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THE ADAPTIVE ECOLOGY OF THE SPECIES GROUPS OF THE GENUS *LEPTODACTYLUS* (AMPHIBIA, LEPTODACTYLIDAE)[1]

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Frogs of the Neotropical genus *Leptodactylus* provide a clear example of one way in which a group of amphibians evolved from an almost aquatic to a terrestrial life history. The genus is comprised of approximately 30 species, but the taxonomy and relationships of many of these species are confused. My initial interest in the genus was to attempt to determine if clusters of related species (species groups) could be recognized, and if so, to determine the relationships among the species groups. The following discussion uses as a background the synthesis of the species groups and their interrelationships (Heyer, 1969).

SYNOPSIS AND RELATIONSHIPS AMONG THE SPECIES GROUPS

The five species groups and the species in each group are: 1) Fuscus group—*L. bufonius, fuscus, gracilis, labialis, labrosus, latinasus, mystaceus, mystacinus, poecilochilus, ventrimaculatus*; 2) Marmoratus group—*L. hylaedactylus, marmoratus*; 3) Melanonotus group—*L. dantasi, discodactylus, melanonotus, podicipinus, pustulatus, wagneri*; 4) Ocellatus group—*L. bolivianus, chaquensis, ocellatus*; 5) Pentadactylus group—*L. laticeps, pentadactylus, rhodomystax, rhodonotus, rugosus*. This is a conservative list. The only species group composition considered accurate is the Melanonotus group, as it is the only group to have undergone recent revision (Heyer, in press). Members of each group are distributed in Central and/or South America. The relationships among the species groups are easiest explained visually (Fig. 1).

THE ADAPTIVE ECOLOGY OF THE SPECIES GROUPS

The principal change in mode of life observable in *Leptodactylus* is from riparian (in the broad sense) to terrestrial habitats. Fortunately, the species groups present a series of grades in this process, allowing the probable history of the adaptive shift to be discerned.

Simpson (1947) laid down the foundations of the adaptive zone concept. The adaptive zone hypothesis is a conceptual means of explaining the origin of new adaptive kinds of organisms. The usefulness of the concept has been treated recently in a symposium (Systematic Zoology, Volume 14, Number 4, 1965). Simpson's (1947) basic features of the adaptive zone concept, pertinent to the present discussion, are these: (1) Adaptive zones are subdivisions of the environment based on broad adaptive types as evidenced by taxonomic segments of the biota; (2) Major adaptive zones are separated by discontinuities or essentially instable ecological zones; (3) The change from one zone to another is usually undertaken by a small group of organisms at a very rapid evolutionary rate; and (4) A radiation ensues in a newly entered adaptive zone. Once this radiation has occurred, the forms in the transitional zones are comparatively ill-adapted and rapidly become extinct. More recently, workers (particularly Bock, 1965; Hecht, 1965; King, 1965; and von Wahlert, 1965) have concentrated on the processes involved in the transition from

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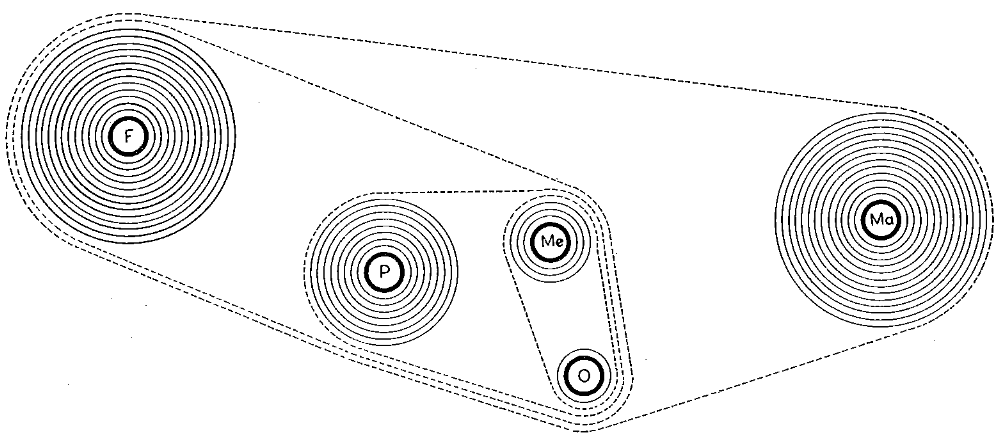


