we believe that the deficiency of β-galactosidase is the fundamental enzymic defect in generalized gangliosidosis (*14*). Assays of tissues and body fluids for β-galactosidase activity should provide a means for determining both homozygotic patients and heterozygotic carriers of the abnormal gene.

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Lactate Dehydrogenase Isozymes in Parthenogenetic Teiid Lizards (Cnemidophorus)

Abstract. *Heterozygosity occurs at the lactate dehydrogenase* b-*locus in two diploid parthenogenetic species of* Cnemidophorus. *Each such species produces two different B subunits, one of which is also found in two sexual species and in two triploid parthenogenetic species; the other occurs also in a third sexual species. Interspecific hybridization between sexual species carrying different* b-*alleles and producing different B subunits may be responsible for the heterozygosity at the lactate dehydrogenase* b-*locus in diploid parthenogenetic* Cnemidophorus.

Interspecific hybridization has been implicated in the origin of all natural instances of vertebrate parthenogenesis. Morphological considerations have fostered the speculation that *Poecilia formosa,* a diploid gynogenetic teleost, resulted from a cross between *P. sphenops* and *P. latipinna* (*1*). The suspected hybrid origin of triploid gynogenetic ambystomatid salamanders has been recently documented by biochemical evidence (*2*). Hybridization has been hypothesized for the origin of a triploid gynogenetic teleost, *Poeciliopsis* Cy (*3*), and of parthenogenetic species of the lizard genus *Lacerta* (*4*).

Lowe and Wright (*5*) proposed hybrid origins for parthenogenetic species of *Cnemidophorus* on the basis of karyotypic evidence that haploid chromosome complements from distinct sexual species were combined in certain parthenogenones. The evidence of hybridization was strongest in *C. neomexicanus*; its diploid chromosome complement could be partitioned into distinct haploid sets matching closely the haploid chromosomes of *C. tigris* and *C. inornatus,* two sympatric sexual species with quite different chromosome morphologies.

Our preliminary electrophoretic analysis of a variety of proteins from three sexual and four parthenogenetic species of *Cnemidophorus* supports the proposed hybrid origin of *C. neomexicanus* and suggests a similar hybrid origin for a second diploid parthenogenetic species, *C. tesselatus,* class E (*5, 6*).

Lizards used by us were captured alive in southern New Mexico and western Texas during August 1967. Enzyme studies were performed on various tissues fresh from the lizard body or after storage in a freezer. Glass-ground tissue homogenates containing 25 mg of tissue per milliliter of gel buffer were centrifuged at 40,000g for 30 minutes. Samples of the supernatant were subjected to electrophoresis on vertical starch gel and analyzed for specific enzyme activity according to reported techniques (*7*). A twofold dilution of the prescribed (*7*) gel buffer was used, with a voltage gradient of 6 volt/cm for 15 to 16 hours. Serum and red-cell proteins were examined by reported procedures (*8*), with substitution of agarose electrophoresis (*9*) in the separation of serum proteins.

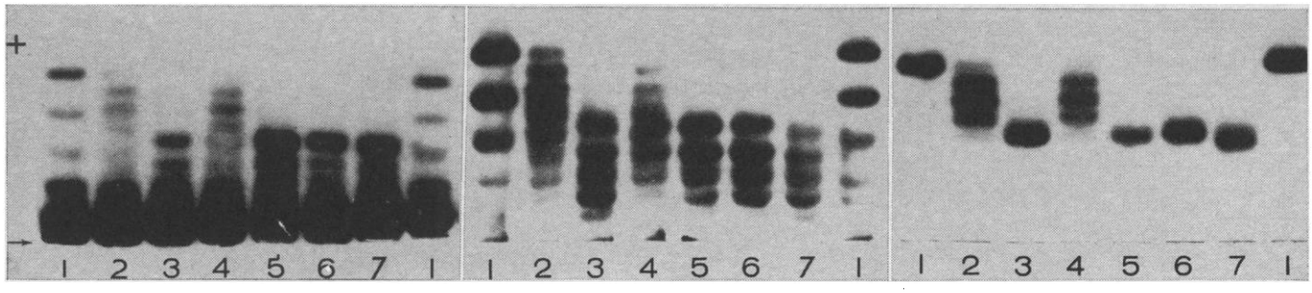
All lizards contributing tissues to this study are deposited in the Museum of Comparative Zoology, Harvard University; identification of the species has been confirmed (*10*). In the case of the lactate dehydrogenase (LDH) patterns, at least three individuals from each of the seven species have been analyzed without detection of infraspecific differences.

Malate dehydrogenase isozymes from the seven species exhibited indistinguishable electrophoretic mobilities; likewise, hemoglobin and serum albumin showed no differences. Lactate dehydrogenase isozymes, however, showed differences: in each tissue studied, the seven species were divided among three distinct electrophoretic patterns (Figs. 1–3).

In most vertebrates, LDH isozymes arise from the association of two different subunits, A and B, to form five possible tetramer combinations: A_0B_4(LDH-1); A_1B_3(LDH-2); A_2B_2-(LDH-3); A_3B_1(LDH-4); and A_4B_0-(LDH-5) (*11*). Genetic studies have shown that the synthesis of A and B subunits is under the control of structural genes at two distinct loci: *a* and *b* (*12–14*). It is assumed that these principles apply to LDH isozymes of the species we discuss.

