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PHYLOGENY OF *PLEURODEMA* (ANURA: LEPTODACTYLIDAE): A BIOGEOGRAPHIC MODEL

By

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Modern biogeographic thinking is undergoing drastic modifications with the reassessment of Croizat's (1964) conceptual contributions by Brundin (1966), Croizat, Nelson, and Rosen (1974), Ball (1975), and Rosen (1975). Recent studies on frogs within the Neotropical Realm (Duellman, 1972; Duellman and Crump, 1974; Heyer, 1973) have provided additional support for the importance of climatic fluctuation and concomitant ecological modifications in the patterns of distribution and differentiation of organisms in the American tropics as postulated by Haffer (1969), Vanzolini and Williams (1970) and Müller (1973). With the exception of Müller (1973), who formulated a series of dispersal centers throughout South America, the biogeographic concerns have been primarily with the tropical regions, to the neglect of temperate South America.

Southern South America has an endemic and evolutionarily important frog fauna, consisting primarily of telmatobiine leptodactylids. The major exception is the leptodactyline genus *Pleurodema* containing 14 species, only two of which occur in the tropics. *Pleurodema bufonina* is the southernmost frog, reaching the Straits of Magellan at 53° S Lat.; two species range northward in the Andes to Perú, and one extends to Panamá and the Caribbean coast of South America (13° N Lat.). *Pleurodema* are small (< 60mm),

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toad-like anurans; many species are fossorial. These small frogs exhibit a diversity of reproductive behavior and combinations of morphological traits that provide ideal material for a phylogenetic study.

The data for the present paper have been derived from our studies on the morphology of adults and tadpoles, mating calls, breeding behavior, and karyotypes, and from the extensive literature on the genus. These data form the basis for a phylogenetic construct that, in combination with information on past and present climatic and vegetation patterns in southern South America, provide the basis for the biogeographic model.

ACKNOWLEDGMENTS

Our field studies on *Pleurodema* were accomplished independently. Veloso is indebted to Mario Penna for assistance in recording calls and to Nelson Diaz for measuring frogs. Duellman's field work in South America was supported by a grant (No. 1304) from the National Geographic Society. In the field he was ably assisted by Dana K. Duellman, John E. Simmons, and Linda Trueb. Stephan Halloy also assisted in collecting specimens in Argentina and Chile, and Raymond F. Laurent kindly guided us to a locality for *P. tucumana*. Through the courtesy of Nelly Carillo de Espinoza, Duellman was able to examine specimens in the Museo de Historia Natural "Javier Prado" in Lima. The research was completed at The University of Kansas and supported by a grant (No. 3272) from the General Research Fund of the Graduate School, The University of Kansas. Veloso's travel to Kansas was made possible by the Programa Multinacional de Genética, OEA. We are grateful to John E. Simmons for his laboratory assistance; José M. Cei for data on certain Argentinian specimens; W. Ronald Heyer, John D. Lynch, Jaime Péfaur, and Edward O. Wiley for helpful suggestions; and Linda Trueb for executing the illustrations.

MATERIALS AND METHODS

We have relied on the literature for data on *P. bibroni*, *guayapae*, and *kriegi*; we have had no field experience with these species or with *P. diploistris* and *nebulosa*. Of the other 10 species, we have examined the large collections in the Museum of Natural History at The University of Kansas (KU) and in the Museo Javier Prado in Lima, Perú (MJP).

Tape recordings were made on Uher 4000-L recorders at a speed of 19 cm/sec and were analyzed by means of a Sonograph Model 7029 (Kay Electric Co.). Chromosomes were obtained from squashes of corneal epithelium in the manner described by Bogart (1970). Measurements of chromosomes were made from projected

negatives by means of a map measurer. Each arm of both homologous chromosomes was measured in order to construct the idiograms. Nomenclature of centromeric position is that proposed by Levan, Fredga, and Sandberg (1964).

HISTORICAL RESUMÉ

Although frogs of the genus *Pleurodema* have been recognized as a distinct genus since 1838, when Tschudi proposed the generic name for the Uruguayan species, *P. bibroni*, there has been great taxonomic confusion at the species level. Throughout most of the literature on the Chilean and Uruguayan species, they have been known as *P. bibroni* and *P. darwini*, respectively. Donoso-Barros and Cei (1962) and Donoso-Barros (1969b) showed that the correct name for the Chilean species is *P. thaul* and for the Uruguayan species, *P. bibroni*. Parker (1927) provided the first systematic review of the genus, and Vellard (1960) treated the Andean species in Perú. Gorham (1966) listed 11 species in the genus, one of which (*verrucosa*) was placed in *Ischnocheila* by Lynch (1971). The most recent review of the genus was by Gallardo (1968), who resurrected *P. borellii* from the synonymy of *P. cinerea*; Barrio and Rinaldi de Chieri (1970) did not recognize *P. borellii* as distinct from *P. cinerea*. Lynch (1971) reviewed the generic relationships of the leptodactylid frogs and placed *Pleurodema* in the Leptodactylinae; he treated *P. sagittifer* (Schmidt, 1857) as a *species inquirenda*. Dunn (1944) questionably assigned *P. sagittifer* named from "Neu-Grenada" to the synonymy of *P. marmorata*, not an unreasonable assertion in that several species named by Schmidt and supposedly originating from Panamá and Colombia have subsequently been found only in Perú and Bolivia.³ All trivial names associated with the genus *Pleurodema* and their current status are listed in Table 1.

Cei (1962) summarized the existing knowledge of *P. thaul* (as *P. bibroni*). Veloso, Galleguillos, and Diaz (1973) analyzed the karyotypes of allopatric populations of *P. thaul*. Cei and Codoceo (1957) and Cei (1961) reported on the reproductive cycle of *P. bufonina*. Cei and Roig (1961) discussed the distribution of *P. bufonina*; this species was reported from additional Patagonian localities in Chile by Donoso-Barros (1969a), Webb and Greer (1969), and Veloso, Diaz, and Galleguillos (1973). Cei (1972a) presented an analysis of serological variation in *P. bufonina*. Barrio (1964) utilized differences in mating calls for distinguishing three cryptic species of *Pleurodema* in the subandean desert region in Argentina.

³ Cochran and Goin (1970:486) referred one specimen (USNM 144910) from Barranquilla, Colombia, to *P. sagittifer*. Examination of the specimen reveals that it unquestionably is *P. brachyops*.

TABLE 1.—Alphabetical Synonymy of the Species of *Pleurodema*.

Trivial Name, Original Generic Name, Author, Date	Current Name
<i>alpina</i> (<i>Paludicola</i>) Andersson, 1906	<i>cinerea</i>
<i>andicola</i> (<i>Pleurodema</i>) Philippi, 1902	<i>thaul</i>
<i>andina</i> (<i>Pleurodema</i>) Philippi, 1902	<i>thaul</i>
<i>aspera</i> (<i>Pleurodema</i>) Philippi, 1902	<i>thaul</i>
<i>belli</i> (<i>Pleurodema</i>) Philippi, 1902	<i>thaul</i>
<i>bibroni</i> (<i>Pleurodema</i>) Tschudi, 1838	<i>bibroni</i>
<i>borellii</i> (<i>Paludicola</i>) Peracca, 1895	<i>borellii</i>
<i>brachyops</i> (<i>Lystris</i>) Cope, 1868	<i>brachyops</i>
<i>bufonina</i> (<i>Pleurodema</i>) Bell, 1843	<i>bufonina</i>
<i>carbonaria</i> (<i>Pleurodema</i>) Philippi, 1902	<i>thaul</i>
<i>cinereum</i> (<i>Pleurodema</i>) Cope, 1877	<i>cinerea</i>
<i>coquimbensis</i> (<i>Pleurodema</i>) Philippi, 1902	<i>thaul</i>
<i>darwini</i> (<i>Pleurodema</i>) Bell, 1843	<i>bibroni</i>
<i>diplostiris</i> (<i>Cystignathus</i>) Peters, 1870	<i>diplostiris</i>
<i>elegans</i> (<i>Pleurodema</i>) Bell, 1843	<i>thaul</i>
<i>frenata</i> (<i>Paludicola</i>) Cope, 1890	<i>thaul</i>
<i>fusca</i> (<i>Pleurodema</i>) Philippi, 1902	<i>thaul</i>
<i>glandulosa</i> (<i>Pleurodema</i>) Philippi, 1902	<i>thaul</i>
<i>gracilis</i> (<i>Pleurodema bibroni</i> var.) Philippi, 1902	<i>thaul</i>
<i>guayapae</i> (<i>Pleurodema</i>) Barrio, 1964	<i>guayapae</i>
<i>infusata</i> (<i>Pleurodema marmorata</i>) Vellard, 1960	<i>marmorata</i>
<i>kriegi</i> (<i>Paludicola</i>) Müller, 1926	<i>kriegi</i>
<i>longipes</i> (<i>Pleurodema</i>) Philippi, 1902	<i>thaul</i>
<i>marmoratus</i> (<i>Leiuperus</i>) Duméril and Bibron, 1841	<i>marmorata</i>
<i>montevidense</i> (<i>Pleurodema</i>) Philippi, 1902	<i>bibroni</i>
<i>nebulosus</i> (<i>Leiuperus</i>) Burmeister, 1861	<i>nebulosa</i>
<i>phryniscoides</i> (<i>Pleurodema</i>) Philippi, 1902	<i>thaul</i>
<i>plebeya</i> (<i>Pleurodema</i>) Philippi, 1902	<i>thaul</i>
<i>pseudophryne</i> (<i>Pleurodema</i>) Philippi, 1902	<i>thaul</i>
<i>sachsi</i> (<i>Pleurodema</i>) Peters, 1877	<i>brachyops</i>
<i>sagittifer</i> (<i>Leiuperus</i>) Schmidt, 1857	<i>marmorata</i> ?
<i>salarinus</i> (<i>Leiuperus</i>) Bell, 1843	<i>bufonina</i>
<i>thaul</i> (<i>Bufo</i>) Lesson, 1826	<i>thaul</i>
<i>tucumana</i> (<i>Pleurodema</i>) Parker, 1927	<i>tucumana</i>
<i>verrucosa</i> (<i>Pleurodema</i>) Philippi, 1902	<i>thaul</i>
<i>viridis</i> (<i>Leiuperus</i>) Tschudi, 1845	<i>marmorata</i>

Barrio and Rinaldi de Chieri (1970) reviewed the karyological data on *Pleurodema* and showed that *P. bibroni* and *P. kriegi* are polyploids, and Laurent (1975) demonstrated morphometric differences between those species.

ANALYSIS OF CHARACTERS

Morphological, karyological, acoustic, and reproductive characters used in the study are discussed below. Some characters have been used only in a phenetic sense, whereas in others it has been possible to ascertain evolutionary direction from primitive to derived states. The determination of primitive and derived states

depended upon the utilization of the criteria of Wagner (1961) as discussed by Kluge and Farris (1969) and Trueb (1973). Lynch (1971) and Heyer (1975) discussed evolutionary direction in characters in leptodaelylid frogs.

MORPHOLOGICAL STRUCTURE

Morphological features, such as sizes and proportions, dermal modifications, osteological structures, and coloration exhibit various combinations of differences among the species of *Pleurodema*. The more important of these are treated below.

Size and sexual dimorphism.—The species of *Pleurodema* are moderately small frogs, ranging in snout-vent length from 33 mm in males of *P. kriegi* to 56 mm in females of *P. bufonina*. The largest males are in *P. brachyops* (49 mm) and the smallest females in *P. kriegi* (35 mm). Males are smaller than females; the ratio of snout-vent length between the sexes ranges from 1:104 in *P. brachyops* to 1:122 in *P. bufonina*, *thaul* (southern Chile), and *tucumana*.

Dermal Structure.—The skin on the venter is smooth, except for granules on the proximal posteroventral surfaces of the thighs. The skin on the dorsum is smooth (*P. brachyops*, *diplolistris*), shagreened (*P. bufonina*, *tucumana*), smooth with scattered pustules (*P. guayanae*, *nebulosa*, *thaul* from Argentina and central Chile), smooth with scattered tubercles and folds in scapular region (*P. borellii*, *cinerea*), rugose with folds laterally (*P. bibroni*, *kriegi*), or bearing longitudinal rows of large glandular tubercles (*P. thaul* from southern Chile). Evolutionary trends in dermal conditions are not evident. Certainly scapular and lateral folds must be derived characters. Most likely the dermal conditions are reflections of micro-environmental conditions in which the frogs live.

Lumbar glands.—Many species of *Pleurodema* (*bibroni*, *borellii*, *brachyops*, *bufonina*, *cinerea*, *kriegi*, and *thaul*) have a pair of prominent elevated glands dorsolaterally just posterior to the sacrum. In *P. bufonina* the glands are large and hemi-ovoid (Fig. 1). In the other species the glands are smaller and more globular, protruding posteriorly in some. The glands of *P. bufonina* are usually distinctly darker than the surrounding skin. In the other species part of each gland is black; the rest of the gland is a contrasting color—yellow, red, or pale blue. The physiological function of these glands is unknown. Cei and Espina (1957) reported on the aposematic behavior of *P. thaul*, which lowers the head and elevates the sacral region, thereby displaying the prominent, colored glands, which in this position appear as eyes. Thus, the simulated head gives the impression of a much larger animal. The effect supposedly discourages potential predators. Although this behavior is common in *P. thaul*, we have not observed similar behavior in other species

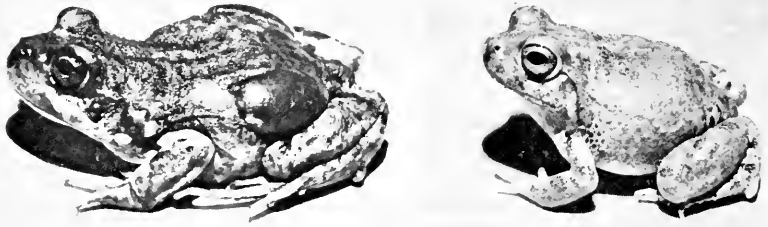


FIG. 1.—Left *Pleurodema bufonina*, ♀, 45 mm snout-vent length, KU 161375. Right *P. tucumana*, ♀, 35 mm snout-vent length, KU 160844.

having lumbar glands. In the leptodactyline frogs lumbar glands are derived characters; such glands are present only in *Pleurodema*.

Tarsal fold.—Most species of *Pleurodema* lack an inner tarsal fold; *P. borellii*, *cinerea*, and *thaul* have a fold on the distal one-fourth of the tarsus, whereas the fold extends more than half the length of the tarsus in *P. bufonina*. Apparently the primitive condition is a short fold; the absence of a fold or presence of a long fold are independently derived characters.

Tarsal tubercle.—Tubercles are absent on the tarsus of all species, except *P. diplolistris*, which has a large conical tubercle proximally on the tarsus. This unique character state obviously is derived.

Inner metatarsal tubercle.—The tubercle is ovoid in most species; enlarged but not compressed in *P. bibroni*, *kriegi*, and *tucumana*; enlarged and compressed in *P. brachyops*, *diplolistris*, *guayapae*, and *nebulosa*. The ovoid condition is considered to be primitive; the enlarged tubercle represents an independently derived state, with the compression of the enlarged tubercle being a progressively derived state.

Tympanic annulus.—All species of *Pleurodema* have an ear; the upper edge of the tympanum is covered by a supratympanic dermal fold. The tympanic annulus is distinct in most species but partially or completely concealed in *P. bibroni*, *guayapae*, *kriegi* and *thaul*. The concealment of the tympanum is considered to be the derived character state.

Prevomerine odontophores.—These structures are present in all species; in some species the odontophores are large and bear numerous teeth, whereas in others they are small and have only two or three teeth. Among the species having small odontophores, the structures are buried in the dermal mucosa in *P. bibroni*, *guayapae*, *kriegi*, *marmorata*, *nebulosa*, *tucumana*. Prominent odontophores are considered to be primitive.

