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**A NEW SPECIES OF LEOPARD FROG (*RANA PIPIENS* COM-  
PLEX) FROM THE PLAINS OF THE CENTRAL  
UNITED STATES**

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Sufficient evidence has accumulated over the last six years to show that the leopard frogs (*Rana pipiens, sensu lato*) of North America actually include several forms that merit recognition as distinct species. Littlejohn and Oldham (1968) showed that four essentially allopatric forms, recognizable on the basis of mating call structure and morphology of adult males, occur in the central United States. These were referred to informally as the northern, western, eastern, and southern call types. Narrow zones of sympatry were located between western and eastern, western and southern, and between eastern and southern call types in Texas. The zone of overlap between western and southern call types was found to be about 16 kilometers wide in north-central Texas, and that between southern and eastern call types was estimated to be about eight kilometers wide in central Texas. Also, Post and Pettus (1967) found an overlap zone only eight kilometers wide between so-called CF (continuous dorsolateral folds) and DF (displaced dorsolateral folds) complexes (corresponding to the northern and western call types, respectively) in Colorado, and Flury (1972) collected both northern and western call types together in northern Nebraska. Brown and Brown (1972) found the western call type in sympatry with both eastern and northern call types in Illinois, and overlap between western and southern call types in Texas has been confirmed by Purcell (1968), Mecham (1969), Cuellar (1971), and Platz (1972). Platz (1972) found the overlap zone between west-

ern and southern call types in western Texas to be about 56 kilometers wide. Crossing experiments (Mecham, 1969; Cuellar, 1971) have demonstrated genetic differences between certain of the forms, as have the studies on heart muscle lactate dehydrogenase by Salthe (1969). Other taxa apparently occur in the southwestern United States. Mecham (1968*a*, 1968*b*) demonstrated sympatry between so-called northern and southern forms in Arizona. The northern form probably corresponds to the northern call type of Littlejohn and Oldham (Mecham, 1968*b*), but the southern form apparently is distinct from call types in the central United States (Mecham, 1968*a*, 1968*b*, 1971). Platz and Platz (in press) recently identified a third type (the lowland form) in Arizona; sympatry between this third form and the southern form (Arizona), as well as between the northern and southern forms (Arizona), were detected through analysis of hemoglobins.

Three of the call types identified by Littlejohn and Oldham (1968) correspond closely in their distributions to formally recognized subspecies (Mecham, 1969; Platz, 1972). The northern call type represents *R. p. pipiens* Schreber; the eastern call type, *R. p. sphencephala* Cope; and the southern call type, *R. p. berlandieri* Baird. The western call type, included largely within the range of *R. p. berlandieri* by Conant (1958), apparently represents an undescribed taxon. Three taxa, the western call type, *R. p. berlandieri*, and *R. p. sphencephala*, contact one another and retain their distinctness in sympatry; thus, they clearly fulfill the requirements for recognition as separate species. The same is true of the western call type and *R. p. pipiens*. As *R. p. pipiens* and *R. p. berlandieri* are disjunctly allopatric, their relative specific status cannot be subjected to the ultimate taxonomic test. Also, sympatry has yet to be demonstrated between *R. p. pipiens* and *R. p. sphencephala*, although the two taxa presumably come into contact. In both cases, however, the differentiation in mating call structure and other characters is comparable to those of taxa known to maintain their distinctness in sympatry, and it is reasonable to assume that the taxa involved would act as biological species. Sanders and Smith (1971) have proposed specific rank for *R. p. berlandieri*. We propose that all four taxa be treated as species. As no name is available for the western call type (= plains or southern plains type of Mecham, 1969, 1971, Cuellar, 1971, and Platz, 1972, = the DF complex of Post and Pettus, 1966, 1967), a formal description is presented below. A detailed study of the systematic biology of the *Rana pipiens* complex in the United States has been made by Pace (in press).

