

ior of *Micrurus frontalis*, which it resembles in ventral coloration. Goin and Goin (1971) and Azevedo (1960) state that *M. frontalis* adopts a defense position elevating its posterior end in a loop that shows the ventral surface. This behavior occurs in both *M. frontalis* and *L. dorbignyi*; the subcaudal pattern of the latter snake is especially reminiscent of *Micrurus*.

In addition to the mimetic aspects, the coloration and pattern of *Lystrophis dorbignyi* and *Bothrops alternatus* are cryptic in their preferred habitats, such as pastures and low, rocky areas. Possibly both species rely on camouflage as an initial defense. If detected, *Lystrophis* behaviorally mimics *Bothrops* at first, and subsequently switches to coral snake mimicry if the disturbance persists. A similar case of crypsis and pattern and behavioral mimicry in *Pituophis* and *Crotalus* was described by Sweet (1985).

Natural selection strongly favors crypsis as a means of avoiding predation; when crypsis fails, behavioral mimicry has selective value. The present case appears to be unique in that *Lystrophis dorbignyi* "escalates" in its defensive behavior from mimicry of a sympatric *Bothrops* to a startling display of previously hidden colors in a fashion strongly resembling the defense behavior of a sympatric *Micrurus*.

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The Distribution of the *Ambystoma jeffersonianum* Complex in New Jersey

STEPHEN NYMAN,^{1,2} MICHAEL J. RYAN,^{1,3} AND JAMES D. ANDERSON,^{1,4} ¹Department of Zoology and Physiology, Rutgers University, Newark, New Jersey 07102, USA, ²Present address: Department of Zoology, University of Rhode Island, Kingston, Rhode Island 02881, USA, ³Present address: Department of Zoology, University of Texas, Austin, Texas 78712, USA, ⁴Deceased.

Three species of the *Ambystoma jeffersonianum* diploid-triploid species complex have previously been reported from New Jersey: *A. jeffersonianum* (Uzzell, 1964), *A. platineum* (Uzzell, 1964; Anderson and Giacosis, 1967), and *A. laterale* (Anderson and Giacosis, 1967). The purpose of this paper is to report the presence of *A. tremblayi* in New Jersey and to present and analyze the distributional relationships of the four species in New Jersey.

We sought salamanders of the *A. jeffersonianum* complex throughout northwestern New Jersey and in the major wetlands of the Passaic River drainage and adjacent areas. Our goals were to ascertain the distributional limits of these salamanders and to determine whether triploids were found at specific localities. Roads were searched on rainy spring and autumn