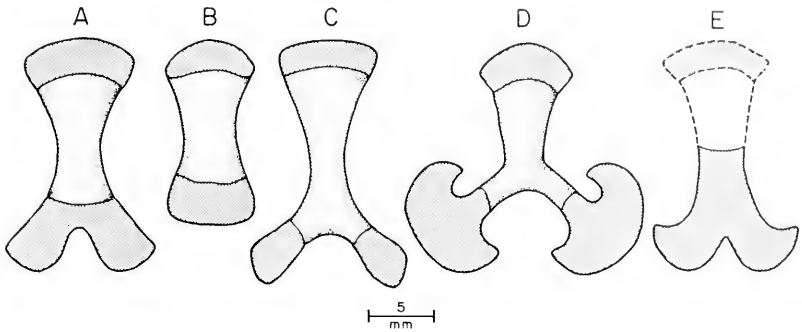


FIG. 2.—Sternal structure in *Pleurodema*: A. *P. thaul* (southern Chile), KU 162287. B. *P. thaul* (southern Argentina), KU 160810. C. *P. brachyops*, KU 167360. D. *P. guayapae* (from Barrio, 1964:483). E. *P. kriegi* (from Galardo, 1968:183).

Sternum.—As in all leptodactylines, the sternal plate is ossified; the cartilaginous xiphisternum is partly calcified and variously shaped (Fig. 2). The following character states are identified by letters on figure 2: A. Primitive—*P. borellii*, *bufonina*, *cinerea*, *thaul* (except in southern Argentina), *tucumana*; B. *P. marmorata*, *thaul* (southern Argentina); C. *P. brachyops*, *diplostris*; D. *P. guayapae*, *nebulosa*; E. *P. bibroni*, *kriegi*. Each of character states B-E probably were derived independently from A. The significance of the differences in sternal structure is not known. Since the sternum is the point of insertion and origin of various pectoral and abdominal muscles, differences in locomotion, burrowing, and/or amplexus might be reflected in its design.

Vocal sacs and slits.—Large median, subgular vocal sacs with lateral expansions are present in all species except *P. bufonina*, which has small vocal slits. All species having vocal sacs have a mating call; *P. bufonina* has a release call. The presence of vocal sacs is primitive; the absence of vocal sacs is derived, correlated with the loss of voice.

Testes.—The testes of breeding males are elongate, convoluted, and unpigmented, except in some populations of *P. thaul*, in which they are pigmented, and in *P. marmorata*, in which they are enormously enlarged (\pm one-third length of body), reniform, and heavily pigmented. The functional significance of this apparently derived condition is unknown.

Coloration.—Most species of *Pleurodema* are dull brown or gray dorsally, usually with some irregular darker markings; the venter is white, except for dark pigment on the throat in males and yellow, pink, or orange in the groin and on the hidden surfaces of the thighs of *P. borellii*, *brachyops*, and *cinerea*. In *P. thaul* (except in southern Chile) and *marmorata* the dorsum is green, tan, orange, or

reddish brown with darker spots. The dorsum is dull gray or brown, and the venter is gray in *P. thaul* from southern Chile. No evolutionary trends in coloration are evident.

KARYOLOGY

With the exception of *P. bibroni* and *kriegi*, the chromosomes of the species of *Pleurodema* are essentially alike. Barrio and Rinaldi de Chieri (1970) noted that *P. borellii* (their *P. cinerea* from Tucumán, Argentina), *bufonina*, *cinerea*, *guayapae*, *nebulosa*, *thaul*, and *tucumana* all have $2N=22$ with a secondary constriction on the eighth pair of chromosomes. Veloso, Galleguillos, and Diaz (1973) reported on interpopulational variation in *P. thaul*; in specimens from Provincia Llanquihue, Chile, secondary constrictions are present on the short arms of pair 8 and on the long arms of pair 9.

We present here a description of the karyotype of *P. marmorata*. Examination of preparations of seven males and two females from Putre, Provincia Tarapacá, Chile, revealed consistent chromosome structure in both sexes. Of the 11 pairs of chromosomes, pairs 1, 5, 9 and 10 are metacentric; pairs 2, 3, 6, 7, 8, and 11 are submetacentric, and pair 4 is subtelocentric (Figs. 3-4). A secondary constriction is present on the short arms of both homologues of pair 8.

Most species of *Pleurodema* are conservative karyologically; the presence of a secondary constriction on the ninth pair in *P. thaul* in southern Chile is the only noticeable divergence. Barrio and Rinaldi de Chieri (1970) reported tetraploidy in *P. bibroni* and *kriegi*; this is a striking departure from the otherwise conservative karyology of the group. As is evident from Barrio and Chieri's fig-

Pleurodema marmorata



Pleurodema thaul



Pleurodema bufonina

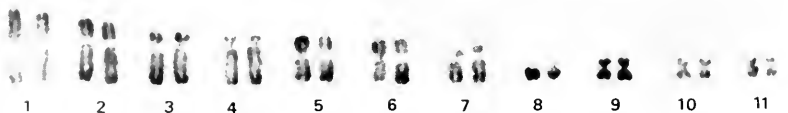


FIG. 3.—Chromosomes of *Pleurodema*.

ures 9 and 11, it is not possible to arrange the chromosomes in groups of fours. There are differences in size and structure of the supposed homologous pairs 1-2 and 15-16 in *P. bibroni* and in pairs 1-2, 11-12, and 15-16 in *P. kriegi*. Thus, Barrio and Rinaldi de Chieri suggested that these species are allopolyploids.

However, a different mechanism possibly is responsible for the differences in the homologs. If a species has a long evolutionary history as a polyploid, new arrangements of genetic material might explain the absence of complete homology (Bogart and Wasserman, 1972). According to Barrio and Rinaldi de Chieri (1970), the

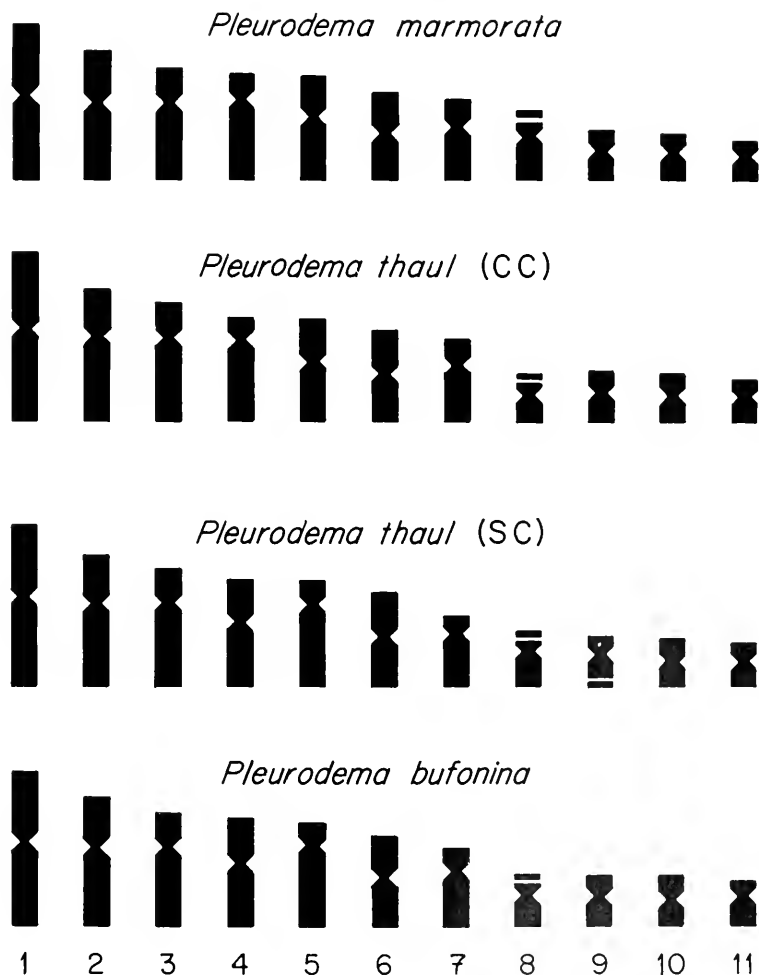


FIG. 4.—Idiograms of *Pleurodema*. Note secondary constriction on long arms of ninth pair in *P. thaul* (southern Chile).

polyploid species are the result of the combination of chromosomes of two parental species. Due to the morphological similarities of these disjunct polyploid species, we assume that the polyploid condition evolved only once, prior to the vicariation of the modern species. The identification of parental species cannot be determined with certainty. Karyologically, any of the diploid species of *Pleurodema* could have been parental species. Structurally and behaviorally, the ideal parental stocks would have had lumbar glands, axillary amplexus, and foam nests. Furthermore, the ancestral stocks should have occurred in western or central Argentina. These criteria are met in their entirety only by *P. borellii*. Assuming *P. borellii* to be one of the parental species involved in the development of the allopolyploid condition, the following alternatives for the second parental species can be explored:

1) *P. tucumana*.—Lumbar glands absent. Presently occurs in sympatry with *P. borellii* in the vicinity of Tucumán, Argentina; no evidence of hybridization in zone of sympatry.

2) *P. nebulosa* and *P. guayapae*.—Lumbar glands absent. Ranges of both species overlap in western Argentina; species hybridize in zone of sympatry (Barrio, 1964).

3) *P. thaul*.—Lumbar glands present; differences in sternal structure from other species; no foam nest. Presently occurs in *Nothofagus* forest.

4) A species having lumbar glands, axillary amplexus, and foam nest, but now extinct.

We view the alternatives in priority of their numerical sequence, except the fourth, which exists as an untestable possibility. *Pleurodema borellii* and *tucumana* occur sympatrically at present and do not interbreed; furthermore, *P. tucumana* lacks lumbar glands. *Pleurodema nebulosa* and *guayapae* form hybrids; thus, because their genetic divergence is not great, they may be relatively recent in origin, more recent than the formation of the polyploid stock that gave rise to *P. bibroni* and *kriegi*. It seems unlikely that *P. thaul* was a parental species. *Pleurodema borellii* and the polyploid species inhabit semi-arid environments, whereas *P. thaul* inhabits *Nothofagus* forest. Furthermore, the differences in reproductive biology seem to eliminate the likelihood of its interbreeding with a species having a foam nest.

On the basis of this evidence it is difficult to explain the polyploid condition of *P. bibroni* and *kriegi* as having arisen by allopolyploidy. The polyploid condition could have arisen in *P. borellii* or a *P. borellii*-like ancestor by autopolyploidy. The latter apparently is a generalized way of polyploid formation in other polyploid anurans (Becak, *et al.*, 1968; Becak, 1970; Becak and Becak, 1974; Bogart, 1976).

REPRODUCTIVE BIOLOGY

Different aspects of reproductive biology in *Pleurodema* can be utilized in speculating on phylogenetic relationships within the genus.

Amplexic position.—Frogs exhibit two basic kinds of amplexus—inguinal and axillary. Inguinal amplexus is considered to be the primitive condition (Lynch, 1973; Rabb, 1973); this amplexic position is characteristic of the archaeobatrachian families and the Australian myobatrachines. Inguinal amplexus was reported in the telmatobiine leptodactylid *Batrachyla leptopus* by Formas (1976), and illustrated in *Telmatobius somuncurensis* by Cei (1972b). Cei (1962) reported inguinal amplexus in *P. thaul* from southern Chile. We have observed inguinal amplexus in *P. thaul* in southern Chile and in *P. bufonina*. These are the only records of inguinal amplexus in New World leptodactylids. All other *Pleurodema* have, or are presumed to have, axillary amplexus. The presence of inguinal amplexus in two species of *Pleurodema* is paradoxical. Although in frogs as a group, inguinal amplexus is primitive, we consider the condition to be derived in *Pleurodema*.

Eggs.—Three different kinds of egg clutch structure are found in *Pleurodema*. In *P. thaul* (except in southern Chile) and *P. marmorata* eggs are deposited in clumps in water, whereas eggs are deposited in short, irregular strings in *P. bufonina* and *thaul* (in southern Chile). This type of egg deposition seems to be associated with inguinal amplexus in *Pleurodema*. All other species have, or are presumed to have, an aquatic foam nest—an advanced reproductive mode (Lynch, 1971). We consider the aquatic clumps of eggs to be primitive (shared with telmatobiines) and eggs in strings (among leptodactylids unique to some *Pleurodema*) and foam nests (characteristic of most leptodactylines) to be derived independently.

Tadpoles.—Tadpoles of *P. thaul* were described by Cei (1962). We have examined tadpoles of *P. brachyops*, *bufonina*, *cinerea*, *marmorata* and *thaul* (southern Argentina, southern and central Chile) and have found that all are alike structurally in having: 1) an ovoid body about as wide as deep; 2) small eyes directed dorso-laterally; 3) sinistral spiracle directed posterodorsally at about mid-length of body; 4) moderately robust caudal musculature about equal to depth of dorsal fin at midlength of tail; 5) a dorsal fin not extending onto body; 6) median vent; 7) small anteroventral mouth with the upper part of the lip bare and elsewhere bearing a single row of small papillae; 8) lips barely folded laterally; 9) two upper and three lower rows of denticles with the second upper row interrupted medially; 10) beaks broadly arched and finely serrate.

All of the tadpoles have a dull grayish brown body with a dark gray belly. The tail is tan or brown with fine dark brown reticu-

lations, least developed in *P. brachyops* and *cinerea* and heaviest in *P. thaul*. In life, gold or greenish flecks or streaks are present ventrolaterally in some tadpoles.

The lack of morphological diversity among these generalized leptodactylid tadpoles limits the use of larval characters in a phylogenetic analysis.

MATING CALL

Barrio (1964) analyzed the mating calls of *P. guayanae*, *nebulosa*, and *tucumana*. Here we present analyses of the mating calls of *P. brachyops*, *cinerea*, *marmorata*, and *thaul* and of the release call of *P. bufonina* (Figs. 5-6).

Pleurodema brachyops.—One individual was recorded at Nueva Gorgona and another at 3.4 km north of Montijo, Panamá. Both were calling while floating in shallow ponds; water temperatures were 25° and 29.5° C, respectively. The call consists of long series of loud snore-like notes, 36-40 ($\bar{x} = 38$) per minute. The notes have a duration of 0.5-1.5 ($\bar{x} = 1.0$) second. The notes are well modulated; the third harmonic at 650-750 ($\bar{x} = 700$) Hz (Hertz) is dominant, and the pulse rate is 60 per second.

Pleurodema cinerea.—Two individuals from the Río Tupiza, Departamento Potosí, Bolivia, were calling from water having a temperature of 16° C; the air temperature was 18.5° C. Nine call groups of two individuals were analyzed. The call is a series of pulsed notes separated by short intervals. The notes are moderately well modulated with 11 harmonics evident between 80 and 8000 Hz. The third harmonic at about 1600 Hz is dominant. The duration of the notes is 0.14-0.20 ($\bar{x} = 0.17$) of a second, and the pulse rate is 50-60 ($\bar{x} = 59.9$) pulses per second.

Pleurodema marmorata.—Two individuals were recorded at Tambo Machay, Departamento Cuzco, Perú, at 11.5° C and at 5 km W of Tincopalca, Departamento Puno, Perú, at 30° C. Fourteen call groups of the four individuals were analyzed. The call consists of a series of moderately long notes having durations of 0.24-0.48 ($\bar{x} = 0.34$) of a second. The notes are moderately well modulated; the harmonics rise during the length of the note. The dominant frequency is at 1600-1900 ($\bar{x} = 1716$) Hz at the beginning of the notes, rising to a mean of 1958 Hz at the end of the notes. A second emphasized harmonic is at 5258 Hz at the beginning, rising to 5861 Hz at the end of the notes. The individuals from Tambo Machay produced 60-80 ($\bar{x} = 70$) pulses per second; those from Tincopalca, 50 pulses per second.

