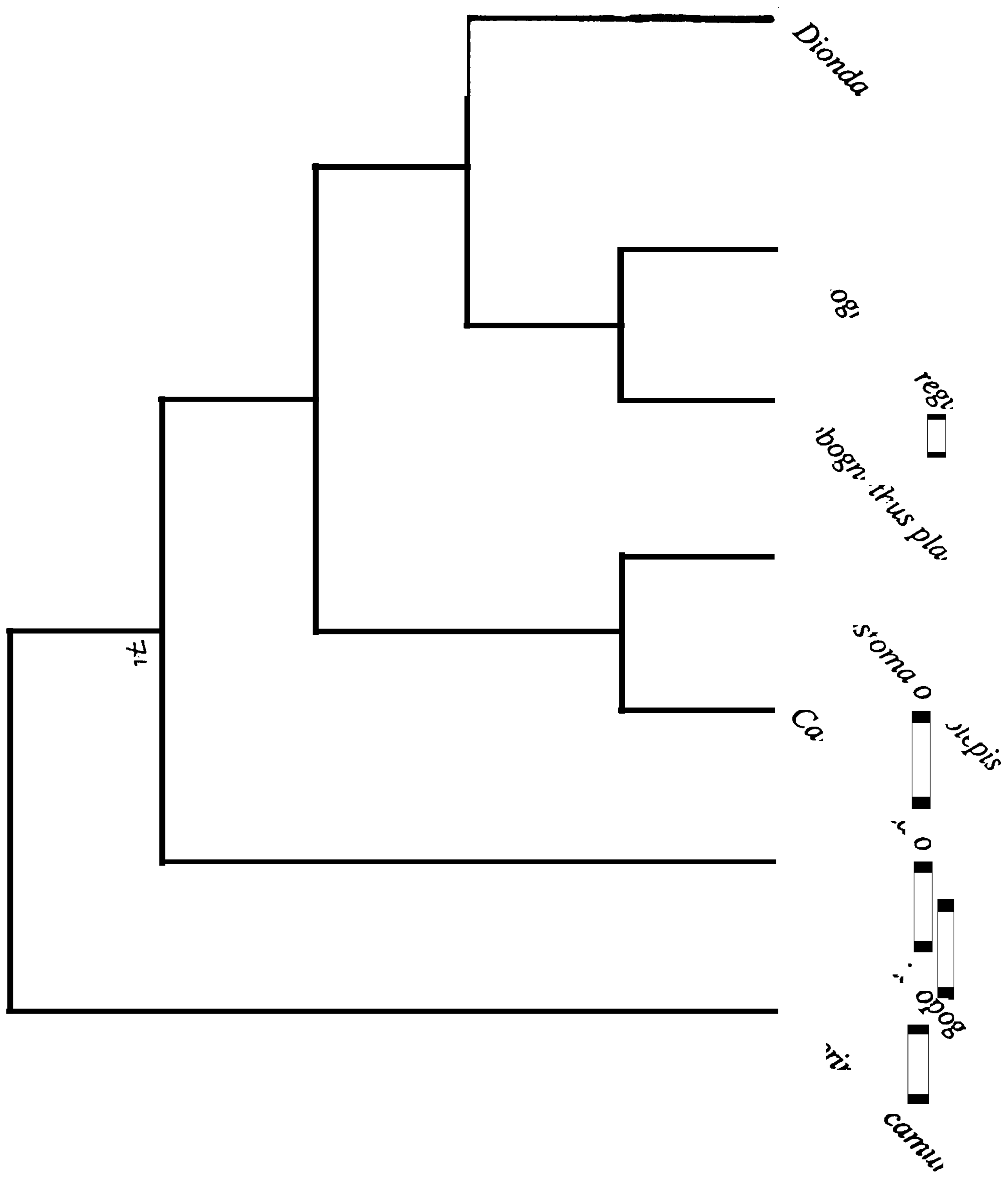
F . 1 (K)