FIG. 1. Relationships among the species groups of the genus *Leptodactylus*. Dark circles indicate point locations of the species groups. F = Fuscus group, P = Pentadactylus group, Me = Melanonotus group, O = Ocellatus group, Ma = Marmoratus group. Solid concentric circles indicate total number of evolutionary advancements for each of the groups. Dashed lines indicate the way in which the groups are related. Of all the groups, the Melanonotus and Ocellatus groups are most closely related to each other. The Pentadactylus group is then related to these two groups, and the Fuscus group is related to the cluster of the three groups. The Marmoratus group is not closely related to the other four groups. Taxonomically interpreted, the genus *Leptodactylus* is composed of two subgenera; the subgenus *Leptodactylus* which includes the Fuscus, Melanonotus, Ocellatus, and Pentadactylus groups, and the subgenus *Adenomera* which includes the Marmoratus species group.

one major adaptive zone to another. These workers emphasize that: (1) Evolutionary changes in transitional zones are via microevolutionary means, although the rate of genetic change is rapid; (2) Ecological shifts are very important, but are not as easily documented as morphological changes; and (3) All transitional forms are fully adapted to the particular environment in which they exist, while at the same time possessing certain characteristics (preadaptations) which allow evolutionary change to a new adaptive type given the proper selective pressures in a suitable environment.

One of the most unusual features of the genus *Leptodactylus*, and one which is shared by certain other leptodactylid genera in South America and Australia, is the foam nest. The nest is constructed of glandular secretions beaten into a froth, the consistency of which is quite like a beaten egg white. The eggs are deposited in the nest during its construction. Many frogs, probably most, are capable of exuding considerable amounts of mucus from the skin and the female reproductive tract. Relatively few have utilized such mucus to form a foam nest. The adaptation appears to be mainly one of behavior, although concurrently there is probably selection for increase in mucus secretion either by an increase in number of mucous glands or an increased production of mucus from existing mucous glands.

Several selective factors act in concert to bring about populational movement into a different adaptive zone. The major forces that would operate on an anuran to place the eggs in a foam nest out of water for any portion of development include: predation on eggs and larvae in a pond-marsh situation, larval competition in a pond-marsh situation, and desiccation of a temporary water source.

The main predators feeding in a pond utilized by most amphibians for reproductive and developmental purposes are not fish, as the ponds used are characteristically seasonal or rather temporary. Water insects, carnivorous tadpoles, and snakes are the major predators. A foam nest, even one floating on top of water, protects the nest contents from many of these predators for as long as the nest is intact. The genus *Leptodactylus* inhabits, and probably inhabited through much of its evolution, regions characterized by markedly seasonal rainfall. Resistance of reproductive products to desiccation is always an important factor in the success of a species living in such an environment, particularly if the rainfall is erratic during the breeding season. While eggs or developing larvae are within a foam nest, most are protected from desiccation because of the insulating effect of the nest. Certain of these nests are rather sturdy. In the summer of 1967, I preserved some nests of *L. melanonotus* by placing the nests on top of a formalin solution in jars. The jars were violently shaken to preserve the eggs, but the nest remained intact. The 3000 mile journey by truck to Los Angeles was not smooth, thus the nests were bounced considerably; yet, I had to dissect the nests with teasing needles in the laboratory in order to count the eggs.

One may visualize the following series of events in a drainage basin characterized by sporadic rainfall. A frog places its eggs in a foam nest during one brief rainy period after which the pond dries up. A subsequent heavy rain comes which destroys the nest and releases just hatched larvae into the newly refilled pond. The offspring of such a frog would have a lower mortality rate than those of a frog laying its eggs directly in the water, assuming comparable periods of egg deposition and larval development. As it probably would take a very heavy rain to destroy the nest, the larvae would be assured of water for the duration of their aquatic development. The Melanonotus and Ocellatus groups reflect the primitive *Leptodactylus* pattern in that the foam nest is placed on top of the water (Fernandez and Fernandez, 1921; Lutz, 1947; pers. obs.). During the breeding season, *L. melanonotus* is a typical riparian frog, feeding and breeding in the water-land interface. The frogs move about only among plants characteristic of the water edge or marsh and breed in water so shallow that when they sit on the bottom, their heads are above water.

The genus *Leptodactylus* has been able to make the transition from a life-history closely tied to water to a more terrestrial ecology. The Pentadactylus group shows the first step towards a more terrestrial life, if the pre-adaptations present in the Melanonotus-Ocellatus groups may be regarded as primitive. Apparently, *L. pentadactylus* congregate at bodies of water only for breeding purposes. The frogs are often found in large burrows and breeding may occur at these burrows or in potholes next to water (Breder, 1946) or at the margins of ponds (Bokermann, 1957). Breder (1946) observed nests of *L. pentadactylus* in potholes, either in contact with small bodies of water or little removed from bodies of water. He also observed that nests were torn apart by torrential rains, and the advanced larvae escaped into the rising water. The advantages that members of the Pentadactylus group share are: (1) the eggs are protected from pond predators, and (2) the eggs are free from desiccation.