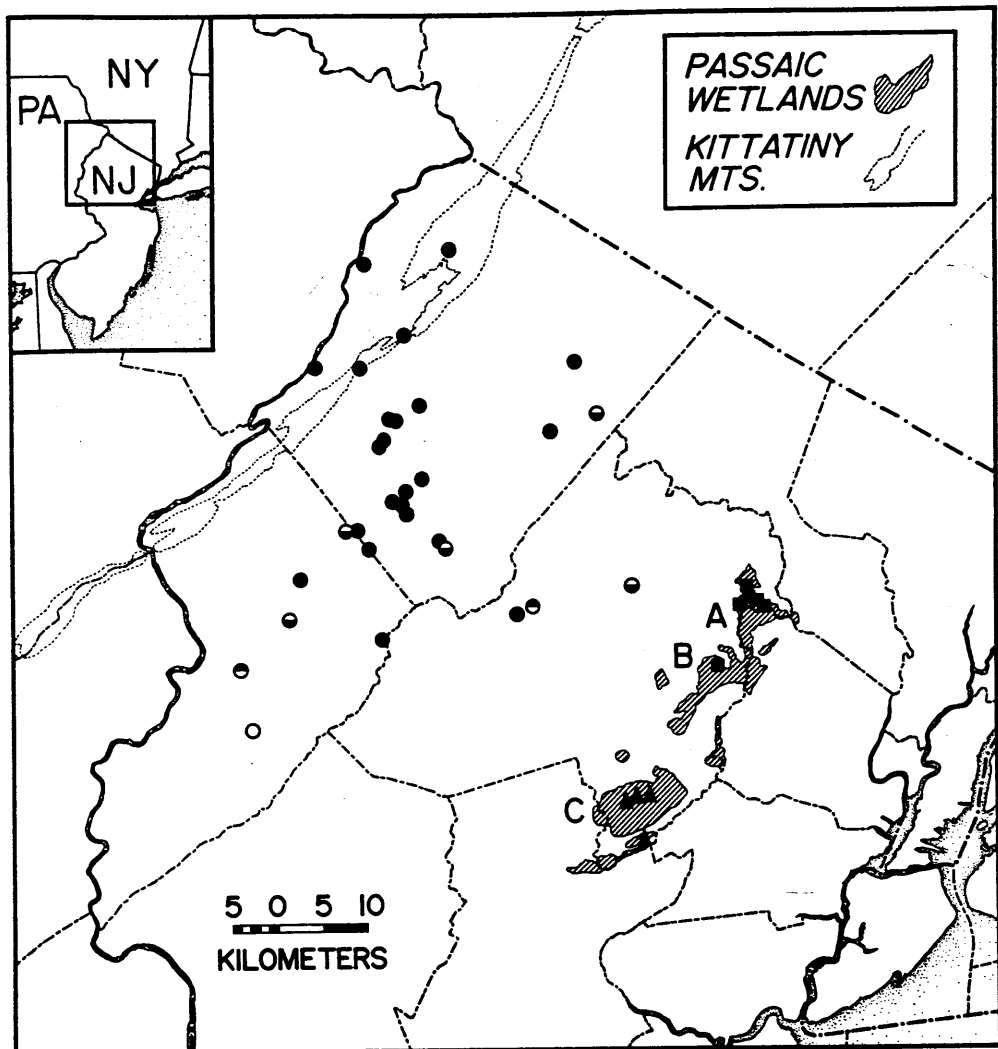


FIG. 1. Localities for members of the *Ambystoma jeffersonianum* complex in New Jersey. Solid circle = *A. jeffersonianum* (AJ) and *A. platineum* (AP) confirmed; circle, top half shaded = AP not confirmed (small sample size); circle, bottom half shaded = AJ from unpublished records, not examined for AP; open circle = AJ approximate location; triangle = *A. laterale* (AL) confirmed; square = AL and *A. tremblayi* confirmed. Wetlands indicated within the basin of glacial Lake Passaic are Great Piece Meadows (and immediately north of it, Bog and Vly Meadows) (A), Troy Meadows (B), and the Great Swamp (C). The main ridge of the Kittatiny Mts. is as defined by the 300 m contour.

nights, likely ponds were checked for the presence of egg masses and larvae, and rocks and logs were turned in the vicinity of pond basins. Triploids were suspected wherever egg masses contained a high percentage of dead, fungus-covered eggs and where females greatly outnumbered males in collections of adult salamanders. Where they occur, triploids are characteristically more abundant than diploids (Uzzell, 1964). A consequence of the scarcity of males is that some females lay eggs without mating or lay over ripe eggs of low viability (Piersol, 1929; Clanton, 1934). The presence of triploids was confirmed primarily

from erythrocyte and erythrocyte nuclear measurements of dried blood smears from adults (methods as in Anderson and Giacosis, 1967, except that slides were unstained).

In northwestern New Jersey, blood smears from large numbers of adult salamanders were obtained from several populations during breeding migrations by road collecting and the use of unbaited minnow traps in ponds in 1976-1978 and 1983. Smaller series of salamanders from road collections and log turning have been obtained in the Passaic River drainage. Six salamanders from the latter region were examined

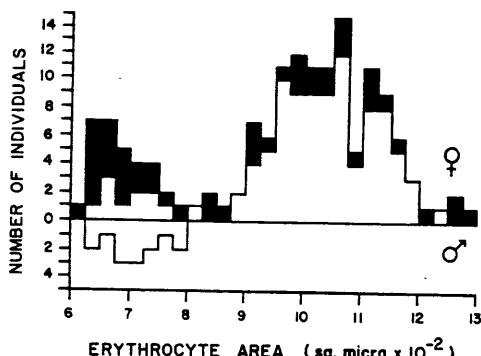


FIG. 2. Frequency distribution of mean erythrocyte areas of *A. jeffersonianum* and *A. platineum* collected by minnow traps on the night of 5-6 March 1976 from Springdale Pond, Sussex Co. (unshaded) and *A. laterale* and *A. tremblayi* collected on the road in Great Piece Meadows, Morris Co., October 1976 (shaded). Salamanders in the latter collection, all indicated here as females, were immatures not distinguished by sex.

electrophoretically for four distinguishing enzyme systems (maltase dehydrogenase-1 (MDH-1), glutamate oxaloacetate transaminase-1 (GOT-1), superoxide dismutase-1 (SOD-1), and Esterase-1 (EST-1)) by J. P. Bogart to confirm identifications based on erythrocyte and erythrocyte nuclear areas. Where adults were unavailable for examination, larvae were identified from erythrocytes suspended in a 4% solution of NaCl and measured as for adults. Larvae so treated fall into two categories which correspond to a diploid and a triploid group. Suitable dried blood smears are difficult to obtain from larvae (Wilbur, pers. comm.; Nyman, pers. observ.).