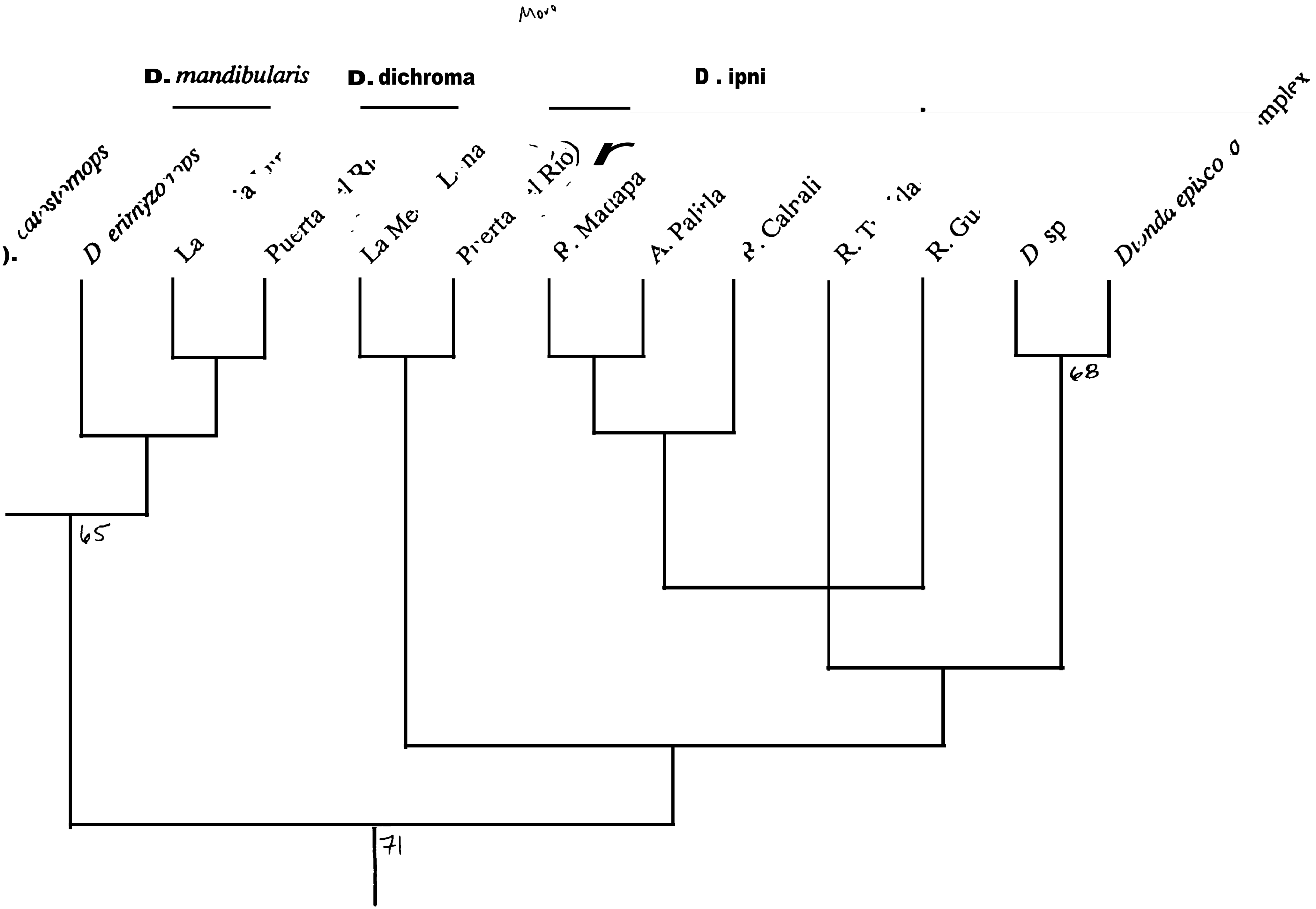
Mauden et l.

Fig. 2
Mayden et al.