A nomenclatorial problem may have been created with the restriction of the type locality of *Rana pipiens* to White Plains, New York,

by Schmidt (1953). Several lines of evidence (oviducts, head measurements, Moore, 1944; Snout shape, Ruibal, 1957; HLDH enzymes, Salthe, 1969) suggest that *Rana sphenocephala* extends into this area. See Pace (in press) for a detailed discussion of nomenclature.

***Rana blairi***, new species  
Plains Leopard Frog  
(Figs. 1-2)

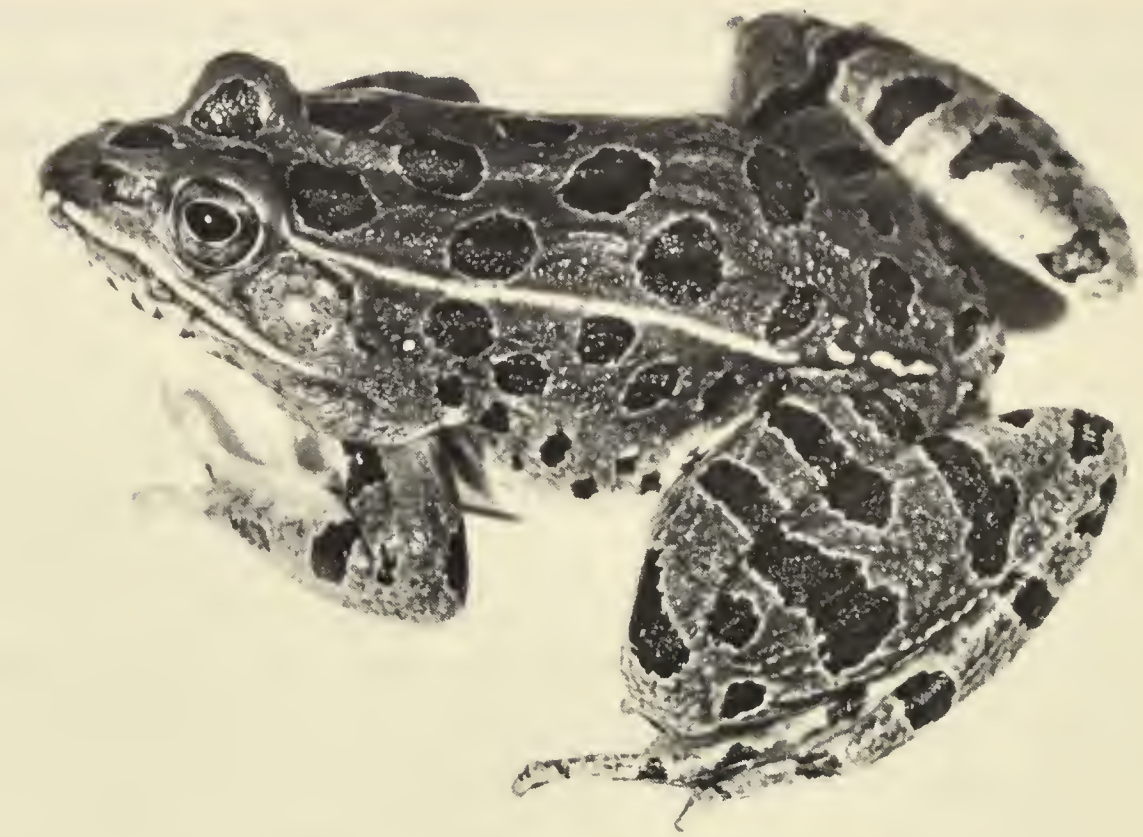
*Holotype*.—Adult male, University of Michigan Museum of Zoology Collection, no. 131690, from 1.6 km. W New Deal, Lubbock Co., Texas, collected by Charles Everett on 6 August 1971.

*Paratypes*.—UMMZ 131691-131693, collected with the holotype, and UMMZ 131694-131697 from 1.6 km. E New Deal, Lubbock Co., Texas, also collected on 6 August 1971 by Charles Everett.