Populations of *A. jeffersonianum* and *A. platineum* were most concentrated within the Ridge and Valley Province upon the broad limestone and shale floor of the Kittatiny Valley, an area of extensive, glaciated karst topography southeast of the Kittatiny Mountains (Appalachian range) (Fig. 1). Most localities were north of the Wisconsin glacial border. These salamanders were found in only one pond on the highlands of the Kittatiny ridge itself, although *Ambystoma maculatum* bred in 15 other ponds and swamps examined in this region. This pattern (*A. maculatum* present, *A. jeffersonianum* complex absent) was repeated elsewhere outside of the Kittatiny Valley, whereas the reverse pattern was only noted once. We took this to mean that *A. jeffersonianum* and *A. platineum* had been restricted in dispersal either by historical barriers, by chance, or, most probably, by unsuitable ecology.

Ambystoma platineum apparently is found wherever *A. jeffersonianum* occurs in northwestern New Jersey. Small sample sizes at some localities precludes a precise determination at this time.

Breeding habitats of *A. jeffersonianum* and *A. platineum* included limestone sinkhole ponds (Anderson and Martino, 1966), kettle ponds, other natural basins, and abandoned quarry pits. Most were ephemeral and

were filled by groundwater, springs, and surface runoff. Pond dimensions were highly variable, with surface areas ranging from less than 0.01 ha to over 6 ha, but most ponds had maximum depths after filling of at least 1 m. No swamps, marshes, streams, or springs and very few ridge-top ponds were utilized, although many of these habitats supported larval *A. maculatum*. *Ambystoma jeffersonianum* and *A. platineum* live terrestrially in upland, well drained, second growth, mixed deciduous woodlands.

Breeding aggregations of *A. jeffersonianum* and *A. platineum* were characterized by the numerical predominance of the unisexual species. Of 146 salamanders caught in minnow traps in a pond near Springdale, Sussex Co., on the night of 5-6 March 1976, *A. platineum* was nearly nine times more numerous than females of *A. jeffersonianum* (Fig. 2). Sampling of salamanders entering and leaving breeding ponds near Swartswood Lake, Sussex Co., in 1977 and 1978 suggests that diploids comprised no more than 10-20% of those breeding aggregations.

Ambystoma laterale was found in four of the major regions of the Passaic River basin: the Great Swamp, Great Piece Meadows, Bog and Vly Meadows, and Troy Meadows (Fig. 1). These areas are a mixture of wooded swamp, marsh, and bog habitats situated between low basaltic ridges (elevation to about 150 m) demarcating the northern and southeastern boundaries of the remnants of a glacial lake (Lake Passaic) formed during the Pleistocene by the impeded flow of the Passaic River.

Erythrocyte analyses of salamanders collected in Great Piece Meadows, Bog and Vly Meadows, and Troy Meadows indicated the presence of *A. tremblayi* in each of these areas. Salamanders from Great Piece Meadows exhibited the same bimodality in frequency distribution of erythrocyte areas within about the same range of values as did *A. jeffersonianum* and *A. platineum* (Fig. 2). Females greatly outnumbered males in breeding migrations in Great Piece Meadows. Of animals found on the road in this area during the entire breeding season in 1980 (24 March to 14 April), 52 were females, 15 were males, and 14 animals killed by automobiles were of unknown sex. Electrophoretic examination has further confirmed the presence of *A. tremblayi* (Table 1). However, *A. tremblayi* is absent from the most extensive wetland within the Passaic basin, the Great Swamp.

Eggs and larvae of *A. laterale* were found in the Great Swamp in small, vernal ponds, abandoned farm ponds, and roadside ditches. Similarly, *A. laterale* and *A. tremblayi* in Troy Meadows bred in shallow vernal ponds. Other aquatic habitats, such as cattail marsh and flooded woodlands, were not extensively surveyed for larvae. *A. laterale* and *A. tremblayi* in Great Piece Meadows bred in a network of shallow pools and runnels in a red maple swamp.