Pleurodema thaul.—Analyses were made of 53 calls of 25 individuals from 13 different localities in Chile, ranging from Pajonales (29°21'S) to Valdivia (39°50'S). Air temperatures were 13.0-19.0

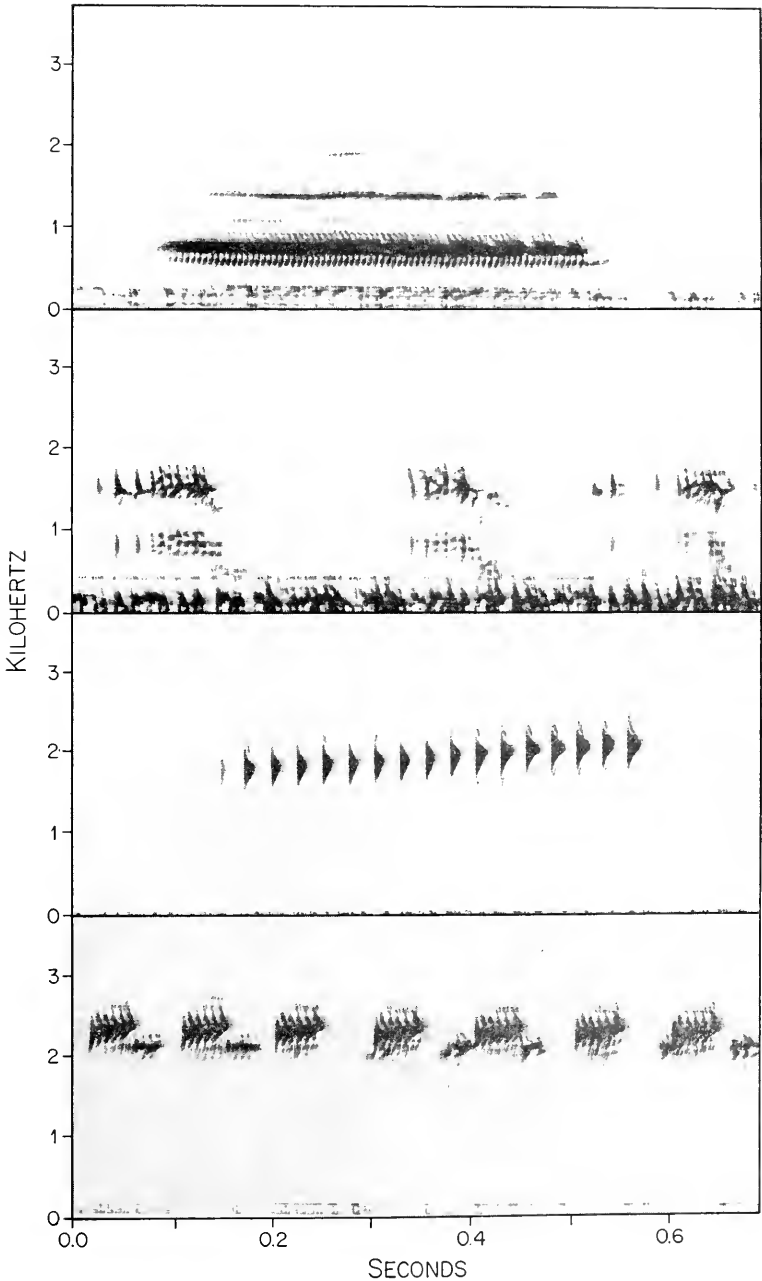


FIG. 5.—Audiospectrograms of mating calls of *Pleurodema*. A. *P. brachyops*, KU Tape 867, 25° C. B. *P. cinerea*, KU tape 1206, 16° C. C. *P. marmorata*, KU tape 1223, 6.5° C. D. *P. thaul*, KU Tape 1213, 16° C.

($\bar{x} = 16.75 \pm 2.25$)° C. The call consists of a modulated trill having a duration of 0.2-9.0 ($\bar{x} = 2.54$) seconds. The second (of five) harmonic at 1500-2300 ($\bar{x} = 2047$) Hz is dominant, and the fourth harmonic at about 5900 Hz also is emphasized. The call durations given above are for single individuals. Males calling in large choruses sometimes call continuously for nearly one minute.

At Cuesta de los Condores, Provincia Talca, Chile, a chorus of four males was observed to have an initially organized chorus structure (as defined by Duellman, 1967). One male emitted short, loud, poorly modulated notes followed by the usual mating call. These two kinds of calls had different harmonic structures. As soon as the trill began, the other individuals began trilling.

Pleurodema bufonina.—Although we have collected males in breeding condition at Laguna del Maule, Provincia Talca, Chile, and Laguna Blanca, Provincia Neuquén, Argentina, we have not heard the species produce a mating call. José M. Cei (pers. comm.) has confirmed these observations on the basis of his extensive experience with this species. However, *P. bufonina* does have a release call and warning vibration; Cei and Espina (1957) reported the presence of warning vibrations in *P. thaul*, an activity also observed by us, but without a release call.

Analyses were made of six release calls by two individuals from Laguna del Maule; the recordings were made in the laboratory at 25° C. The release call consists of two short notes each having a duration of about 0.02 of a second and separated from one another by an interval of about 0.25 of a second and then a longer note about 0.1 of a second in duration. The long note is moderately well modulated, having three or four harmonics. The first harmonic is dominant at about 1000 Hz initially and then declining to about 700 Hz; the pulses are produced at a rate of 140 per second.

ACCOUNTS OF SPECIES

In the following accounts of the species of *Pleurodema*, a brief diagnosis is followed by an account of the ecology and distribution of each species. Additional information is presented in *Remarks*.

Pleurodema bibroni Tschudi

Pleurodema bibroni Tschudi, 1838:85.—Montevideo, Provincia Montevideo, Uruguay.

Diagnosis.—Small species (♂ 38 mm, ♀ 40 mm) showing little sexual dimorphism in size; skin on dorsum weakly rugose with folds laterally; lumbar gland large, prominent; inner tarsal fold absent; inner metatarsal tubercle ovoid; tympanic annulus concealed; pre-vomerine odontophores covered; sternum shallowly notched posteriorly; dorsum gray with large dark spots; belly white; 2N=44.

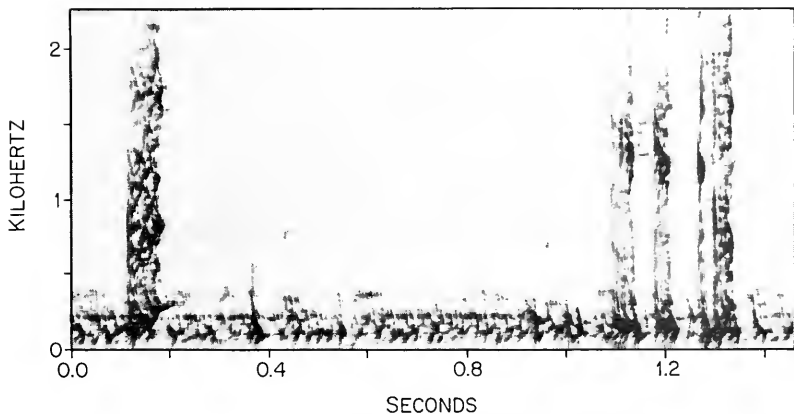


FIG. 6.—Audiospectrogram of release call of *Pleurodema bufonina*, KU Tape 1357, 25° C.

Ecology and Distribution.—Presumably terrestrial and having axillary amplexus and depositing eggs in foam nest. Known only from seasonally wet pampas of southeastern Uruguay from Treinta y Tres to Montevideo.

Remarks.—We have no experience with this species, which was known as *P. darwini* until Donoso-Barros (1969b) demonstrated that the name *P. bibroni* (long associated with a Chilean species) was the correct name for the Uruguayan species.

Pleurodema borellii (Peracca)

Paludicola borellii Peracca, 1895:26.—San Miguel de Tucumán, Provincia Tucumán, Argentina.

Diagnosis.—Large species (♂ 44 mm, ♀ 49 mm) showing only moderate sexual dimorphism in size; skin on dorsum smooth with scattered pustules dorsally and folds laterally; lumbar gland prominent; inner tarsal fold extending about one-fourth length of tarsus; inner metatarsal tubercle ovoid; tympanic annulus distinct; pre-omerine odontophores prominent; sternum deeply incised posteriorly; dorsum orange-tan to grayish tan with brown or dark gray spots; belly white with tan flecks laterally; ventral surfaces of thighs pinkish lavender; $2N=22$ with secondary constriction on eighth pair.

Ecology and Distribution.—Inhabiting sub-humid subtropical environments including broad-leafed deciduous forest and xerophilous scrub forest and breeding in temporary ponds after seasonal rains. Amplexus axillary; eggs deposited in foam nest. Northwestern Argentina from northern Salta and eastern Jujuy through Tucumán to Catamarca and La Rioja, occurring at elevations of 400 to nearly 3000 m.

Remarks.—Parker (1927) considered *P. borellii* to be a junior synonym of *P. cinerea*, but Gallardo (1968) recognized *P. borellii* as a distinct species. Comparison of specimens of *P. cinerea* from the Altiplano of southern Perú and Bolivia with specimens of *P. borellii* from the vicinity of Tucumán, Argentina (± 500 m) reveals few differences. In comparison with *P. cinerea*, *P. borellii* is slightly larger and has proportionately longer legs and feet. The snout in *P. borellii* is slightly narrower and more acuminate than the broader, blunter snout in *P. cinerea*. The yellow coloration in the groin of *P. cinerea* was not observed in *P. borellii*. Although we have recordings of *P. cinerea*, we do not know the call of *P. borellii*. Until such time as decisive evidence is available, we prefer to recognize *P. borellii* and *P. cinerea*, species that live in strikingly different habits.

Gallardo (1968) reported *P. borellii* from La Quiaca on the Altiplano in northern Provincia Jujuy, Argentina. We have specimens from the Altiplano collected at Abra Pampa south of La Quiaca. Our specimens are referable to *P. cinerea*. Other specimens from Río Grande, Provincia Jujuy, also are *P. cinerea*. Consequently, the identifications of all specimens from Provincia Jujuy reported by Gallardo (1968) are suspect.

In the southern part of its range *P. borellii* occurs in sympatry with *P. tucumana*. The two species were found at the same pond at El Cadillal, Provincia Tucumán, Argentina, on the night of 2 December 1974.

Pleurodema brachyops (Cope)

Lystris brachyops Cope, 1868:312.—Río Magdalena, Colombia.

Diagnosis.—Large species (δ 49 mm, ♀ 51 mm) showing little sexual dimorphism in size; skin on dorsum smooth; lumbar gland prominent; inner trasal absent; inner metatarsal tubercle enlarged, compressed; tympanic annulus distinct; prevomerine odontophores prominent; sternum broadly dilated posteriorly with shallow indentation; dorsum pale green or tan with dark brown blotches; belly white; groin and hidden surfaces of legs orange; $2N=22$.

Ecology and Distribution.—Inhabiting savannas, llanos, and xeric scrub forests and breeding in temporary ponds after seasonal rains. Amplexus axillary; eggs deposited in foam nest. Guyana and extreme northern Brasil westward into Venezuelan llanos and along dry north coast of Venezuela and Colombia; savannas of Panamá; coastal islands of Venezuela and Curacao.

Remarks.—This species is distinctive in the genus by having deep orange “flash colors” in the groin and hidden surfaces of the limbs. Also, it is distinctive in having pale blue spots on the otherwise black lumbar gland.

One of us (Duellman) has observed this species in Panamá, Colombia, and Venezuela. Males call while sitting in shallow water or while floating on the surface of the water. Although the lumbar gland is large and distinctively colored, no aposematic behavior displaying the gland was observed.

Pleurodema bufonina Bell

Pleurodema bufonina Bell, 1943:39.—Puerto Deseado, Provincia Santa Cruz, Argentina.

Diagnosis.—Large species (δ 45 mm, ♀ 56 mm) showing extreme sexual dimorphism in size; skin on dorsum shagreened, thick, glandular; lumbar gland enormous, approximately one-third length of body; inner tarsal fold extending at least to midlength of tarsus; inner metatarsal tubercle ovoid; tympanic annulus distinct; prevomerine odontophores prominent; sternum deeply incised posteriorly; dorsum dull brown with or without darker brown spots and/or pale middorsal stripe; venter creamy tan; $2N=22$ with secondary constriction on eighth pair.

Ecology and Distribution.—Terrestrial, frequenting arroyos and margins of lakes in the cold sub-humid or semi-arid Patagonian steppe and tundra. Amplexus inguinal; eggs deposited in short strings in water. Patagonian Argentina and southern Chile from the Straits of Magellan northward to 36° S principally east of the Andes but following tongues of Patagonian habitat through Andean passes at Laguna del Maule (36° S), Laguna La Laja ($37^\circ 30'S$), and Paso Pino Hachado ($36^\circ 40'S$), Chile. Elevational range from sea level to 2300 m.

Remarks.—This is the southernmost frog; its distribution extends to 53° S. Cei and Roig (1961) reported on the distribution and survival in harsh Patagonian environments. Cei and Codoceo (1957) and Cei (1961) noted the seasonally arrested spermatogenetic cycle in the species.

Capurro (1957) reported *P. bufonina* from Isla Chiloé, Chile; examination of the illustration of the specimen reveals that it is *P. thaul*. Cei (1962) reported that M. Codoceo had observed *P. bufonina* and *P. bibroni* (= *P. thaul*) together in Aisén, Chile. Our field work in Chile and Argentina has not revealed the sympatric occurrence of the two species. They are parapatric at Laguna El Maule and at Laguna La Laja. At these Chilean localities there are intrusions of Patagonian vegetation into more mesic Andean scrub and forest. *Pleurodema bufonina* occurs only in the Patagonian vegetation, where *P. thaul* does not occur. The two species also were found in close proximity in Provincia Neuquén, Argentina; there, too, *P. bufonina* was found in the Patagonian steppe, whereas *P. thaul* occurred only in the *Nothofagus* forest.

Although breeding activity has been observed, no mating calls have been heard. Breeding males do not have the laterally distended, pigmented vocal sacs characteristic of most of the other species; small vocal slits are present. Males do have a release call and a warning vibration.

In the northern part of its range *P. bufonina* commonly is found in association with *Bufo spinulosus* Wiegmann. Tadpoles of both species were found in pools in arroyos in Provincia Neuquén, Argentina, in December. At Laguna Blanca, Provincia Neuquén, *P. bufonina* was found beneath rocks at the edge of the lake; terrestrial stages of the primarily aquatic *Telmatobius patagonicus* Cei were under the same rocks.

Pleurodema cinerea Cope

Pleurodema cinereum Cope, 1877:40.—Juliaca, Departamento Puno, Perú.

Diagnosis.—Large species (♂ 42 mm, ♀ 45mm), showing little sexual dimorphism in size; skin on dorsum smooth with scattered pustules; lumbar gland prominent; inner tarsal fold extending about one-fourth length of tarsus; inner metatarsal tubercle ovoid; tympanic annulus distinct; prevomerine odontophores prominent; sternum deeply incised posteriorly; dorsum olive-tan to grayish brown with dark brown to black irregular spots; belly white; groin and hidden surfaces of thighs yellow; 2N=22 with secondary constriction on eighth pair.

Ecology and Distribution.—Inhabiting puna (bunch-grass associations) and semi-arid montane environments and breeding in temporary ponds formed by seasonal precipitation. Amplexus axillary; eggs deposited in foam nest. The Altiplano and some dissected valleys from the Titicaca Basin in southern Perú to northern Argentina, occurring at elevations of 2900-4100 m.

Remarks.—Males call while sitting at the bases of bunch grass in water or floating on the surface of the water. In the Titicaca Basin *P. cinerea* occurs in sympatry with the smaller *P. marmorata*. Comparisons between *P. cinerea* and *P. borellii* are given in the account of the latter species.

Pleurodema diplolistris (Peters)

Cystignathus diplolistris Peters, 1870:648.—Ceará, Brasil.