*Diagnosis*.—A frog of the *Rana pipiens* complex distinguished by a combination of characters including: dorsolateral folds that are usually interrupted posteriorly and deflected medially; absence of oviducts in males; usually a complete pale line on the upper lip; and a mating call (*sensu* Littlejohn and Oldham, 1968) with a uniquely low pulse rate (average of less than six pulses per second below 24°C) and low pulse number (average of less than six pulses per call).

*Description of holotype*.—Adult male with a snout-vent length of 91.3 millimeters; tibia length, 55.0; head width, 31.4; head length 31.5 nostril to edge of upper lip, 7.5; orbit to nostril, 6.6; diameter of tympanum, 8.9. Dorsolateral folds broken posteriorly just anterior to thigh and slightly inset medially, terminating midway above thigh; no vestigial oviducts; webbing on hind foot extending to the base of apical phalanx of fourth toe. External vocal sacs moderately developed; skin smooth on venter, finely granular on posterior surface of thigh, moderately rugose or pustulate on sides, and with low longitudinally oriented plicae on the back. Color (in alcohol) pale cream below and pale brown above, tinged with gray on sides. Venter immaculate except for sparse dark stippling on the throat and upper chest; a pale narrow stripe extending along the upper lip from a point below the posterior margin of the tympanum to a point beyond the naris; dorsolateral folds very pale brown; tympanum with an obscure, pale spot. Dorsum with 18 dark brown, rounded spots with traces of pale, very narrow, borders; spots on sides smaller; transverse dark bars on upper surface of the hind limbs; posterior surface of thighs mottled with dark brown, diffuse spots.

*Variation within the type series*.—Paratypes (three males, four females) agree closely with the holotype in most characters including



1



2

FIG. 1.—Holotype of *Rana blairi*.

FIG. 2.—Paratype of *Rana blairi*, a female (UMMZ 131694) from 1.6 km. E New Deal, Texas.

dorsolateral folds, oviducts, skin texture, extent of webbing, and general coloration. The supralabial stripe varies from well defined to obscure, but can be traced nearly to the tip of the snout in all specimens. A pale tympanic spot is present in all specimens, and varies from obscure to distinct. Pale borders to the spots are very narrow or absent. Dark markings on the posterior surface of the thigh vary from pale, diffuse spotting to heavy mottling. Some fine dark stippling or mottling is present on the throat, particularly to the sides, on all but

two specimens. Coloration in life for all specimens of the type series was pale brown above, paler on the sides, with dark brown spots. Dorsolateral folds, tympanic spots, and supralabial stripes varied from pale brown to pale yellow-brown. The venter was pale white in all specimens except for yellow groin color and a tinge of yellow on the lower abdomen and proximal part of the thigh.

Mean values with ranges for the type series are: snout-vent, males 81.90 (74.6-91.3) millimeters, females 88.07 (84.1-98.7); tibia/snout-vent, males 0.58 (0.55-0.59), females 0.56 (0.53-0.60); head width/head length, males 1.01 (0.99-1.03), females 1.03 (1.00-1.05); head length/snout-vent, males 0.35 (0.33-0.35), females 0.33 (0.32-0.34); nostril-lip/eye-nostril, males 1.11 (1.08-1.14), females 1.08 (1.03-1.11); dorsal spot number, males 19.50 (18-21), females 18.75 (14-22). Mean values for males and females together are: snout-vent,  $87.50 \pm 3.02$ ; tibia/snout-vent,  $0.57 \pm 0.01$ ; head width/head length,  $1.02 \pm 0.01$ ; head length/snout-vent,  $0.34 \pm 0.01$ ; nostril-lip/eye-nostril,  $1.09 \pm 0.01$ ; dorsal spot number,  $19.10 \pm 0.92$ .