Terrestrial habitats in the Great Swamp and Troy Meadows consist of scattered areas of second growth hardwood forest on low ridges and knolls one to five meters above the marsh and wooded swamp. Although similar areas may exist and provide terrestrial habitat for salamanders in Great Piece Meadows, *A. laterale* and *A. tremblayi* in spring and autumn migrations were found moving to and from a steep, basaltic

TABLE 1. Electrophoretic phenotypes for four enzyme systems diagnostic for diploid salamanders of the *Ambystoma jeffersonianum* complex and for six salamanders from the Passaic River basin, New Jersey. "F" and "S" refer to fast and slow migrating allozymes, respectively. The number of letters indicates dosage of each allele.

Identity of specimen(s)	SOD-1	GOT-1	EST-1	LDH-1
<i>A. laterale</i> (AMNH 114796), Great Piece Meadows, N.J.	FF	FF	FF	FF
<i>A. tremblayi</i> (AMNH 114797-114800), Great Piece Meadows, N.J.	FFS	FFS	FFS	FFS
<i>A. tremblayi</i> (AMNH 114801), Troy Meadows, N.J.	FFS	FFS	FFS	FFS
Most <i>A. laterale</i> , many localities ¹	FF	FF	FF	FF
Most <i>A. jeffersonianum</i> , many localities ¹	SS	SS	SS	SS

¹ Bogart, unpublished data.

ridge which forms a crescent along the northern and western boundaries of this wetland. The hill is vegetated with weedy, second growth to mature, mixed deciduous woods.

On a local scale, aspects of the distribution of *A. tremblayi* (absent from the Great Swamp, but present in the same basin further north, and apparently absent from Long Island) fit the in situ origin hypothesis originally proposed by Uzzell (1964), but questioned by Uzzell and Goldblatt (1967). On the broader scale, however, the in situ origin of triploids seems implausible because triploids occur over a region far more extensive than that where both parental species overlap or are proximate in distribution (Morris and Brandon, 1984). Alternatively, the triploids may have dispersed along with their diploid hosts or invaded the ranges of the diploid species. As such, *A. tremblayi* may have once occurred more extensively, such as in the Great Swamp, but has since become locally extinct.

In New Jersey, distances of only 13-15 km each separate populations of *A. jeffersonianum* and *A. platineum* from populations of *A. laterale* and *A. tremblayi*, and populations of *A. laterale* from areas where both *A. laterale* and *A. tremblayi* occur. The situation is similar elsewhere, particularly in New England, eastern New York, and Ontario, Canada, where the species occur in a seemingly desultory pattern of areas in which one or the other diploid species is found, with or without its associated triploid species (Uzzell, 1964; Uzzell and Goldblatt, 1967; Weller and Menzel, 1979; Morris and Brandon, 1984; Joseph Pratt, pers. comm.).

We propose that the present distribution, in New Jersey at least, is the result of ecological sorting of the species of the complex. Whereas New Jersey *A. jeffersonianum* and *A. platineum* occurred in well drained uplands, *A. laterale* and *A. tremblayi* were associated with lowlands bordering swamps and marshes. *Ambystoma laterale* and *A. tremblayi* bred in flood plain pools, ponds, and swamps. Flood waters inundated some of these areas in winter and sometimes after the onset of the salamanders' breeding, yet breeding pools in all areas were shallow and early to dry. In Great Piece Meadows the deepest breeding pools were less than 0.6 m deep and most held only 15-25 cm of standing water. Fish, particularly *Umbra pygmaea* (eastern mudminnow), were found in these pools with the larval salamanders. *Ambystoma jeffersonianum* and *A. platineum* were restricted to ponds and have not been found in flood plain habitats within their range

in New Jersey. Although habitat should not be used a priori to assume a corresponding ecology, habitat differences observed in New Jersey are in agreement with published accounts of the habitats of these species throughout their ranges as summarized by Weller et al. (1978).