Diagnosis.—Small species (♂ 40 mm, ♀ 43 mm) showing little sexual dimorphism in size; skin on dorsum smooth; lumbar gland absent; inner tarsal fold absent; inner metatarsal tubercle enlarged, compressed; tympanic annulus distinct; prevomerine odontophores prominent; sternum broadly expanded and shallowly notched posteriorly; dorsum tan with irregular brown spots; venter white.

Ecology and Distribution.—Occurring in the arid *caatinga* of northeastern Brasil (states of Ceará and Bahia).

Remarks.—We have not observed this species in the field; there are no reports in the literature on its life history and karyology. Presumably the species has 22 chromosomes and exhibits axillary amplexus with eggs deposited in foam nests. *Pleurodema diplolistris* is unique among species in the genus by having a prominent tarsal tubercle.

Pleurodema guayapae Barrio

Pleurodema guayapae Barrio, 1964:478.—Cuayapa, near Patquia, Provincia La Rioja, Argentina.

Diagnosis.—Small species (♂ 38 mm, ♀ 42 mm) showing little sexual dimorphism in size; skin on dorsum pustulate; lumbar gland absent; inner tarsal fold absent; inner metatarsal tubercle enlarged, compressed; tympanic annulus concealed; prevomerine odontophores covered; sternum with posterior osseous bifurcation; dorsum brownish pink with small dark spots; venter white; $2N=22$ with secondary constriction on eighth pair.

Ecology and Distribution.—A fossorial species living in arid and semi-arid habitats and breeding in temporary pools after brief seasonal rains. Amplexus axillary; eggs in foam nest. Central Argentina from southwestern Santiago del Estero to central La Rioja, including extreme southern Catamarca and northwestern Córdoba.

Remarks.—Barrio (1964) distinguished this species from *P. nebulosa* on the basis of the mating call. He discovered hybrids between *P. guayapae* and *P. nebulosa* at Guayapa. The mating call of the hybrid is intermediate between those of the parental species. The ranges of the two species overlap only in the central part of Provincia La Rioja. The range of *P. guayapae* lies completely within that of *P. tucumana*.

Pleurodema kriegi (Müller)

Paludicola kriegi Müller, 1926:194.—Sierra Grande, Provincia Córdoba, Argentina.

Diagnosis.—Small species (♂ 33 mm; ♀ 35 mm) showing little sexual dimorphism in size; skin on dorsum slightly rugose with folds laterally; lumbar gland large, prominent; inner tarsal fold absent; inner metatarsal tubercle ovoid; tympanic annulus concealed, prevomerine odontophores covered; sternum shallowly notched posteriorly; dorsum dull reddish gray with large black spots; belly white becoming ochre on chest and reddish yellow on undersides of legs; $2N=44$.

Ecology and Distribution.—Probably terrestrial, inhabiting semi-arid habitats; presumably having axillary amplexus and depositing

eggs in foam nests. Known only from the Sierra Grande and Pampa de Achala, western Córdoba, Argentina.

Remarks.—We have no experience with this species, which Parker (1927) synonymized with *P. cinerea*. Gallardo (1968) re-described essentially topotypic specimens and placed *P. kriegi* in the synonymy of *P. darwini* (= *P. bibroni*). Barrio and Rinaldi de Chieri (1970) noted the tetraploid condition of *P. kriegi* and recognized the species as being distinct from *P. bibroni*, which also is tetraploid. They noted secondary constrictions on the 15th pair of chromosomes of both species and also on the 12th pair of *P. kriegi*, although the latter constriction is not evident in their figure. Laurent (1975) noted slight differences in proportions and in coloration. The ranges of the two species are separated by a distance of nearly 1000 km and includes the pampas of eastern Argentina, a region well known herpetologically.

Pleurodema marmorata (Duméril and Bibron)

Leiuperus marmoratus Duméril and Bibron, 1841:421.—Potosí, Departamento Potosí, Bolivia.

Diagnosis.—Small species (♂ 38 mm; ♀ 46 mm) showing moderate sexual dimorphism in size; skin on dorsum smooth with scattered pustules; lumbar gland absent; inner tarsal fold absent; inner metatarsal tubercle ovoid; tympanic annulus usually distinct; prevomerine odontophores covered; sternum rounded posteriorly; dorsum gray, tan, green, red, or brown with dark green, brown, or black markings; venter white; $2N=22$ with secondary constriction on eighth pair.

Ecology and Distribution.—Inhabiting wet and dry *puna* (bunch-grass associations) between 3000 and 5000 m. Amplexus axillary; eggs deposited in masses in shallow temporary or permanent ponds. Ranging from central Perú to central Bolivia and extreme northeastern Chile, occurring on the western slopes of the Cordillera Oriental, the Altiplano and the Cordillera Occidental.

Remarks.—Vellard (1960) recognized three subspecies of this highly variable species. Examination of Vellard's specimens plus extensive series from throughout the range in the collections at the Museum of Natural History, The University of Kansas, reveals that *P. marmorata* is a highly variable species and that within-population variation in proportions and coloration frequently is greater than between-population variation. Consequently, we prefer not to recognize taxonomically any populations within *P. marmorata*.

In the Titicaca Basin in southern Perú *P. marmorata* occurs sympatrically with *P. cinerea*, a larger species depositing eggs in foam nests. Comparison of series of *P. marmorata* from the sympatric zone (Santa Rosa, Departamento Puno, Perú) with specimens

from north of the range of *P. cinerea* (Departamento Ayacucho, Perú) revealed that southern specimens are larger and have proportionately longer feet than the northern ones. No detailed morphometric analysis of samples from throughout the range was undertaken.

Calling males were observed at many localities in Perú. Males sit on the ground at the edge of shallow pools or sit in shallow water. None was observed calling while floating in the water.

This species reaches higher elevations in the Andes than any other amphibian. We have observed it to elevations of 4675 m, and Vellard (1960) stated that it reaches 5000 m. At these high elevations, the frogs usually are found beneath rocks—frequently on wet ground with small pools of water that freeze nightly. In the Cordillera Occidental in central Perú and northern Chile, and in the Cordillera in Bolivia we have found numerous individuals beneath rocks covered with snow. One individual was observed hopping across a snow field by day. Males were heard calling when the air temperature was 1° C.

Pleurodema nebulosa (Burmeister)

Leiuperus nebulosus Burmeister, 1861:532.—Mendoza, Provincia Mendoza, Argentina.

Diagnosis.—Small species (♂ 36 mm; ♀ 40 mm) showing little sexual dimorphism in size; skin on dorsum weakly pustulate; lumbar gland absent; inner tarsal fold absent; inner metatarsal tubercle enlarged, compressed; tympanic annulus distinct ventrally; pre-vomerine odontophores covered; sternum with posterior osseous bifurcation; dorsum pinkish gray with black flecks; venter white; 2N=22 with secondary constriction on eighth pair.

Ecology and Distribution.—A fossorial species living in arid habitats and breeding in temporary rain pools. Amplexus axillary; eggs in foam nest. Western Argentina from southwestern Catamarca to central Mendoza, including western San Luis, with disjunct populations in southwestern Córdoba and northern La Pampa.

Remarks.—Barrio (1964) discovered the sympatric occurrence of and hybridization of cryptic species at Guayapa (see account of *P. guayapae*). The two species differ structurally in the concealment of the tympanic annulus in *P. guayapae* and in mating calls.

Pleurodema thaul (Lesson)

Bufo thaul Lesson, 1826:64.—Concepción, Provincia Concepción, Chile.

Diagnosis.—Small to large species depending upon population, showing moderate sexual dimorphism in size; skin on dorsum smooth, pustulate, or with rows of large pustules; lumbar gland prominent; inner tarsal fold extending about one-fourth length of

tarsus; inner metatarsal tubercle ovoid; tympanic annulus partly concealed; sternum rounded or deeply incised posteriorly; dorsum green, gray, or tan with darker markings, or dark grayish brown with or without faintly darker markings; venter white or gray; $2N=22$ with secondary constriction on eighth pair (also on ninth pair in some populations).

Ecology and Distribution.—Occurring in humid and subhumid austral forests and subhumid chaparral (*matorral*) vegetation from Aisén northward to La Serena, Provincia Coquimbo, and thence with discontinuous populations northward to Copiapó, Provincia Atacama, Chile; in Argentina occurring in austral forests along the eastern base of the Andes. Elevational range from sea level to 1500 m. Amplexus axillary or inguinal; eggs deposited in strings or masses in water.

Remarks.—We regard *P. thaul* as a composite species of at least three forms differing in size, proportions, coloration, karyology, amplexic position, and eggs. These three forms we designate solely by their geographic positions—Southern Chile (SC), Central Chile (CC), and southern Argentina (SA). The three forms are diagnosed, as follows—

Southern Chile (SC): Large frogs (δ 40 mm, ♀ 53 mm) having extreme sexual dimorphism in size; snout narrowly rounded in dorsal profile; skin on dorsum bearing longitudinal rows of large tubercles; sternum deeply incised posteriorly; nuptial pad well developed; dorsum predominately dull dark brown or gray, some individuals having paler brown with large dark spots; venter gray; secondary constrictions on eighth and ninth pair of chromosomes; amplexus inguinal; eggs deposited in short strings in water.

Central Chile (CC): Moderate-sized frogs (δ 44 mm, ♀ 48 mm) exhibiting minor sexual dimorphism in size; snout broadly rounded in dorsal profile; skin on dorsum smooth with or without small pustules; sternum deeply incised posteriorly; nuptial pad poorly developed; dorsum gray with small dark green spots or tan or dark green with small dark brown spots; venter white; secondary constriction on eighth pair of chromosomes; amplexus axillary; eggs deposited in masses in water.

Southern Argentina (SA): Moderate-sized frogs (δ 41 mm; ♀ 48 mm) exhibiting considerable sexual dimorphism in size; snout broadly rounded in dorsal profile; skin on dorsum smooth with or without small pustules; sternum round posteriorly; nuptial pad well developed; dorsum gray, green, or tan with dark brown or green irregular spots; venter white; secondary constriction on eighth pair of chromosomes; amplexus axillary; eggs deposited in masses in water.

In addition to these three forms we also note the existence of a

morph presently known only from an isolated saline pond in the desert at Pajonales in northern Provincia Coquimbo, Chile. Frogs from this locality have completely smooth skin dorsally and a pale coloration with yellow in the inguinal region.

The southern Chilean form occurs throughout Provincia Llanquihue and on Isla Chiloé; presumably this is the form in the extreme south in Aisén. The central Chilean form ranges from the Río Bio-Bio northward to La Serena. The southern Argentinian form occurs in the western parts of Provincia Neuquén and Provincia Río Negro. In south-central Chile between Concepción and Valdivia there is a confusing array of *Pleurodema* with respect to polymorphism in dorsal pustules and coloration.

Cei and Capurro (1957) and Cei (1958) analyzed the variation in coloration and morphological features in *P. thaul*, and Cei (1958) concluded that additional studies on this polymorphic species should be able to define distinct taxa. Our major contribution to the problem has been the discovery of differences in sternal conditions, amplexic positions, egg deposition, and karyotypes—all characters used at the specific level in *Pleurodema*. However, we refrain from taxonomic recognition of the forms at this time due to our incomplete knowledge of the distribution and variation within the forms, especially in the region from Concepción to Valdivia. Furthermore, once the variation within the taxa is better known it is necessary to determine the accurate assignment of Philippi's (1902) many specific names, all of which now reside in the synonymy of *P. thaul*. The presently confusing array of variation in populations between Concepción and Valdivia perhaps is indicative of the existence there of representatives of both the northern and southern forms. There are no apparent barriers to gene flow in *Pleurodema* from Provincia Llanquihue to central Chile (vicinity of Santiago), although the Río Bio-Bio is the northern boundary for some species restricted to the austral forests. Possibly an additional taxon exists in this region.

In southern Chile and Argentina this species occurs in *Nothofagus* and *Araucaria* forests; farther north in the lowlands it occurs in chaparral (*matorral*) associations and in relict stands of *Nothofagus*. The species also occurs in the deeply incised Andean Valleys in central Chile where it attains elevations of 1500 m. In two of these valleys (Laguna del Maule and Laguna La Laja), *P. thaul* is parapatric with *P. bufonina*, which occurs only in the Patagonian vegetation in the upper parts of the valleys. Although the species has been found on the western slopes of passes in southern Chile to elevations of 1010 m, it has not been found on the tops of Paso de Petrohue (980 m) and Paso de Puyehue (1479 m), where potential gene flow might occur between populations in southern Chile and southern Argentina.

Pleurodema tucumana Parker

Pleurodema tucumana Parker, 1927:468.—Tapia, Provincia Tucumán, Argentina.

Diagnosis.—Large species (♂ 40 mm, ♀ 53 mm) showing extreme sexual dimorphism in size; skin on dorsum weakly granular; lumbar gland absent; inner tarsal fold absent; inner metatarsal tubercle enlarged, not compressed; tympanic annulus distinct; prevomerine odontophores usually covered; sternum deeply incised posteriorly; dorsum brown with irregular dark brown spots; venter white; $2N=22$, probably with secondary constriction of eighth pair.

Ecology and Distribution.—A fossorial species inhabiting sub-humid to arid habitats and breeding in temporary pools after seasonal rains. Amplexus axillary; eggs in foam nest. Central Argentina from northern Tucumán and western Santiago del Estero through southeastern Catamarca and northwestern Córdoba to central La Rioja.

Remarks.—The range of *P. guayapae* is completely encompassed within the range of *P. tucumana*. In central La Rioja both species occur in sympatry with *P. nebulosa*. In Tucumán *P. tucumana* occurs with *P. borellii*; at El Cadillal, Provincia Tucumán, both species were observed at the same pond on the night of 2 December 1974 (Duellman, per. observ.).

INTRAGENERIC RELATIONSHIPS

Using the cladistic approaches of Hennig (1966), we have attempted to determine branching sequences and sister groups of *Pleurodema*. In this method the phylogeny of a group is reconstructed by defining vicariance events; all species on a polytypic branch share derived characters and differ from species on the other branch (sister group) in one or more derived characters.

In the following list of characters, the primitive state is designated 0; derived states are 1, 2, *etc.*, as noted. The characters are described in the foregoing section on character analysis, and the character states are tabulated in Table 2.

A. Amplexic position.

0. Axillary

1. Inguinal

B. Egg deposition (1 and 2 independently derived)

0. Masses

1. Strings

2. Foam nest

C. Lumbar gland

0. Absent

1. Present

- D. Chromosomes
 - 0. 22
 - 1. 44
- E. Tarsal fold (1 and 2 independently derived)
 - 0. Short
 - 1. Long
 - 2. Absent
- F. Inner metatarsal tubercle (1 and 2 independently derived; 3 derived from 2)
 - 0. Ovoid
 - 1. Small
 - 2. Enlarged
 - 3. Enlarged and compressed
- G. Tympanic annulus
 - 0. Prominent
 - 1. Concealed
- H. Prevomerine odontophores
 - 0. Prominent
 - 1. Covered
- I. Sternum (each state independently derived)
 - 0. Figure 2A
 - 1. Figure 2B
 - 2. Figure 2C
 - 3. Figure 2D
 - 4. Figure 2E

Four characters (A-D) were used to generate cladograms defining six major branches in *Pleurodema* (Fig. 7); each branch contains one to four species and represents a monophyletic group.

Group A.—*P. marmorata* (character states for A-D = 0000)

Group B.—*P. diplolistris*, *guayapae*, *nebulosa*, *tucumana* (0200)

Group C.—*P. thaul* (SA), *thaul* (CC) (0010)

Group D.—*P. bufonina*, *thaul* (SC) (1110)

Group E.—*P. borellii*, *cinerea*, *brachyops* (0210)

Group F.—*P. bibrioni*, *kriegi* (0211)

Two equally parsimonious phyletic arrangements of these groups are possible; each requires five evolutionary steps, and each contains one pair of convergences. In the first alternative (Fig. 7A) the deposition of eggs in foam nests occurs in two phyletic lines, whereas in the second alternative (Fig. 7B) the development of lumbar glands occurs twice. We favor the first alternative because it is most reasonable biologically. Within the Leptodactylinae large lumbar glands are unique to certain species of *Pleurodema*, whereas foam nests are common in leptodactylines and also occur in other families. Thus, it seems more reasonable to assume the development of foam nests in two phyletic lines of *Pleurodema* than to require the evolution of lumbar glands independently to two phyletic lines.