*Distribution.*—Distribution is centered in the Great Plains, and includes northwestern Texas and eastern New Mexico, the western two-thirds of Oklahoma, all of Kansas with the possible exception of the southeastern corner, eastern Colorado, most of Nebraska, southern Iowa, apparently large parts of Missouri, and much of Illinois. Distribution in Texas, Oklahoma, and Kansas is shown by the map of Littlejohn and Oldham (1968). Western limits of the range in New Mexico are not positively known, but one of us (Mecham) has identified specimens from the Sacramento Mountains (Lincoln County) in the southern part of that state. Post and Pettus (1966) recorded *R. blairi* (as the DF complex) as far west as western Las Animas and Pueblo counties in southern Colorado. Distribution of males lacking vestigial oviducts (Moore, 1944) indicates that *R. blairi* extends as far north as northern Nebraska; Flury (1972) collected it with *R. pipiens* at Valentine, Nebraska. Distribution in Illinois appears to be largely associated with the prairie peninsula; Brown and Brown (1972) found *R. blairi* as far south as Jackson County and as far north as LaSalle County in that state. Pace (in press) has provided distribution maps and details of localities for leopard frog taxa, including *R. blairi*, in the United States.

*Comparisons.*—Mating call structure. Characteristics of mating calls of *R. blairi* including those of a series recorded at the type locality are given in Table 1. Also included for comparison are characteristics of mating calls of some other members of the *R. pipiens* complex. The initial calls of a series and single calls tend to be longest

and were chosen as the basis for call duration figures in the table. A sound spectrogram of two mating calls recorded at the type locality is given in Fig. 3. A sound spectrogram of a call sequence (including mating call or mating trill, low trills, grunts and grinds) as well as oscillograms of individual pulses of the mating call and low trill have been furnished by Mecham (1971); Littlejohn and Oldham (1968) provided an oscillogram of mating call pulses.

The most distinctive characteristic of the mating call of *R. blairi* is the uniquely low pulse rate, which averages less than six pulses per second below 24°C. In other taxa of the complex pulse rates are always higher and never overlap those of *R. blairi* at comparable temperatures (Table 1). The number of pulses per call (which can be extracted from Table 1 as pulse rate  $\times$  call duration + 1) is also unusually low. Mean pulse number at the type locality for single calls and first calls in a series was only 4.76 (range 3 to 7) and subsequent calls in a series usually contained only three or four pulses. Mating calls of *R. blairi* resemble more closely those of the lowland form (*sensu* Platz and Platz, in press) than those of other taxa examined, but pulse rates are well below those of the lowland form at comparable temperatures.

Morphology and pattern. Some of the more diagnostic morphological and pattern characteristics of *R. blairi* are compared with those of other taxa of the *R. pipiens* complex in Table 2. The broken and displaced dorsolateral folds of *R. blairi*, as noted by Littlejohn and Oldham (1968), have a diagnostic value of about 95 per cent in separating that form from *R. pipiens* and *R. sphenoccephala*, both of which have continuous folds. Vestigial oviducts appear to be consistently absent in males of *R. blairi*, whereas they are almost always present in *R. pipiens* (Moore, 1944, examined one sample from Maine that lacked them). Oviducts also are present in males of *R. berlandieri* over most of Texas, although males from trans-Pecos Texas may lack them (McAllister, 1962), and the same is true for presumed *R. berlandieri* from some areas in México (Cuellar, 1971). Specimens of *R. blairi* possess a usually well-defined labial stripe that extends from the posterior angle of the upper jaw to a point near the tip of the snout. It is always distinct in young animals, but occasionally becomes obscure in adults. A similar stripe appears to be present generally in *R. pipiens* and *R. sphenoccephala* (Wright, 1949; Cuellar, 1971). In *R. berlandieri* (Cuellar, 1971; Platz, 1972) and in southern and lowland forms in Arizona (Mecham, 1968*a*, 1968*b*; Platz and Platz, in press) a labial stripe is indicated posteriorly, but is less well defined, and becomes indistinct and diffuse anterior to the eye. Some yellow pigment may

TABLE 1.—Comparison of some characteristics of mating calls of *Rana blairi* and some other members of the *Rana pipiens* complex. Mean values are given above ranges that are in parentheses.