Each of three sexual species, *C. tigris, C. gularis,* and *C. inornatus,* and of two triploid parthenogenetic species, *C. uniparens* and *C. exsanguis,* produces no more than the predicted five isozymes in tissues where both A and B subunits are developed (Figs. 1 and 2). These species differ in that the fastest band, corresponding to LDH-1 (A_0B_4), of *C. tigris* (No. 1 in Figs. 1 and 2) exhibits greater mobility than the fastest band in each of the other four species (Nos. 3, 5, 6, and 7 in Figs. 1 and 2). Variation in LDH-5 (A_4B_0) mobility among the species studied has not been detected. The relative mobility of the individual bands in electrophoretic patterns from the above five species supports the interpretation that these species synthesize similar A subunits, but that *C. tigris* produces a variant B subunit that we shall call B′.

Two diploid parthenogenetic species, *C. neomexicanus* and *C. tesselatus* (Nos.



Figs. 1–3. Fig. 1 (left). Electrophoretic patterns of LDH isozymes from skeletal muscle. (1) *Cnemidophorus tigris* female [Harvard University Museum of Comparative Zoology (MCZ) 100087; Socorro County, N.M.]; (2) *C. tesselatus* 2*n* parthenogenone (MCZ 100090; Sierra County, N.M.); (3) *C. gularis male* (MCZ 100108; Kent County, Texas); (4) *C. neomexicanus* 2*n* parthenogenone (MCZ 100092; Socorro County, N.M.); (5) *C. uniparens* 3*n* parthenogenone (MCZ 100110; Sierra County, N.M.); (6) *C. inornatus* male (MCZ 100082; Otero County, N.M.); (7) *C. exsanguis* 3*n* parthenogenone (MCZ 100105; Otero County, N.M.). Electrophoretic patterns of LDH isozymes from liver (Fig. 2, middle) and heart (Fig. 3, right); specimens as in Fig. 1.

4 and 2 in Figs. 1 and 2), exhibit more than five isozymes in liver and skeletal muscle, the suggestion being that more than two distinct subunits are associating to form tetramers. The location of the fastest and slowest bands in these species' patterns suggests the presence of A and B′ subunits; the number of bands resolved calls for an additional subunit of intermediate mobility, such as B. Although theory predicts formation of 15 isozymes when three subunits randomly associate into tetramers, overlapping migration, and variation in proportion of isozymes formed, may account for the resolution of fewer than 15 bands in liver and skeletal muscle from *C. neomexicanus* and *C. tesselatus*.

The presence of both B and B′ subunits in *C. neomexicanus* and *C. tesselatus* is indicated by isozyme patterns from heart and kidney. In the heart and kidney of all species except *C. neomexicanus* and *C. tesselatus*, electrophoresis reveals a single band corresponding to LDH-1 and presumably containing only B-type subunits (Nos. 1, 3, 5, 6, and 7 in Fig. 3). The *a*-locus in these lizard tissues is apparently silent, and the dominant production of the fastest subunit facilities analysis of hybrid patterns involving allelism at the *b*-locus. In heart and kidney from *C. neomexicanus* and *C. tesselatus* (Nos. 2 and 4 in Fig. 3), electrophoresis shows five isozyme bands whose staining intensity approximates the binomial proportions of 1 : 4 : 6 : 4 : 1 that theory predicts when equal amounts of two different subunits randomly form tetramers. It is concluded that these five isozymes have the following tetramer composition, in order of increasing mobility: $B_4B'_0$, $B_3B'_1$, $B_2B'_2$, $B_1B'_3$, $B_0B'_4$. This conclusion is further justified by the matching mobilities of the slowest and fastest isozymes, in the *C. neomexicanus* and *C. tesselatus* heart and kidney patterns, with the LDH-1 of *C. gularis* and *C. inornatus* and with the LDH-1 of *C. tigris*, respectively.

Heterozygosity at the *b*-locus has been described within populations of humans (*13, 15*), pigeons (*16*), and fish (*17*). In each instance electrophoretic analysis of heterozygotes has revealed complex LDH isozyme patterns similar to those seen in *C. neomexicanus* and *C. tesselatus*.

Lactate dehydrogenase patterns are known from several artificially produced interspecific hybrids. Rats and mice synthesize electrophoretically distinct A subunits, and hybrid somatic cells, produced by fusion in tissue culture of cells from the two species, exhibit the expected hybrid isozyme patterns (*18*). Speckled trout and lake trout synthesize different A subunits, and the splake, an artificial hybrid of these species, forms hybrid LDH isozymes as a result of heterozygosity at the *a*-locus (*19*). Two frog species, *Rana pipiens* and *R. palustris*, have B subunits of different electrophoretic mobility, and hearts from hybrid tadpoles produced in the laboratory show hybrid isozyme patterns (*20*) strikingly similar to those in *C. neomexicanus* and *C. tesselatus*.

Repeated attempts (*20*) have failed to hybridize in vitro B subunits from *R. pipiens* and *R. palustris*. Using the same method and a recently introduced urea-mediated freeze-thaw technique (*21*) we have likewise failed to achieve in vitro hybridization of B-type subunits from *C. gularis* and *C. tigris* and from *C. inornatus* and *C. tigris*.

It is reasonable to conclude that the hybrid LDH patterns seen in parthenogenetic species of *Cnemidophorus* result from the occurrence of both a *C. tigris*–like *b*′-allele and a *C. inornatus*– or *C. gularis*–like *b*-allele in individuals of *C. neomexicanus* and *C. tesselatus*. Interspecific hybridization of the sort implicated in the origin of *C. neomexicanus* (*5*) is considered responsible for the heterozygosity demonstrated at the LDH *b*-locus in these two diploid parthenogenetic species.

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