TABLE 2.—Character States of 13 Characters in *Pleurodema*.
(See text for explanation)

Character	<i>bibroni</i>	<i>borellii</i>	<i>brachyops</i>	<i>buffonina</i>	<i>cinerea</i>	<i>diploblistris</i>	<i>guayanae</i>	<i>krigei</i>	<i>marmorata</i>	<i>nebulosa</i>	<i>thaul</i> (SA)	<i>thaul</i> (CC)	<i>thaul</i> (SC)	<i>tucumana</i>
A	0	0	0	1	0	0	0	0	0	0	0	0	1	0
B	2	2	2	1	2	2	2	2	0	2	0	0	1	2
C	1	1	1	1	1	0	0	1	0	0	1	1	1	0
D	1	0	0	0	0	0	0	1	0	0	0	0	0	0
E	2	0	2	1	0	2	2	2	2	2	0	0	0	2
F	2	0	3	0	0	3	3	2	0	3	0	0	0	2
G	1	0	0	0	0	0	1	1	0	0	1	1	1	0
H	1	0	0	0	0	0	1	1	1	1	0	0	0	1
I	3	0	2	0	0	2	4	3	1	4	1	0	0	0

INTERGENERIC RELATIONSHIPS

According to Lynch (1974) and Heyer (1975), *Pleurodema* is a primitive leptodactyline. Lynch (1971: 207) stated: "The Leptodactylinae are derived from the relative primitive Alsodini (*Eupsophus*). The most primitive leptodactyline (*Pleurodema*) is very similar to *Eupsophus*. The two genera differ in the sternal apparatus, breeding biology, and loss of the quadratojugal. *Pleurodema* has an osseous sternal style (as do all other leptodactylines); these two characters clearly ally *Pleurodema* with the Leptodactylinae, although its close relationship with *Eupsophus* is obvious and could be used to support the argument that the Leptodactylinae are only a tribe of the Telmatobiinae." It should be noted that Lynch's *Eupsophus* includes frogs now placed in *Alsodes*, *Eupsophus*, *Phrynosus*, and *Telmatobius*. In Heyer's (1975) cladistic arrangements of derived characters of leptodactylid frogs, *Pleurodema* clustered with the telmatobiine genera *Batrachyla*, *Batrachophrynosus*, *Eupsophus*, and *Telmatobius* in two cladograms, and with the leptodactyline genus *Physalaemus* in a third cladogram.

It is constructive to compare *Pleurodema* with *Alsodes nodosus* (*Eupsophus nodosus* of Lynch, 1971). Veloso and Iturra (1976) provided karyological evidence for the separation of *Alsodes* and *Eupsophus*. The latter is considered to be a primitive telmatobiine having species with 28, 30, and 34 chromosomes, many of which are telocentric, thereby giving fundamental numbers of 46, 54, and 58. All *Alsodes*, except *A. nodosus*, have 26 metacentric and submetacentric chromosomes, whereas *A. nodosus* has 22 metacentric and submetacentric chromosomes; thus, *Alsodes* have fundamental numbers of 52 and 44. Most other telmatobiines have 26-34 chromo-

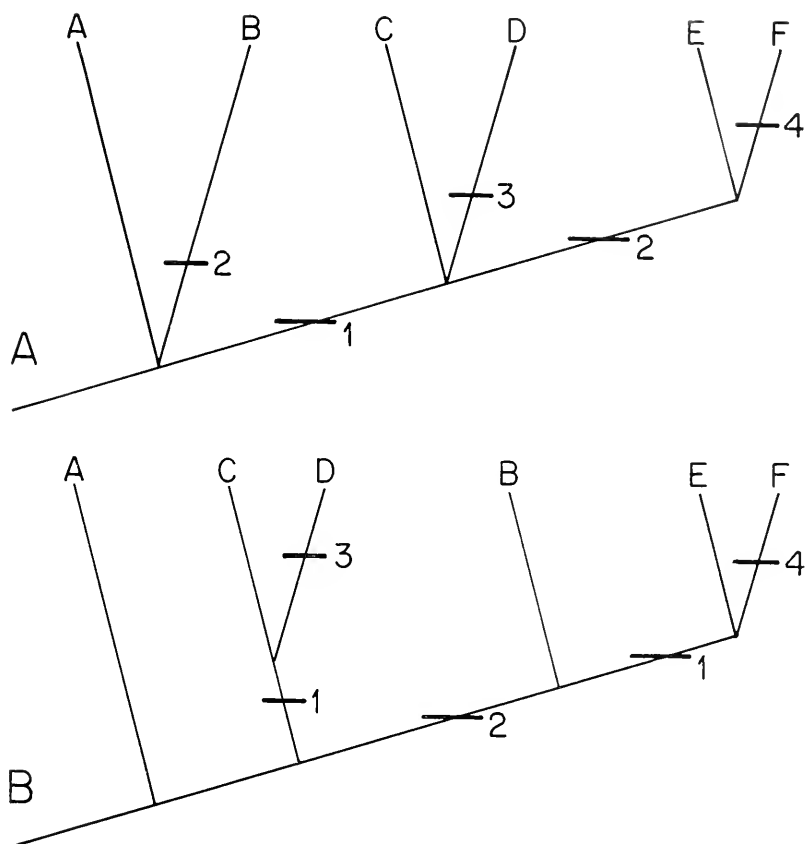


FIG. 7.—Alternative phylogenies of six species groups of *Pleurodema* based on characters A-D. Character shifts are: 1. Development of lumbar glands. 2. Eggs deposited in foam nest. 3. Inguinal amplexus and eggs laid in strings. 4. Polyploidy. See text for species composition of groups.

somes; only *Alsodes nodosus* and *Telmatobius somuncurensis* (Cei, 1969) have 22 chromosomes.

With the exception of the tetraploid species (*P. bibroni* and *kriegi*), all *Pleurodema* have 22 metacentric and submetacentric homomorphic chromosomes with a secondary constriction on pair 8. The 22 chromosomes of *Alsodes nodosus* are more variable in size than those of *Pleurodema*; in *A. nodosus* the fourth pair is heteromorphic, and a secondary constriction is present on pair 2. Karyologically, *Pleurodema* and *Alsodes nodosus* could have had a common ancestor, but it is more reasonable to postulate an independent derivation of 22 chromosomes in *Pleurodema* from an *Eupsophus* stock.

Structurally *Alsodes nodosus* is distinctly different from *Pleuro-*

dema. It is a moderately large, terrestrial species; males have spinous nuptial adpersities on the thumb and chest. Males have a mating call, and amplexus is axillary; large unpigmented eggs are deposited in clumps in streams in the Pacific lowlands and lower Andean slopes of central Chile. The large tadpoles have two upper and three lower rows of denticles.

Among the species of *Eupsophus*, *vertebralis* has 28 chromosomes (fundamental number 54), *roseus* 30 (46), and *vanzolinii* 34 (58).⁴ It is easiest to derive the chromosome complement of *Pleurodema* from a stock resembling *Eupsophus roseus*. This small terrestrial species inhabits humid *Nothofagus* forest in southern Chile. Males have a mating call but lack nuptial adpersities. Amplexus is axillary, and the eggs are unpigmented; presumably they are deposited in water.

Comparison of characters of the primitive telmatobiines (Tribe Telmatobiini, including *Alsodes*, *Batrachophrynus*, *Eupsophus*, *Hylorina*, *Linnomedusa*, and *Telmatobius*) with *Pleurodema* and the subfamily Leptodactylinae (exclusive of *Pleurodema*) reveals that *Pleurodema* is intermediate between the other groups in some characters, shares some character states with one or the other group, and differs from both groups in some characters (Table 3). The morphological and karyological evidence supports Lynch's (1971) contention that *Pleurodema* can be considered as a primitive leptodactyline and possibly allied with the telmatobiine *Eupsophus*. The inguinal amplexus exhibited by two species of *Pleurodema* is unusual among New World leptodactylids. Formas (1976) reported inguinal amplexus in *Batrachyla leptopus*, and Cei (1972b) illustrated inguinal amplexus in *Telmatobius somuncurensis*. Eggs in short strings, as found in *Pleurodema bufonina* and *P. thaul* (SC) are unique in the Leptodactylidae. We interpret these reproductive differences (inguinal amplexus and eggs in strings) as adaptive modifications that are divergent from the major evolutionary trends in the Telmatobiinae-Leptodactylinae lineage.

With the exception of *Pseudopaludicola* and some *Pleurodema*, all leptodactylines deposit eggs in foam nests. Heyer (1969) noted evolutionary adaptations in nests in the *Leptodactylus* complex. The trend is from foam nests floating in water to nests in hollows that fill with water; in these instances aquatic tadpoles are present. In *Adenomera* a foam nest is constructed on land and there are no aquatic larvae.

Bogart (1974) discussed the evolutionary significance of karyotypes of the *Leptodactylus* complex. Noting the presence of 24 and

⁴ Iturra and Veloso (1976) reported 34 chromosomes in *Eupsophus coppiingeri* from the Sierra Nahuelbuta, Chile. The frogs in the Sierra Nahuelbuta were named as *Eupsophus vanzolinii* by Donoso-Barros (1974).

TABLE 3.—Comparison of Three Groups of Leptodactylid Frogs.

Character	Telmatobiini	<i>Pleurodema</i>	Leptodactylinae
Stemal Style	Cartilaginous	Osseous	Osseous
Quadratojugal	Present	Absent	Present or absent
Cotyler Type	II	I or II	II
Pupil	Horizontal or vertical	Horizontal	Horizontal
Larval Vent	Median	Median	Median or dextral
Amplexus	Axillary	Axillary or inguinal	Axillary
Eggs	Water	Water or foam	Water or foam
Chromosomes	22-34	22	22-26

26 chromosomes in *Adenomera* and 22 chromosomes in *Leptodactylus*, he suggested that *Adenomera* was a primitive leptodactyline and that the subfamily might have evolved through a lineage from *Eupsophus* and *Batrachyla* through *Eleutherodactylus* to *Adenomera* and thence *Leptodactylus*. Heyer and Diment (1974) criticized Bogart's hypothesis, noting that his proposed lineage is contrary to all other evidence in the leptodactylines. Bogart's phylogeny is based solely on karyotypes—only one set of characters—to the exclusion of data on morphology, life history, and ecology. When all suites of characters are considered, the primitive chromosome number in the Leptodactylinae must be 22. Thus, 24 and 26 chromosomes in *Adenomera* must be derived, an hypothesis consistent with the derived morphological and ecological characters of the genus.

Pleurodema has 22 chromosomes with a secondary constriction on pair number 8; the same chromosome structure is common in *Leptodactylus* (Bogart, 1974). The floating foam nests of *Pleurodema* are the same as the floating nests of *Leptodactylus* and *Physalaemus*. *Pleurodema* seems to be an ideal ancestral leptodactyline, except that the quadratojugal is absent. This element is absent only in one other genus of leptodactylines, *Pseudopaludicola*, the only other leptodactyline depositing eggs in water.

THE BIOGEOGRAPHIC MODEL

Ideally, biogeographic hypotheses should be deductive (Ball, 1975), not inductive narratives. In order to make our biogeographic model meaningful to the interpretation of the paleogeography of other groups of organisms, we provide a narrative of: 1) the physiographic, climatic, and vegetational history of southern South America, and 2) the distributional history of the diverging groups of *Pleurodema*.

The primitive telmatobiine leptodactylids are restricted to, or are most diverse in, the austral *Nothofagus* forests, whereas the leptodactylines are primarily non-forest frogs, inhabiting savannas, grasslands, and deserts. Thus, the histories of the austral forests and

the austral xeric vegetation formations are pertinent to the evolution of the leptodactylid frogs.

THE CHANGING STAGE

The Tertiary is characterized by gradual cooling and drying subsequent to the Eocene (Axelrod and Bailey, 1969; Wolfe, 1971). The austral forests with such characteristic floristic elements as *Araucaria*, *Laurelia*, and *Nothofagus* have existed in southern South America at least since the Eocene (Cooper, 1960; Cerceau-Larrival, 1968). It is now generally conceded that this austral flora had a Gondwanian dispersal (Raven and Axelrod, 1974)—one that also involved leptodactylid frogs (Lynch, 1971; Savage, 1973). The austral flora was more widespread in the early Tertiary than it is now; in the Oligocene *Araucaria*, *Laurelia*, and *Nothofagus* occurred northward to at least 30° S. Lat. in Chile, and *Nothofagus* was widely distributed in Patagonia (Jeannel, 1967).

Solbrig (1976) hypothesized the existence in middle latitudes of South America since the early Tertiary of a tropical deciduous or semideciduous forest with some xerophytic adaptations. He termed this the Tertiary-Chaco Paleoflora and hypothesized that this flora persists with modifications to the present.

Prior to the Miocene there was no uplift of the Andes; climates in southern South America were more equitable than now and climatic belts extended across the continent. Volcanic activity in Chubut and Santa Cruz in southern Argentina and the uplift of the Bolivian cordillera were initiated in the Miocene (Harrington, 1962; Aubodin, *et al.*, 1973). With the initiation of the Andean uplift in the Miocene, the climates east of the Andes were modified. According to Solbrig (1976), in the Miocene there was a wide expansion of the Argentinian pampas with *Nothofagus* forest adjacent to the pampas; the *Nothofagus* forest was restricted to about its present distribution east of the Andes. Also, semi-desert zones developed between mountains in the western part of the continent and in northern Patagonia.

In the Pliocene there was strong volcanic uplift of the Andes (Petersen, 1958; Rutland, *et al.*, 1965) and increased rain shadow effects east of the mountains. In the Pliocene the Chacoan vegetation expanded northeastward, possibly giving rise to the dry *caatinga* formation in northeastern Brasil; semidesert associations developed along the eastern face of the Andes and in the south separated the *Nothofagus* forests from the pampas (Solbrig, 1976). The semideserts were the precursors of the modern Patagonian and *monte* vegetations. Also, during the Pliocene the bunch-grass association (*puna*) developed in the Andes.

Throughout Miocene and Pliocene times there was a continued

desiccation of the climates along the Pacific coast from central Chile to northern Perú with the restriction or elimination of elements of the Tertiary-Chaco Paleoflora, leaving many disjunct distributions as far north as southern Ecuador (Jeannel, 1967). The development of the extreme xeric conditions of the Atacama Desert and the restriction of the chaparral type of vegetation to central Chile occurred in the Pleistocene, when the Andean Orogeny thrust the cordilleras to their present heights, and the cold Humboldt Current assumed its present course.

Montane glaciation and associated climatic depression was widespread throughout the Andes; three or four glacial stages are recognized (Vuilleumier, 1971). The only major continental glacier extended completely across Patagónia between 41° and 42° S Lat. (Jeannel, 1967). However, the basaltic Somuncurá Plateau was not glaciated (Cei, 1969). The lowlands of southern Chile were dissected by tongues of montane glaciers.

During the Pleistocene the climatic regimes of southern South America alternated between cold and temperate probably with corresponding latitudinal shifts in vegetation. In central Argentina the changes involved drier (interglacial) and wetter (glacial) epochs. Pleistocene and Holocene events in tropical South America also involved alternating wet and dry epochs resulting in expansion of forests and restriction of non-forest habitats in the humid interglacials and expansion of non-forest habitats and restriction of forests in the dry glacial periods. Van der Hammen and González (1969), Van der Hammen (1961), Vanzolini and Williams (1970), and Haffer (1974 and numerous sources cited therein) have documented these climatic fluctuations on the basis of palynological evidence, floristics, and patterns of avian and saurian speciation and distribution. If not before the Pleistocene, at least during Pleistocene dry periods, there existed a dry corridor connecting the Chacoan xerophytic vegetation with the dry Caribbean lowlands and llanos of Venezuela, vegetation formations that existed at least since the Pliocene (Solbrig, 1976; Sarmiento, 1976).