Locality	Individuals (No.)	Temperature (°C)	Call duration (sec)	Pulse rate (No./sec)	Pulse duration (msec)	Pulse rise time (msec)
<i>Rana blairi</i>						
Texas, New Deal (type locality)	10	22.0-24.0	0.70 (0.36-1.00)	5.3 (4.8-6.1)	28.6 (24-34)	9.7 (7-16)
Texas <sup>1</sup>	7	20-25	0.66 (0.48-0.89)	5.6 (4.6-6.8)	27.0 (23-35)	9.1 (7-11)
Illinois <sup>2</sup>	5	21.8-22.5	0.68 (0.57-0.77)	5.1 (4.9-5.3)	24.0 (19.8-29.0)	—
<i>Rana pipiens</i>						
Colorado <sup>1</sup>	4	12-16	3.75 (3.30-4.73)	13.7 (12.9-14.6)	17.8 (16-20)	2.0 (2)
Illinois <sup>2</sup>	5	17.6-18.2	2.90 (2.48-3.39)	19.4 (17.0-21.2)	7.3 (6.9-7.5)	—
<i>Rana sphenocephala</i>						
Texas <sup>1</sup>	7	20-25	0.41 (0.31-0.52)	14.8 (14.3-15.3)	39.4 (33-50)	24.3 (20-30)
Illinois <sup>2</sup>	2	21.5-21.8	0.46 (0.39-0.53)	12.0 (11.8-12.3)	42.1 (41.9-42.3)	—
<i>Rana berlandieri</i>						
Texas <sup>1</sup>	7	20-25	0.64 (0.47-0.83)	28.2 (26.0-31.3)	19.1 (16-22)	9.7 (9-11)
Texas, McAllen <sup>3</sup>	4	22.9-23.1	0.54 (0.41-0.62)	22.3 (20.4-25.8)	18.3 (17.0-19.5)	4.3 (3.5-5.5)
Lowland form (of Platz and Platz, in press)						
Arizona, Wikieup <sup>3</sup>	6	20.0-22.5	0.58 (0.44-0.74)	9.6 (8.6-11.1)	30.3 (25-33)	12.1 (11-15)
Southern form (of Mecham, 1968a, 1968b, 1971; Platz and Platz, in press)						
Mexico, Chihuahua, Casas Grandes <sup>3</sup>	2	21.0-23.6	1.36 (0.84-1.75)	34.6 (31.0-38.7)	14.7 (10.0-18.0)	0.9 (0.8-1.0)

<sup>1</sup>Data of Littlejohn and Oldham (1968).<sup>2</sup>Data of Brown and Brown (1972).<sup>3</sup>Data of Mecham (unpublished).

occur also on the lower abdomen and ventral thigh of mature *R. blairi* of both sexes, at least on the southern high plains (see description), but such coloration is very limited when present, and is not to be compared with the pronounced ventral yellow or yellow-brown of Arizona southern and lowland forms (Mecham, 1968a, 1968b; Platz and Platz, in press). Ventral yellow appears to be absent generally in *R. pipiens*, *R. sphenocephala*, and Texas specimens of *R. berlandieri* (Wright and Wright, 1949; our observations). However, some presumed *R.*