Mayden [redacted]




Mora
D. mandibularis
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D . ipni
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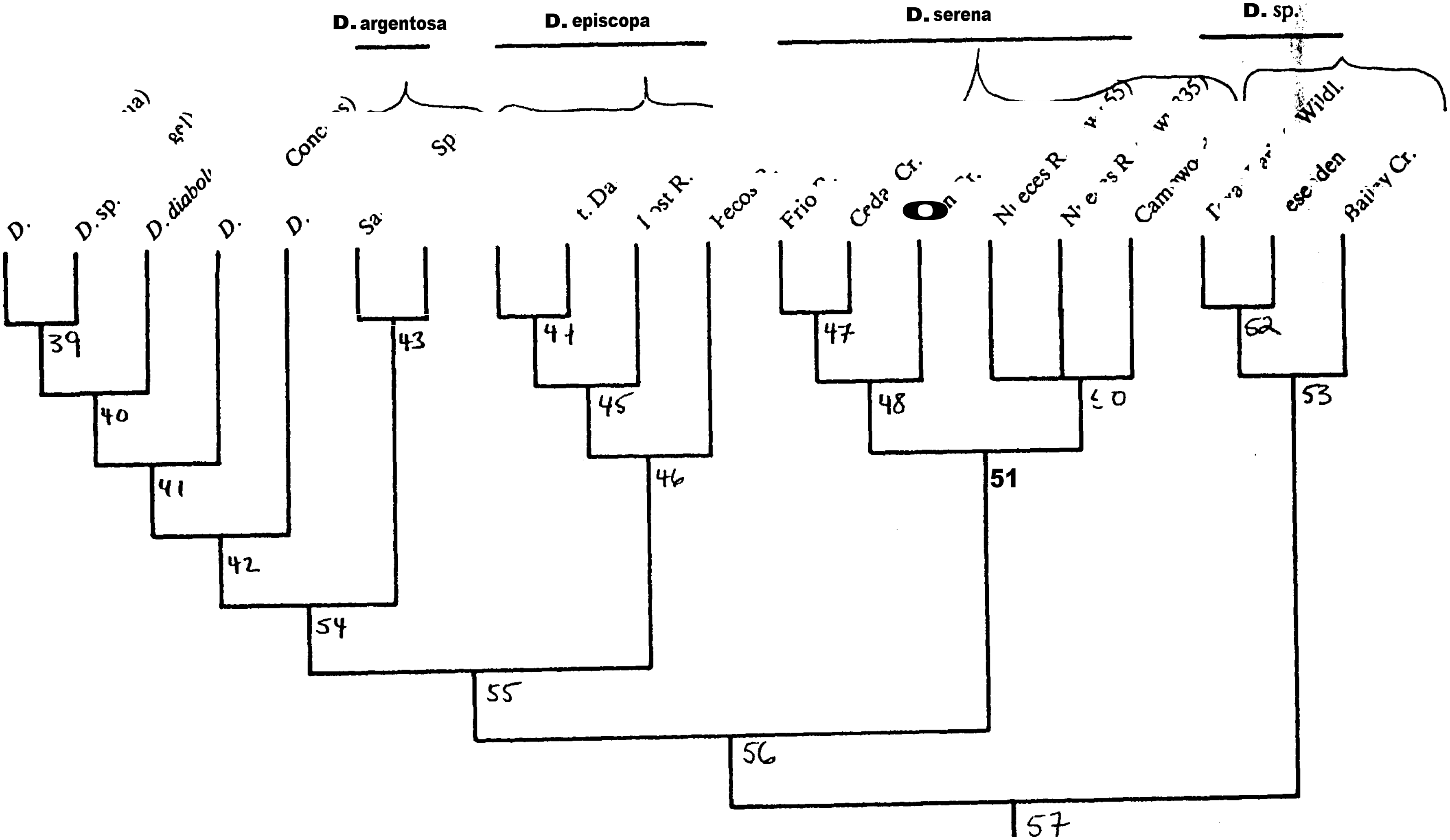
D. argentosa
D. episcopa
D. serena
D. sp.
D. sp.
D. diabol
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Pecos
Frio
Ceda Cr.
Nueces R
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Camwo
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Bailey Cr.
Wildl.
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