These historical events resulted in the present climatic and vegetational patterns that exist today (Fig. 8).

EARLY LEPTODACTYLINAE EVOLUTION

At least three genera of telmatobiine frogs were present in the early Tertiary in Patagónia—*Caudiverbera* from the Lower Eocene and Lower Oligocene; *Eupsophus* and *Neoprocoela* from the Lower Oligocene (Schaeffer, 1949). Lynch (1971) suggested that *Neoprocoela* possibly is related to *Telmatobius* or *Batrachophrynus*, both of which now occur only in the Andes. Thus, at least by the early Oligocene considerable radiation of the telmatobiines had oc-

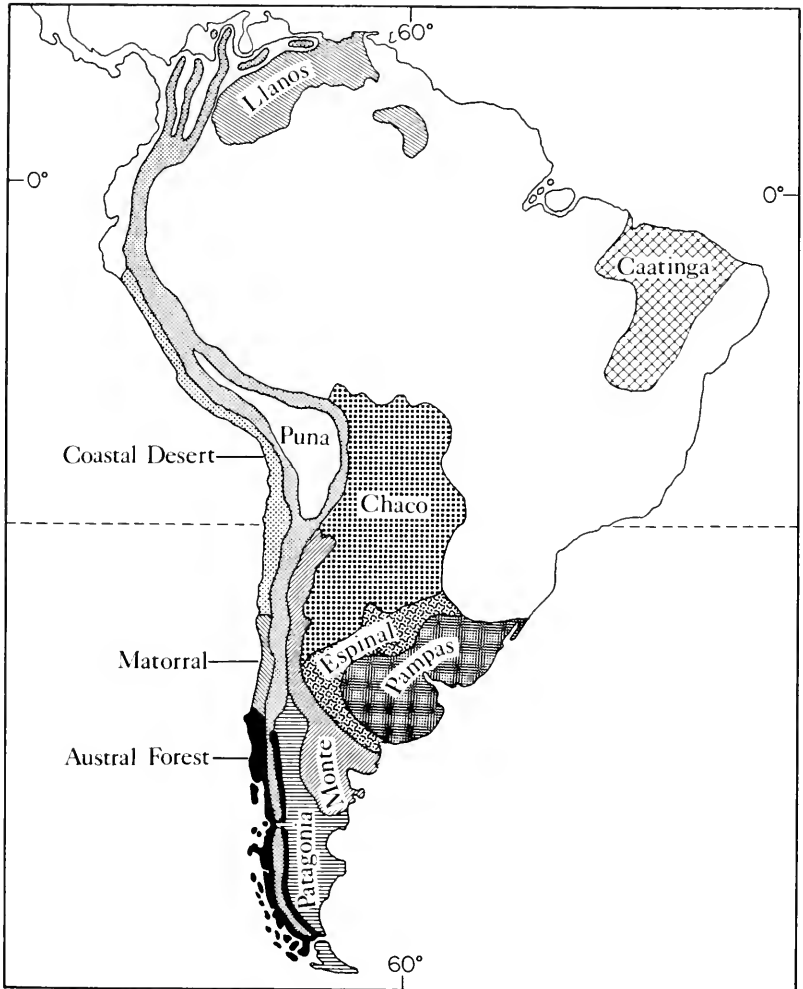


FIG. 8.—Phytogeographic map of South America showing distribution of major xeric formations and austral forests; montane formations stippled (adapted from Solbrig, 1976, and Haffer, 1974).

curred. The existence of Oligocene fossils of *Eupsophus* (primitive telmatobiine relative of *Pleurodema*) is suggestive that *Pleurodema* could have existed at that time. Thus, we begin the history of differentiation and dispersal of *Pleurodema* in the Oligocene. In the following discussion various evolutionary lineages are referred to by the designations used in figures 9, 11, and 13.

We assume that the primitive *Pleurodema* stock was dispersed through the equitable austral forests in southern South America. Early in the history of the genus a divergence resulted in one stock

lacking lumbar glands (A) and one stock having lumbar glands (B). At this time it is not possible to associate the development of lumbar glands with any adaptive modifications of the frogs for different environmental conditions nor for differences in reproductive biology.

We may assume that the stock lacking lumbar glands (A) dispersed northward and encountered the expanding Tertiary-Chaco Paleoflora (Fig. 9). With the beginning of the Andean uplift in the Miocene this stock could have been dispersed so as to be affected by the Andean rainshadow. Those populations in the higher, more mesic habitats retained the primitive habit of depositing eggs in masses in water (A1), whereas those populations at lower elevations east of the rising cordillera evolved the habit of building foam nests (A2). The former stock (A1) continued to disperse northward in developing montane environments with the continuing uplift of the Andes; its restriction to more mesic habitats resulted in its occurrence only in the central Andes. This is the species now known as *P. marmorata*. In the early Pliocene the lowland stock (A2) dispersed through the expanding *monte*-vegetation into northeastern Brasil, where through subsequent isolation beginning in the late Pliocene, a population (A4) evolved into *P. diplolistris*. The southern stock (A3) diverged with adaptations to more xeric (A6) and less xeric habitats (A5); the latter became *P. tucumana*. The remaining stock in western Argentina (A6) inhabited increasingly arid deserts. Probably during the Pleistocene this stock became fragmented into at least two isolates (A7, A8). Barriers to gene flow might have been one or more of the uplifting north-south mountain ranges, such as the Sierra del Valle Fertil, or river valleys carrying glacial runoff. Isolation was sufficiently effective so as to result in the differentiation of *P. nebulosa* and *P. guayapae*. Thus, within the stock of *Pleurodema* lacking lumbar glands (A) there are five species, three of which (*P. guayapae*, *nebulosa*, and *tucumana*) inhabit the *monte* in Argentina and two of which are widely disjunct geographically—one in the central Andes (*P. marmorata*) and one in the *caatinga* in northeastern Brasil (Fig. 10).

The *Pleurodema* stock having lumbar glands (B) underwent a pattern of dispersal and differentiation similar to the former stock (Fig. 11). Early in the evolutionary history of the group there was differentiation in the reproductive biology. A stock (B1) remaining in the temperate austral forests retained the primitive habit of depositing masses of eggs in water, whereas the stock (B2) entering the drier Tertiary-Chaco vegetation developed the habit of depositing eggs in foam nests. This differentiation probably occurred in the Miocene when the first uplift of the Andes interrupted the easterly flow of the moisture-laden prevailing westerlies. Following the stock with the primitive reproductive biology (B1), we find another

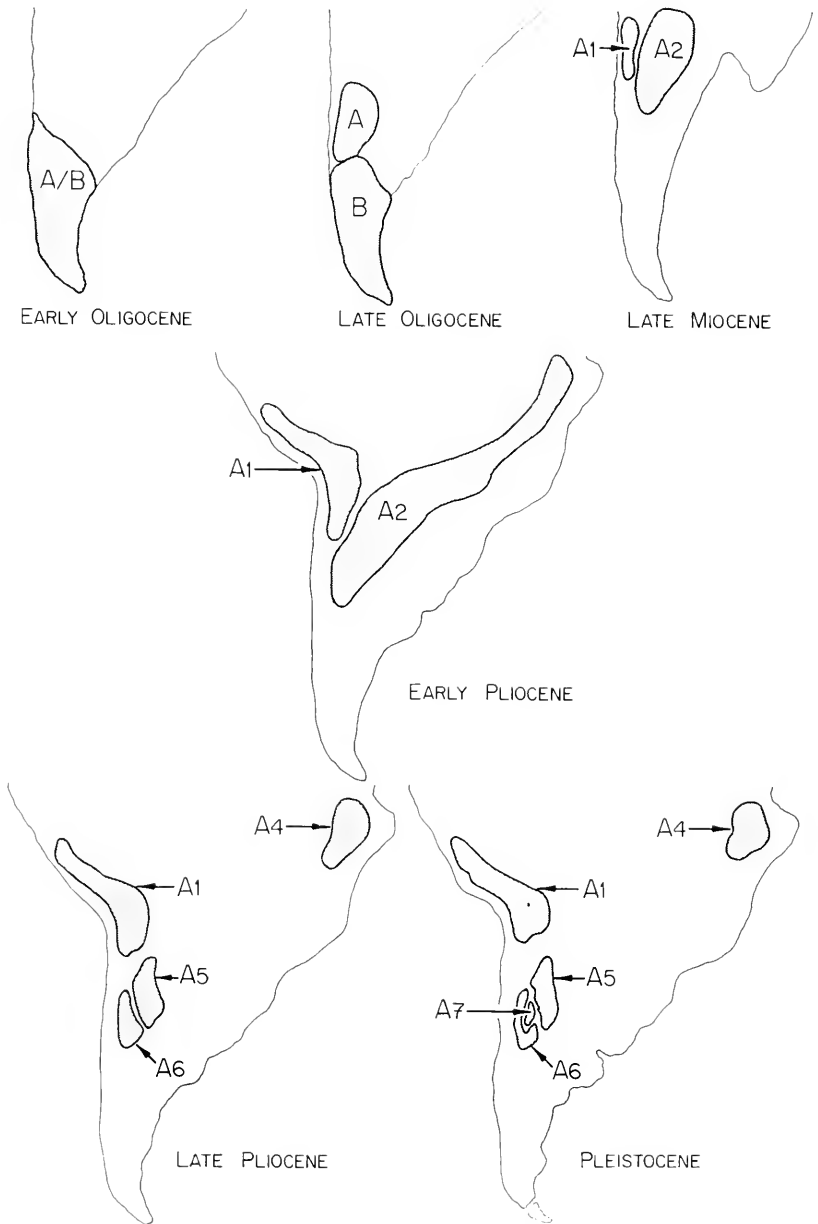


FIG. 9.—Paleogeography of *Pleurodema*. A = group lacking lumbar glands; B = group having lumbar glands. Numbers correspond to those in discussion in text and to branches in figure 13.

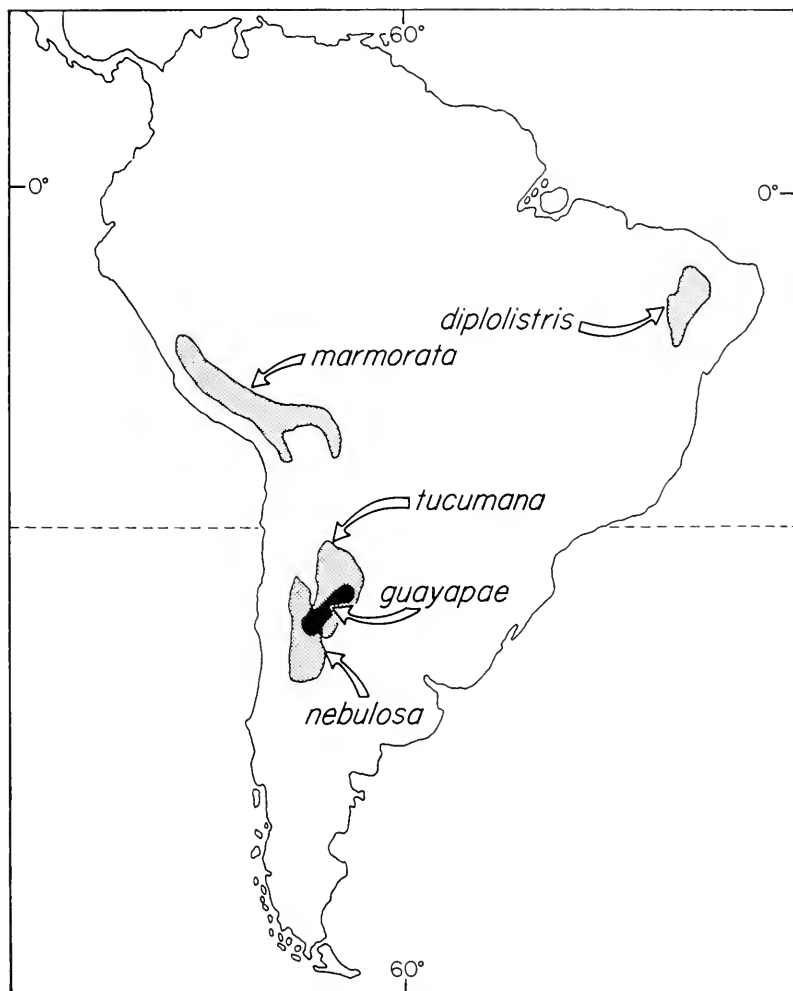


FIG. 10.—Distribution of species of *Pleurodema* lacking lumbar glands.

divergence in manner of oviposition with one stock (B3) retaining the primitive method and the other (B4) depositing eggs in strings. The former stock (B3) remained in the ancestral habitat (*Nothofagus* forest); with the climatic fluctuations in the Pleistocene and Holocene this stock became fragmented into populations in southern Argentina (B13) and in central Chile with disjunct populations as far north as Copiapó (B12). The other stock (B4) depositing eggs in strings seems to represent a reproductive adaptation like that characteristic of *Bufo*, that is to disperse many eggs through several adjacent shallow pools of water. This reproductive strategy

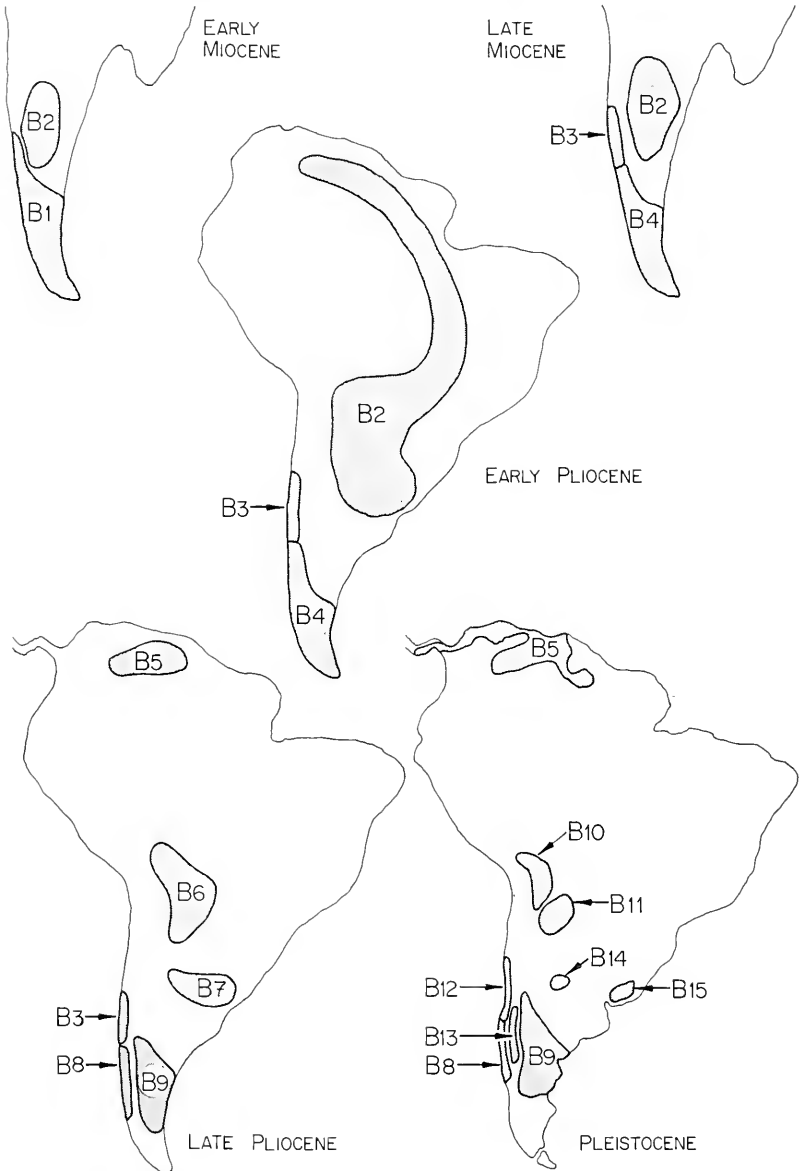


FIG. 11.—Paleogeography of *Pleurodema* having lumbar glands. Numbers correspond to those in discussion in text and to branches in figure 13.—See figure 9 for letter designations.