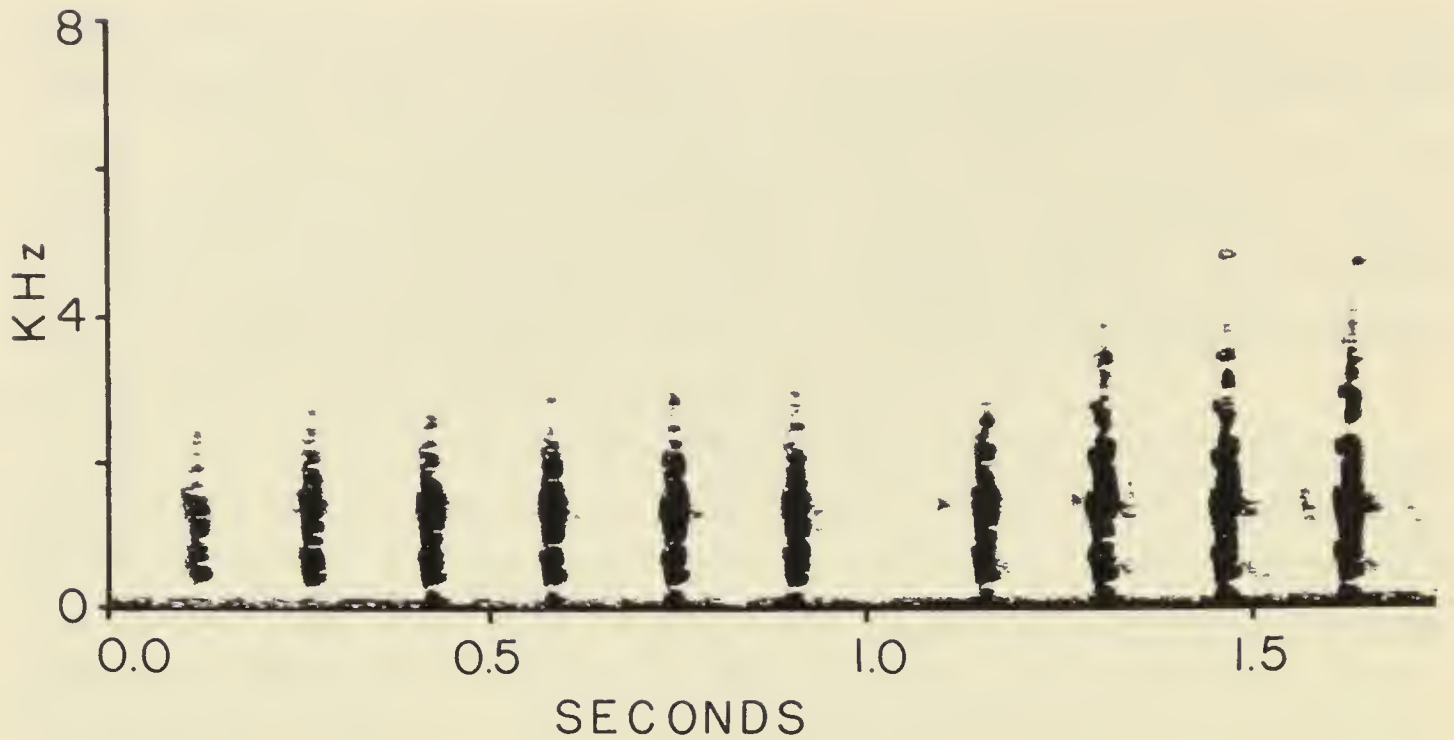


FIG. 3.—A sound spectrogram (Kay 6061-A Sona-Graph, narrow filter band) of two mating calls (trills) of *Rana blairi*, recorded at the type locality on 22 May 1971 at a temperature of 23.0°C.

*berlandieri* in México may be yellow-legged (Sanders and Smith, 1971).

Protein variation. Salthe (1969), in an extensive study of lactate dehydrogenases in North American leopard frogs, found a number of electrophoretic variants of heart muscle lactate dehydrogenase (HLDH). The distribution of these variants conforms in part to the distribution of the various call types. *Rana blairi* and *R. pipiens* both

TABLE 2.—Summary of certain morphological and pattern characteristics of *Rana blairi* and some other members of the *Rana pipiens* complex as indicated by information presented by Brown and Brown (1972), Cuellar (1971), Littlejohn and Oldham (1968), McAllister (1962), Mecham (1968a, 1968b), Moore (1944), Platz (1972), Platz and Platz (in press), Post and Pettus (1966), and Wright and Wright (1949), unless otherwise documented in the text.