The known distribution of triploids (Uzzell and Goldblatt, 1967; Morris and Brandon, 1984) suggests range contraction. Discrimination against triploids in mating by males of the complex (Uzzell, 1969) could have resulted in local extinctions of triploids. The significance of ecological factors in the distribution of triploids is not known. Despite few comparative studies, differences in the ecology and life history of diploids and triploids have been reported (number of eggs/mass, egg weight, time of breeding, embryonic and larval developmental rates; Uzzell, 1964; Wilbur, 1971, 1977; Pennak, 1978). Controlled experiments are needed to ascertain whether these or other possible ecological differences could have contributed to the present distribution.

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TABLE 1. Subfamily Ceratophryinae. Within each subgenus of the genus *Ceratophrys* the species marked with an asterisk (*) are designated by Lynch (1982) as each other's closest relative.

<i>Chacophrys</i>	<i>Lepidobatrachus</i>	<i>Ceratophrys</i>
<i>pierottii</i>	<i>asper</i>	<i>Ceratophrys</i> (Subgenus)
	<i>laevis</i>	* <i>aurita</i>
	<i>llanensis</i>	* <i>ornata</i>
		<i>cranwelli</i>
		<i>Stombus</i> (Subgenus)
		* <i>calcarata</i>
		* <i>cornuta</i>
		<i>stolzmanni</i>

amine Lynch's hypotheses using an independent data base, namely genetic relationships inferred from micro-complement fixation (MCF) analyses of serum albumins. Data derived from MCF studies of serum albumin evolution have been shown to directly estimate amino acid differences between homologous albumins, and hence to constitute a phylogenetic data base (Wilson et al., 1977; Maxson and Maxson, 1986). Such comparative molecular studies have contributed to our understanding of phylogenetic relationships among diverse amphibians (for example Maxson, 1984a; Maxson and Roberts, 1984, 1985; Hutchinson and Maxson, 1986).

Albumin antisera prepared to the albumin of *Ceratophrys aurita* (from São Paulo, Brasil) and *C. calcarata* (from Colombia) were available (Maxson and Heyer, 1982). New albumin antisera were made to *Chacophrys pierottii* (Totoralejos, Cordoba, Argentina) and *Lepidobatrachus laevis* (Filadelfia, Paraguay). Antigens of three of the four remaining species of *Ceratophrys* were available for comparison: *C. cranwelli* (Filadelfia, Paraguay), *C. ornata* (laboratory bred), and *C. cornuta* (Rondonia, Brasil). Antisera were prepared and all MCF comparisons performed according to standard procedures (Champion et al., 1974; Maxson et al., 1979). The available antigens were cross reacted to the panel of four antisera (Table 2).

The immunological distances obtained to the *C. aurita* antiserum indicate that the three species that Lynch associated with the subgenus *Ceratophrys* (*aurita*, *ornata*, and *cranwelli*) are most closely related to one another. By contrast, *C. calcarata*, in the subgenus *Stombus*, does not appear to be any more closely related to *C. cornuta* than it is to the three species in the subgenus *Ceratophrys*. Instead, *C. cornuta* albumin appears equally distant from both representative antisera for the two subgenera. Morphologically the two subgenera are separated on the basis of the subgenus *Ceratophrys* having a dorsal shield while the subgenus *Stombus* lacks the dorsal shield and has a more lateral tarsal fold, more pronounced otic crests, and more extensive webbing between the toes. The albumin data, therefore, do not entirely support all the relationships indicated by Lynch for the species of *Ceratophrys* (see Tables 1 and 2).

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Relationships of Frogs in the Leptodactylid Subfamily Ceratophryinae

LINDA R. MAXSON¹ AND RODOLFO RUIBAL², ¹*Department of Ecology, Ethology, and Evolution, University of Illinois, Urbana, Illinois 61801, USA;* ²*Department of Biology, University of California, Riverside, California 92521, USA.*

There are currently three South American genera of frogs recognized in the subfamily Ceratophryinae: *Ceratophrys*, *Lepidobatrachus*, and *Chacophrys* (Table 1). Lynch (1982) separated the six species of *Ceratophrys* into two subgenera, each with three species. Within each subgenus two of the species have been designated each other's closest relative based on morphological considerations. Lynch also suggested that the genus *Chacophrys* be suppressed because he hypothesized that *Chacophrys pierottii* was an intergeneric hybrid between *Ceratophrys cranwelli* and *Lepidobatrachus llanensis*.

As part of a continuing molecular study of phylogenetic relationships among leptodactylid frogs (Heyer and Maxson, 1982; Maxson and Heyer, 1982, 1986), material was on hand that enabled us to ex-