is mostly associated with xeric situations, where ephemeral water is shallow, but it also can be effective in wet areas, thereby eliminating the migration of adults to breeding sites but instead permit-

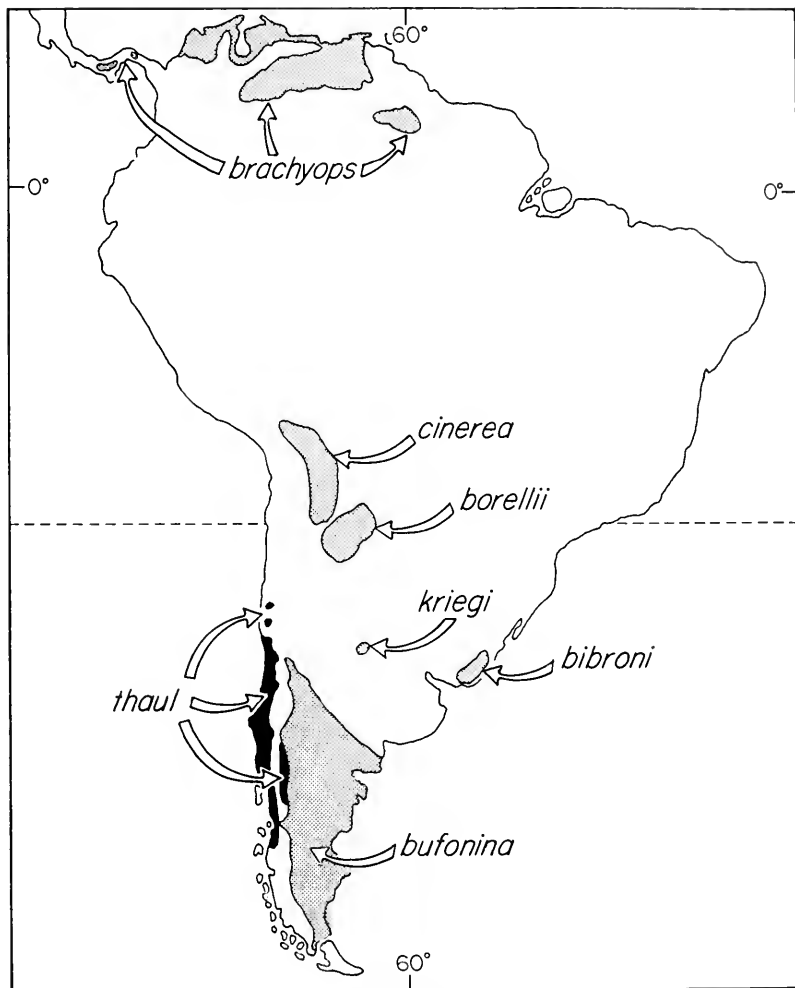


FIG. 12.—Distribution of species of *Pleurodema* having lumbar glands.

ting breeding to take place throughout the wet habitat. Thus, this stock (B4) was suited for life in the temperate austral forests across southern South America. Progressive climatic desiccation and cooling resulted in the restriction of the austral forests to the western part of the continent by the end of the Mioene. The developing Patagonian vegetation in the Pliocene was the site of divergence resulting in one species restricted to the wet austral forests (B8) and another dispersing through the expanding Patagonian scrub (B9). Thus, the austral stock of *Pleurodema* having lumbar glands (B1) evolved into four species—*P. bufonina* in the Patagonian scrub

and the three "kinds" of *P. thaul* in the austral forests (Fig. 12).

The more northern stock (B2) of *Pleurodema* having lumbar glands and depositing eggs in foam nests spread through the xeric *monte*-vegetation (Fig. 11). This stock (B2) dispersed northeastward through non-forested habitats (probably in early Pliocene) and reached the xeric regions of northern South America. Subsequent isolation and differentiation resulted in a vicariant population (B5) in northern Venezuela and Colombia; this is the population now known as *P. brachyops*. With the increasing elevation of the Andes and the evolution of the *puna*-vegetation in the Pliocene, the stock in northern Argentina (B6) differentiated into a highland species inhabiting the *puna* (B10) and a lowland species in the *monte* (B11). Probably in the late Pliocene along the *monte-pampa* ecotone in central Argentina the polyploid condition arose in one stock (B7); the parental species possibly was the more western stock (B6). The polyploid stock (B7) dispersed eastward across the pampas and with the development of drier habitats in eastern Argentina became separated into disjunct populations in central Argentina (B14) and in Uruguay (B15). Thus, the xeric-adapted northern stock of *Pleurodema* with lumbar glands (B2) evolved into five species—*P. bibroni*, *borellii*, *brachyops*, *cinerea*, and *kriegi* (Fig. 12).

The adaptive radiation of *Pleurodema* has involved the modification of the reproductive biology in response to xeric environments. This radiation corresponds to the evolution and dispersal of the Tertiary-Chaco Paleoflora and the receding of the austral *Nothofagus* forests. The entire radiation of the genus has taken place since the beginning of the Oligocene (Fig. 13). Most differentiation has taken place through vicariation, either in direct response to changing environments or to relictualism due to changes in intervening environments. The polyploid stock probably resulted from auto-polyploidy.

The other genera of leptodactylines are distributed in tropical regions essentially north of the main distribution of *Pleurodema*. According to the phylogenetic arrangement of leptodactylines presented by Heyer (1975:31), *Adenomera*, *Lithodytes*, *Vanzolinius*, and *Leptodactylus* form a group closely allied with *Physalaemus* and *Pleurodema*; these two groups are more distantly related to a third group containing *Edalorhina* and *Pseudopaludicola*.⁵ *Leptodactylus* is widespread and diverse in tropical non-forest environ-

⁵Two additional genera (*Hydrodactyle* and *Limmomedusa*) were placed in the Leptodactylinae by Lynch (1971) and Heyer (1975), but their relationships are questionable. Since neither monotypic genus seems to be important in the major picture of leptodactyline radiation, they are not considered further in this discussion.

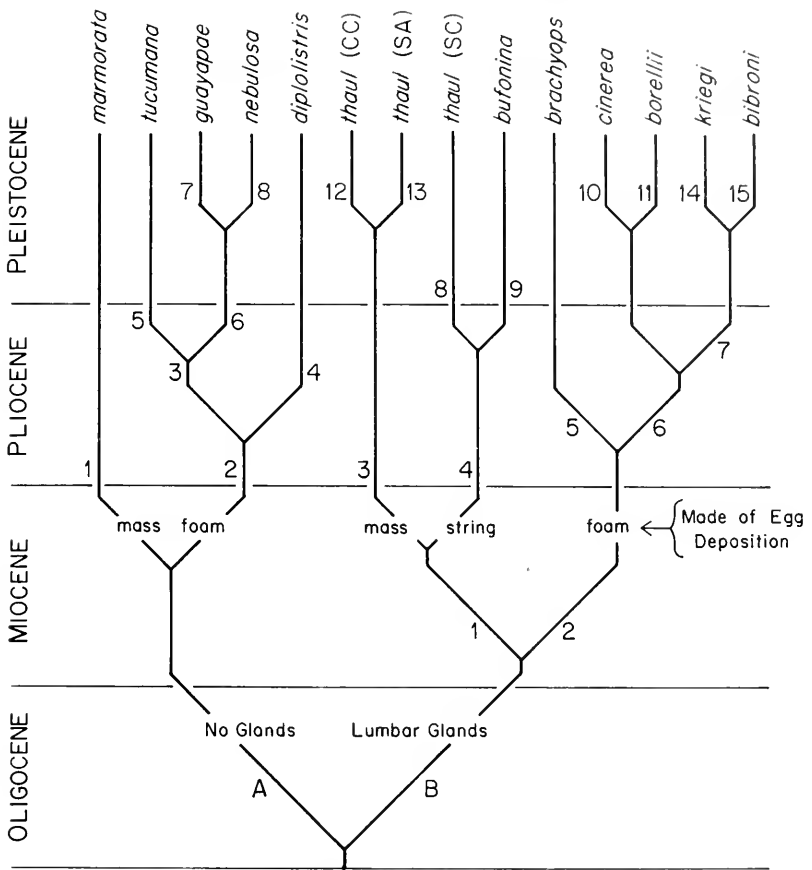


FIG. 13.—Evolutionary scheme of the species of *Pleurodema* with respect to reproductive biology and geological time. The numbers and letters correspond to the paleodistributions shown in figures 9 and 11 and to the stocks discussed in the text.

ments from northern Argentina to México; some species also inhabit humid tropical forests. *Adenomera*, *Lithodytes*, and *Vanzolinius* all apparently were derived from a *Leptodactylus* stock; these three genera inhabit tropical forests, principally in the Amazon Basin. *Edalorhina* and *Pseudopaludicola* inhabit humid tropical forests peripheral to the Amazon Basin. *Physalaemus* is widespread in the American tropics but is most diverse in non-forest environments, especially in eastern and southern Brasil.

Pleurodema, *Physalaemus*, and *Leptodactylus* all have foam nests. *Pleurodema* is primarily temperate in its distribution, whereas the other two genera are tropical. *Pleurodema borellii* and *tucumana* occur sympatrically with *Physalaemus biligonigerus* and *Lep-*

todactylus chaquensis and *latinus* in the vicinity of Tucumán, Argentina; *P. tucumana* occurs with these same species plus *Leptodactylus bufonius*, *laticeps*, and *mystaceus* in the Bañado de Figueroa in north-central Argentina. Of course the northern species of *Pleurodema* (*brachyops* and *diplostris*) occur sympatrically with several species of *Leptodactylus* and *Physalaemus*. Therefore, it is obvious that the major radiation of *Pleurodema* occurred in temperate habitats south of the tropical habitats in which the radiation of other leptodactylines occurred.

Although *Pleurodema* occupies a geographical position intermediate between the telmatobiines and leptodactylines and shows a transition between the reproductive behavior of the two subfamilies, the genus probably cannot be considered to be ancestral to the other leptodactylines. The absence of a quadratojugal in *Pleurodema* and its presence in all other leptodactylines, except *Pseudopaludicola*, seems to preclude the evolution of other leptodactylines from *Pleurodema*. Thus, it seems most reasonable to assume that the earliest leptodactyline stock arose from an *Eupsophus*-like telmatobiine stock. This early leptodactyline stock diverged into one stock lacking a quadratojugal and became *Pleurodema*; the other stock retained the quadratojugal and subsequently evolved into the other leptodactylines. This stock probably dispersed northward with the expanding tropical elements of the Tertiary-Chaco Paleoflora.

RESUMEN

Las especies de anfibios leptodactílidos del género *Pleurodema* se caracterizan por la presencia de un esternón calcificado, diapófisis sacrales ligeramente dilatadas, nasales grandes y en contacto medial, y ausencia de cuadratoyugales. A esto se agrega en algunas especies la presencia de glándulas lumbares bien desarrolladas. Entre los caracteres específicos que distinguen a estas especies se incluyen: 1) presencia o ausencia de glándulas lumbares, 2) características de los repliegues cutáneos y tubérculos, 3) presencia y extensión del pliegue tarsal, 4) forma del tubérculo metatarsal interno, 5) anillo timpánico diferenciado, 6) prominencia de los ondontóforos prevomerianos, 7) estructura del xiphisternón, 8) presencia o ausencia de ranuras y sacos vocales, 9) número de cromosomas, 10) modalidad de ovipostura, 11) canto nupcial, 12) posición ampléxica, 13) coloración.

Utilizando nueve de estos caracteres para un análisis cladístico, es posible reconocer 14 especies de *Pleurodema*. Estas especies son colocadas en seis grupos:

1. *Pleurodema marmorata*.—Glándulas lumbares ausentes, anexo axilar, huevos depositados en racimo; $2N=22$; Andes del Centro del Perú y del Norte de Chile.

2. *Pleurodema diplostris*, *guayapae*, *nebulosa*, y *tucumana*.—

Glándulas lumbares ausentes; amplexo axilar; huevos depositados en nido de espuma; $2N=22$; desiertos del Oeste de Argentina y Caatinga del Nordeste del Brasil.

3. *Pleurodema thaul* (Chile Central y Sur de la Argentina).—Glándulas lumbares presentes; amplexo axilar; huevos depositados en racimo; $2N=22$; estepas y bosques temperados de Chile Central y Sur de la Argentina.

4. *Pleurodema bufonina* y *thaul* (Sur de Chile).—Glándulas lumbares presentes; amplexo inguinal; huevos depositados en rosario; $2N=22$; Patagonia y bosques australes de *Nothofagus*.

5. *Pleurodema brachyops*, *borellii*, y *cinerea*.—Glándulas lumbares presentes; amplexo axilar; huevos depositados en nido de espuma; $2N=22$; Altiplano del Sur del Perú y Norte de la Argentina; vertiente oriental de la Cordillera de los Andes del Noroeste de Argentina; llanos y bosques xéricos del extremo Norte de Suramérica y Panamá.

6. *Pleurodema bibroni* y *kriegi*.—Glándulas lumbares presentes; amplexo axilar; huevos depositados en nido de espuma; autopolioides con 44 cromosomas; Oeste de Córdoba, Argentina y Sudeste del Uruguay.

Entre los problemas taxonómicos que resta por resolver en *Pleurodema*, se pueden citar los siguientes: ¿Son *Pleurodema cinerea* y *borellii* especies distintas o es posible encontrar en la vertiente oriental de la Cordillera de los Andes zonas donde estas especies hibridizan? ¿Son *P. bibroni* y *kriegi* especies distintas o solamente poblaciones disyuntas de una misma especie? ¿Cuales son los límites distribucionales de las tres especies que ahora son referidas como *P. thaul*? ¿Que nombres, si los hay, están disponibles para denominar los diferentes taxa?

Pleurodema comparte numerosas características con los géneros *Alsodes* y *Eupsophus* (Telmatobiinae). La presencia de $2N=22$ cromosomas en *Alsodes nodosus* permite sostener las relaciones de *Pleurodema* con telmatobiinae. Por otra parte, *Pleurodema* parece estar muy cercano al grupo ancestral de Leptodactylinae. En esta subfamilia, el número cromosómico $2N=22$ esta ampliamente representado.

Ecológica y distribucionalmente *Pleurodema* es intermedio entre los telmatobinos (principalmente distribuidos en los bosques australes) y los leptodactilinos (principalmente distribuidos en sabanas tropicales y otros ambientes no boscosos). La modalidad de depositar los huevos en nido de espuma es el principal modo de reproducción de estos últimos. Esta modalidad evoluciona dos veces en *Pleurodema*. La presencia de amplexo inguinal en una de las líneas fleticas de *Pleurodema* es considerada como una especialización que no refleja las relaciones con los arqueobatracios caracterizados por esta modalidad ampléxica.

La historia evolutiva de *Pleurodema* está relacionada con los cambios climáticos que ocurrieron durante el Terciario en el extremo sur del Continente Sudamericano. Estos cambios consistieron en la gradual desecación de la parte sur del continente y continuaron hasta el Eoceno. Cambios graduales como los señalados y otros abruptos, determinados por el levantamiento de la cadena andina, resultan en la restricción de los bosques australes en la expansión y diversificación de la Paleoflora Chaco-Terciaria (Solbrig, 1976). Una vez que *Pleurodema* invade los ambientes xéricos (monte, pampas, y matorrales patagónicos), se desarrolla la modalidad de ovipostura en nido de espuma (Fig. 13). Los actuales esquemas de distribución de estas especies son el resultado de la creación de modernas zonas de vegetación debido a fluctuaciones climáticas del Pleistoceno y el Holoceno.