Species or form	Dorsolateral folds	Oviducts in males	Labial stripe	Yellow pigment (abdomen, thigh)
<i>R. blairi</i>	displaced	absent	complete	occasional, slight
<i>R. pipiens</i>	continuous	present	complete	absent
<i>R. sphenoccephala</i>	continuous	absent, except in peninsular Florida	complete	absent
<i>R. berlandieri</i> (United States)	displaced	present, except in trans-Pecos Texas	incomplete	absent
Southern form (of Mecham, 1968, 1971)	displaced	variable	incomplete	well developed
Lowland form (of Platz and Platz, in press)	displaced	absent	incomplete	well developed



possess a single HLDH variant (PIP I). PIP I, however, does not occur in either *R. berlandieri* or *R. sphenoccephala*, although both of these taxa are highly polymorphic for HLDH. On the basis of HLDH, *R. blairi* is readily distinguishable from both *R. berlandieri* and *R. sphenoccephala*, but not from *R. pipiens*.

Platz (1972) compared serum proteins in the plains leopard frog and *R. berlandieri*, which was found to have a single fast migrating albumin band; the plains type has a slower double band. A slight difference in relative frequency of slow and fast migrating transferrins also was found.

*Etymology.*—The species is named in honor of W. Frank Blair because of his early suggestion that there were cryptic "*Rana pipiens*" species in the southwestern United States (a suggestion which lead directly to the discovery of *R. blairi* in Texas in 1963), and more generally in recognition of his contributions to our knowledge of the systematics and evolutionary biology of anurans.

*Remarks.*—Although some natural hybridization may occur within areas of contact between *R. blairi* and certain of the other taxa of the *R. pipiens* complex, reproductive isolation always appears to be complete enough to preserve the essential integrity of each form. Platz (1972) considered that only 12 of a sample of 138 frogs from the contact zone between *R. blairi* and *R. berlandieri* could be hybrids on the basis of electrophoretic analysis. Littlejohn and Oldham (1968) detected only three presumed hybrid mating calls in recorded samples of *R. blairi* and *R. berlandieri* that included at least 25 males of each taxon, and found no evidence of hybridization where *R. blairi*, *R. berlandieri*, and *R. sphenoccephala* come together in Johnson County, Texas. Brown and Brown (1972) found no evidence of hybridization between sympatric *R. blairi* and *R. sphenoccephala* in Mason County, Illinois. Brown and Brown (1972) recorded no hybrids between sympatric *R. blairi* and *R. pipiens* in La Salle County, Illinois, and Post and Pettus (1967) found no evidence of hybridization between the taxon described herein and *R. pipiens* where their ranges contact in southeastern Colorado.

Experimental crosses by Mecham (1971) and Oldham (unpublished) between *R. blairi* and *R. sphenoccephala* produced only slight variations from normal development, as did crosses by Purcell (1968) between the new taxon and presumed *R. pipiens* from Arizona. Crosses with *R. berlandieri* (Mecham, 1969; Oldham, unpublished; Purcell, 1968), however, gave much more pronounced abnormalities, particularly using females of *R. blairi* and males of *R. berlandieri*. In two such crosses with specimens from the contact zone, abnormali-

ties were so severe as to block development in all embryos (Purcell, 1968). Hybrid males produced from both reciprocal crosses between *R. blairi* and *R. berlandieri*, however, proved to be fertile (Mecham, 1969). These results indicate that developmental incompatibility, and perhaps hybrid sterility, are not highly effective as isolating mechanisms between *R. blairi* and other members of the complex, although developmental incompatibility, at least, may contribute to reproductive isolation from *R. berlandieri*. Reproductive isolation of *R. blairi*, therefore, must depend largely upon premating factors, although adaptive inferiority of hybrids could also play a role.

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