LITERATURE CITED

- AUBOUIN, J., BORRELLO, A. V. CECIONI, G., CHARRIER, R., CHOTIN, P., FRUTOS, J., THIELE, R., VICENTE, J.-C. 1973. Esquisse paléogéographique et structurale des Andes Méridionales. *Rev. Geog. Phys. Geol. Dynam.*, 15:11-72.
- AXELROD, D. I., BAILEY, H. P. 1969. Paleotemperature analysis of Tertiary floras. *Paleogeog. Paleoclim. Paleoecol.*, 6:163-195.
- BALL, I. R. 1975. Nature and formulation of biogeographical hypotheses. *Syst. Zool.*, 24:407-430.
- BARRIO, A. 1964. Especies crípticas del género *Pleurodema* que conviven en una misma área, identificadas por el canto nupcial (Anura: Leptodactylidae). *Physis*, 24:471-489.
- BARRIO, A., RINALDI DE CHERI, P. 1970. Estudios citogenéticos sobre el género *Pleurodema* y sus consecuencias evolutivas (Amphibia, Anura, Leptodactylidae). *Ibid.*, 30:309-319.
- BECAK, M. L. 1970. Further studies on polyploid amphibians (Ceratophryidae). *Chromosoma*, 31:377-385.
- BECAK, M. L., BECAK, W. 1974. Studies on polyploid amphibians—karyotype evolution and phylogeny of the genus *Odontophrynus*. *J. Herp.*, 8:337-341.
- BECAK, W., BECAK, M. L., LANGLADA, F. G. 1968. Artificial triploid hybrids by interspecific mating of *Odontophrynus* (Amphibia, Anura). *Experimentia*, 24:1162-1164.
- BELL, T. 1843. Part V. Reptiles. in DARWIN, C. The zoology of the voyage of the H.M.S. Beagle, under the command of Captain Fitzroy, R.N., during the years 1832 to 1836. Smith, Elder and Co., London: 1-51.
- BOGART, J. P. 1970. Systematic problems in the amphibian family Leptodactylidae (Anura) as indicated by karyotypic analysis. *Cytogenetics*, 9:369-383.
- BOGART, J. P. 1974. A karyosystematic study of frogs of the genus *Leptodactylus* (Anura: Leptodactylidae). *Copeia*, 1974 (3):728-737.
- BOGART, J. P. 1976. Polyploid amphibians: three more diploid-tetraploid cryptic species of frogs. *Science*, 193:334-335.
- BOGART, J. P., WASSERMAN, A. 1972. Diploid-polyploid cryptic species pairs: a possible clue to evolution by polyploidization in anuran amphibians. *Cytogenetics*, 11:7-24.

- BRUNDIN, L. 1966. Transantarctic relationships and their significance as evidenced by chironomid midges, with a monograph of the subfamilies Podonominae and Aphroteniinae and the austral Heptagyiae. Kgl. Svenska Vetensk. Handl., 11:1-472.
- BURMEISTER, C. H. C. 1861. Reise durch die La Plata-Staaten, 2:1-538.
- CAPURRO, L. F. 1955. *Pleurodema bufonina*. Inv. Zool. Chilenas, 2:147-149.
- CEI, J. M. 1958. Polimorfismo y distribución geográfica en poblaciones chilenas de *Pleurodema bibroni* Tschudi. *Ibid*, 4:300-327.
- CEI, J. M. 1961. *Pleurodema bufonina* Bell, anfibio australe con ciclo spermatogenético discontinuo autoregulata. Arch. Zool. Italiano, 46:167-180.
- CEI, J. M. 1962. Batracios de Chile. Ed. Univ. Chile, Santiago: 1-128+i-cviii.
- CEI, J. M. 1969. La meseta basáltica de Somuncurá, Río Negro. Herpetofauna endémica y sus peculiares equilibrios biocénóticos. Physis, 28:257-271.
- CEI, J. M. 1972a. Herpetología Patagónica. IV. Distribución geográfica y diferenciación serológica poblacional de *Pleurodema bufonina* (Bell). *Ibid.*, 31:423-430.
- CEI, J. M. 1972b. Herpetología Patagónica. V. Las especies extra-cordilleras del género *Telmatobius*. *Ibid*, 31:431-449.
- CEI, J. M., ESPINA, S. 1957. La vibración sexual preventiva ("warning vibration") en *Pleurodema* chilenas. Inv. Zool. Chilenas, 4:15-21.
- CEI, J. M., CAPURRO, L. 1957. La distribución de los patrones de coloración en *Pleurodema bibroni* en relación con la distribución geográfica y el habitat. *Ibid*, 3:156-161.
- CEI, J. M., CODOCEO, M. 1957. Probable discontinuidad del ciclo espermatogenético de *Pleurodema bufonina*. *Ibid*, 4:77-82.
- CEI, J. M., ROIG, V. 1961. Sobre la presencia de un batracio característico de la fauna Patagónica en Territorio Mendocino. Bol. Estud. Geog. Univ. Cuyo, 8:129-134.
- CERCEAU-LARRIVAL, T. 1968. Contribution palynologique et biogéographique a l'étude biologique de l'Amérique australe. in DELAMIERE DEBOUTTEVILLE, C., RAPOPORT, E. (eds.). Biologie de l'Amérique australe, 4. Cent. Natl. Recher. Scient., Paris: 111-197.
- COCHRAN, D. M., GOIN, C. J. 1970. Frogs of Colombia. Bull. U.S. Natl. Mus., 288:1-655.
- COOPER, R. A. 1960. Southern hemisphere Mesozoic and Tertiary Podocarpaceae and Fagaceae and their paleogeographic significance. Proc. Roy. Soc. London, 152:491-500.
- COPE, E. D. 1868. Sixth contribution to the herpetology of tropical America. Proc. Acad. Nat. Sci. Philadelphia, 20:305-313.
- COPE, E. D. 1877. Synopsis of the cold-blooded Vertebrata, produced by Prof. James Orton during his exploration of Peru in 1876-77. Proc. Amer. Philos. Soc., 17:33-49.
- CROIZAT, L. 1964. Space, time, form, the biological synthesis. Privately published, Caracas.
- CROIZAT, L., NELSON, G., ROSEN, D. E. 1974. Centers of origin and related concepts. Syst. Zool., 23:265-287.
- DONOSO-BARROS, R. 1969a. Nota distribucional sobre *Pleurodema bufonina* Bell. Bol. Soc. Biol. Concepción, 41:155.
- DONOSO-BARROS, R. 1969b. Posición nomenclatural de un leptodactylido Uruguayo (Amphibia-Anura). *Ibid*, 41:161-162.
- DONOSO-BARROS, R. 1974. Nuevos reptiles y anfibios de Chile. *Ibid*, 48:217-229.
- DONOSO-BARROS, R., CEI, J. M. 1962. The taxonomic position of three common Chilean frogs. Herpetologica, 18:195-203.
- DUELLMAN, W. E. 1967. Social organization in the mating calls of some Neotropical anurans. Amer. Midl. Nat., 77:156-163.

- DUELLMAN, W. E. 1972. South American frogs of the *Hyla rostrata* group (Amphibia, Anura, Hylidae). *Zool. Mededel.*, 47:177-192.
- DUELLMAN, W. E., CRUMP, M. L. 1974. Speciation in frogs of the *Hyla parviceps* group in the upper Amazon Basin. *Occas. Papers Mus. Nat. Hist. Univ. Kansas*, 23:1-40.
- DUMÉRIL, A. M. C., BIBRON, G. 1841. *Erpétologie générale*, Paris, 8: 1-792.
- DUNN, E. R. 1944. Los géneros de anfibios y reptiles de Colombia, Primera parte: Anfibios. *Caldasia*, 2:497-529.
- FORMAS, J. R. 1976. Descriptions of *Batrachyla* (Amphibia, Anura, Leptodactylidae) tadpoles. *J. Herp.*, 10:221-225.
- GALLARDO, J. M. 1968. Sobre la validez de algunas especies argentinas de *Pleurodema* (Anura, Leptodactylidae). *Physis*, 28:135-144.
- GORHAM, S. W. 1966. Liste der resenten Amphibien und Reptilien. *Das Tierreich*, 85:1-222.
- HARRINGTON, H. J. 1962. Paleogeographic development of South America. *Bull. Amer. Assoc. Petrol. Geol.*, 46:1773-1814.
- HAFFER, J. 1969. Speciation in Amazonian forest birds. *Science*, 165:131-137.
- HAFFER, J. 1974. Avian speciation in tropical South America. *Publ. Nuttall Ornith. Club*, 14:1-390.
- HENNIG, W. 1966. *Phylogenetic systematics*. Univ. Illinois Press, Urbana: 1-263.
- HEYER, W. R. 1969. The adaptive ecology of the species groups of the genus *Leptodactylus* (Amphibia, Leptodactylidae). *Evolution*, 23:421-428.
- HEYER, W. R. 1973. Systematics of the *marmoratus* group of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae). *Contri. Sci. Los Angeles Co. Mus.*, 251:1-50.
- HEYER, W. R. 1975. A preliminary analysis of the intergeneric relationships of the frog family Leptodactylidae. *Smithsonian Contri. Zool.*, 199:1-55.
- HEYER, W. R., DIMENT, M. J. 1974. The karyotype of *Vanzolinius discodactylus* and comments on usefulness of karyotypes in determining relationships in the *Leptodactylus*-complex (Amphibia: Leptodactylidae). *Proc. Biol. Soc. Washington*, 87:327-336.
- ITURRA, P., VELOSO, A. 1975. Citotaxonomía en especies del grupo del *Eupsophus rosceus* (Amphibia-Leptodactylidae). Descripción del cariotipo de *Eupsophus coppingeri*. *Gunther. XVIII Reunión An. Soc. Biol. Chile*: 25-26 (abstract).
- JEANNEL, R. 1967. Biogéographie de l'Amérique australe. *in* DELAMERE DEBOUTTEVILLE, C., RAPOPORT, E. (eds.). *Biologie de l'Amérique australe*, 3. *Cent. Nat. Recher. Scient.*, Paris: 401-460.
- KLUGE, A. G., FARRIS, J. S. 1969. Quantitative phyletics and the evolution of anurans. *Syst. Zool.*, 18:1-32.
- LAURENT, R. F. 1975. Diferencias biométricas entre dos poblaciones similares de *Pleurodema*. *Acta Zool. Lilloana*, 31:99-106.
- LESSON, R. P. 1826. *in* LESSON, R. P., GARNOT, P. *Zoologie 2*, *in* DUPERRY, C. *Voyage autour du monde pendant les années 1822-23-24-25, sur le corvette la Coquille*. Paris: 1-65.
- LEVAN, A., FREDKA, A., SANDBERG, A. 1964. Nomenclature for centromeric position on chromosomes. *Hereditas*, 52:201-220.
- LYNCH, J. D. 1971. Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. *Misc. Publ. Mus. Nat. Hist. Univ. Kansas*, 53: 1-238.
- LYNCH, J. D. 1973. The transition from archaic to advanced frogs. *in* VIAL, J. L. (ed.). *Evolutionary biology of the anurans: contemporary research on major problems*. Univ. Missouri Press, Columbia: 133-182.

- MÜLLER, L. 1926. Neue Reptilien und Batrachier der Zoologischen Sammlung des Bayerischen Staats. Zool. Anz., 65:193-200.
- MÜLLER, P. 1973. The dispersal centres of terrestrial vertebrates in the Neotropical Realm. Junk, The Hague: 1-244.
- PARKER, H. W. 1927. A revision of the frogs of the genera *Pseudopaludicola*, *Physalaemus*, and *Pleurodema*. Ann. Mag. Nat. Hist., (9)20:450-478.
- PERACCA, M. G. 1895. Viaggio del dott. Alfredo Borelli nella Rep. Argentina e nell Paraguay. Rettili ed Anfibi. Bol. Mus. Zool., 10 (195):1-32.
- PETERS, W. 1870. Mitteilungen über Amphibien des Königlich Zoologischen Museums. Monats. Akad. Wiss. Berlin, 1870:640-652.
- PETERSEN, U. 1958. Structure and uplift of the Andes of Peru, Bolivia, Chile, and adjacent Argentina. Bol. Soc. Geol. Peru, 33:57-143.
- PHILIPPI, R. A. 1902. Suplemento a los Batraquios Chilenos descritos en la Historia Fisica i Política de Chile de don C. Gay. Santiago: 1-161.
- RABB, G. B. 1973. Evolutionary aspects of the reproductive behavior of frogs. in VIAL, J. L. (ed.). Evolutionary biology of the anurans: contemporary research on major problems. Univ. Missouri Press, Columbia: 213-227.
- RAVEN, P. H., AXELROD, D. I. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Garden, 61:539-673.
- ROSEN, D. E. 1975. A vicariance model of Caribbean biogeography. Syst. Zool., 24:431-464.
- RUTLAND, R. W. R., GUEST, J. E., GRASY, R. L. 1965. Isotopic ages and Andean uplift. Nature, 208:677-678.
- SARMIENTO, G. 1976. Evolution of arid vegetation in tropical America. in GOODALL, D. W. (ed.). Evolution of desert biota. Univ. Texas Press, Austin: 65-99.
- SAVAGE, J. M. 1973. The geographic distribution of frogs: patterns and predictions. in VIAL, J. L. (ed.). Evolutionary biology of the anurans: contemporary research on major problems. Univ. Missouri Press, Columbia: 351-445.
- SOLBRIG, O. T. 1976. The origin and floristic affinities of the South American temperate desert and semidesert regions. in GOODALL, D. W. (ed.). Evolution of desert biota. Univ. Texas Press, Austin: 7-49.
- TRUEB, L. 1973. Bones, frogs, and evolution. in VIAL, J. L. (ed.). Evolutionary biology of the anurans: contemporary research on major problems. Univ. Missouri Press, Columbia: 65-132.
- TSCHUDI, J. 1838. Classification der Batrachier. Mem. Soc. Sci. Nat. Neuchâtel, 5(2):1-99.
- VAN DER HAMMEN, T. 1961. The Quaternary climatic changes of northern South America. Ann. New York Acad. Sci., 95:673-683.
- VAN DER HAMMEN, T., GONZÁLEZ, E. 1960. Upper Pleistocene and Holocene climate and vegetation of the "Sabana de Bogotá." Leiden Geol. Mededel., 25:262-315.
- VANZOLINI, P. E., WILLIAMS, E. E. 1970. South American anoles: the geographic differentiation and evolution of the *Anolis chrysolepis* species group (Sauria, Iguanidae). Arch. Zool. Univ. São Paulo, 19:1-298.
- VELLARD, J. 1960. El género *Pleurodema* en los Andes Peruanos. Mem. Mus. Hist. Nat. Javier Prado, 10(7):1-12.
- VELOSO, A., GALLEGUILLAS, R., DIAZ, N. 1973. Karyotypic analysis of allopatric populations of *Pleurodema thaul* (Lesson). Amphibia, Leptodactylidae. Caryologia, 26:69-76.
- VELOSO, A., ITURRA, P. 1976. Chromosome evidence for different phyletic lines in the frog genus *Eupsophus* (Amphibia: Leptodactylidae). Herp. Rev., 7:99-100 (abstract).

- VUILLEUMIER, B. S. 1971. Pleistocene changes in the fauna and flora of South America. *Science*, 173:771-780.
- WAGNER, W. H., JR. 1961. Problems in the classification of ferns. *in* Recent advances in botany. Univ. Toronto Press, Toronto: 841-844.
- WEBB, R. G., GREER, J. K. 1969. Amphibians and reptiles from Malleco Province, Chile. *Publ. Mus. Michigan St. Univ.*, 4:193-226.
- WOLFE, J. A. 1971. Tertiary climatic fluctuations and methods of analysis of Tertiary floras. *Paleogeog. Paleoclim. Paleoecol.*, 9:27-57.