The next adaptive step appearing in the Fuscus group is placing the foam nest on land in a burrow fashioned by the male. The males call from these burrows located just under the surface of the soil. The burrows usually have a single access hole to the surface. The female is attracted to the burrow where mating takes place and the foam nest is formed. Larval development is initiated in the burrow, but the larvae are either liberated into an adjacent pond when a heavy rain floods the burrow, or perhaps flooded from the burrow when the level of the adjacent pond rises (Dixon and Heyer, 1968; Fernandez and Fernandez, 1921; Lutz, 1947).

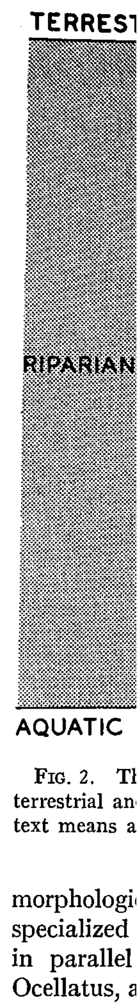
In addition to the adjustment to erratic rainfall, a significant advantage of the terrestrial foam nest was demonstrated in a series of observations on *L. labialis* in western Mexico. On July 11, 1967, Dr. James R. Dixon and I stopped at a dam 2.4 km E and 9.6 km S of the town of Colima on the road from Colima to Tecoman in the state of Colima. The dam contained no standing water and the earth was cracked, but the cracks were moist. The only frogs calling in the daytime were several male *Leptodactylus*. One of the males captured at that time was calling from a 20 × 30 mm, almost spherical burrow. Very early in the morning of July 12, after a very heavy thunderstorm, water rose behind the dam wall. We returned to the dam in the evening while it was still raining lightly, at which time there was a frenzy of breeding activity. Frogs of six species including *L. labialis,* were calling and mating in the pond. I sampled the pond on the morning of July 14, and the tadpoles of *L. labialis* were noticeably advanced over those of *Bufo marmoreus* and *Hypopachus variolosus,* the other larvae that had hatched. On July 24, metamorphosing *L. labialis* were leaving the pond, the first species that we observed to do so. We found several foam nests of *L. labialis* near the dam, some of which contained larvae capable of swimming. *L. labialis* had been able to mate before standing water was present. The eggs had matured in the nest and hatched; the larvae had developed functional mouthparts and enclosed the gills. When the rains came and the pond filled, the larvae were released from their nests and had a temporal advantage over the other species utilizing the pond. The advanced stage of development when the pond first formed resulted in an early metamorphosis for *L. labialis.*

The reproductive behavior of *L. bufonius,* as reported by Cei (1949), contrasts with that of *L. labialis* in certain respects. Cei reported that the females excavate a burrow and call males; in *L. labialis,* the only specimens we found in burrows without nests were calling males. Nevertheless, the main advantages that the Fuscus group has with respect to early development are: (1) the eggs are not taken by pond or ground surface feeding predators, (2) the eggs are freer from desiccation than those of the exposed nests of the Melanonotus, Ocellatus, and Pentadactylus groups (the surface of a nest will encrust if exposed long enough and any eggs located in the encrusted foam are destroyed), (3) the larvae possibly avoid much food and space competition in the pond, and (4) the larvae metamorphose before many other species using the same pond.

The Marmoratus group has the most specialized type of reproductive behavior and larval development. Foam nests are laid in almost spherical incubating chambers like those of the Fuscus group. The larvae hatch and depend entirely on the large yolk stores of the egg for growth (Lutz, 1947). The larvae do not have tooth row denticles in the mouthparts and lack the spiracle characteristic of aquatic *Leptodactylus* larvae (Heyer and Silverstone, in prep.). The larvae metamorphose within the incubating chamber without ever having a free-living aquatic period of growth and development. The Marmoratus group is entirely independent of standing bodies of water during the life cycle; the species of this group are truly terrestrial.

The shift from an aquatic to a terrestrial life in frogs involves a significant number of changes and any intermediate form might be predicted to be ill-adapted to its environment. Nevertheless, a change from a riparian to a terrestrial life history, as evidenced by the genus *Leptodactylus,* can be explained by calling on relatively few genetic changes. Most of the genetic changes within *Leptodactylus* leading to a terrestrial life are behavioral, e.g. whipping mucous secretions into foam, or digging a burrow for the nest. Associated with these modifications of behavior are larger eggs and a reduction in the total number of eggs produced (Fig. 2).

The importance of the ecologic shift towards terrestriality in the genus *Leptodactylus* is reflected by certain adaptive



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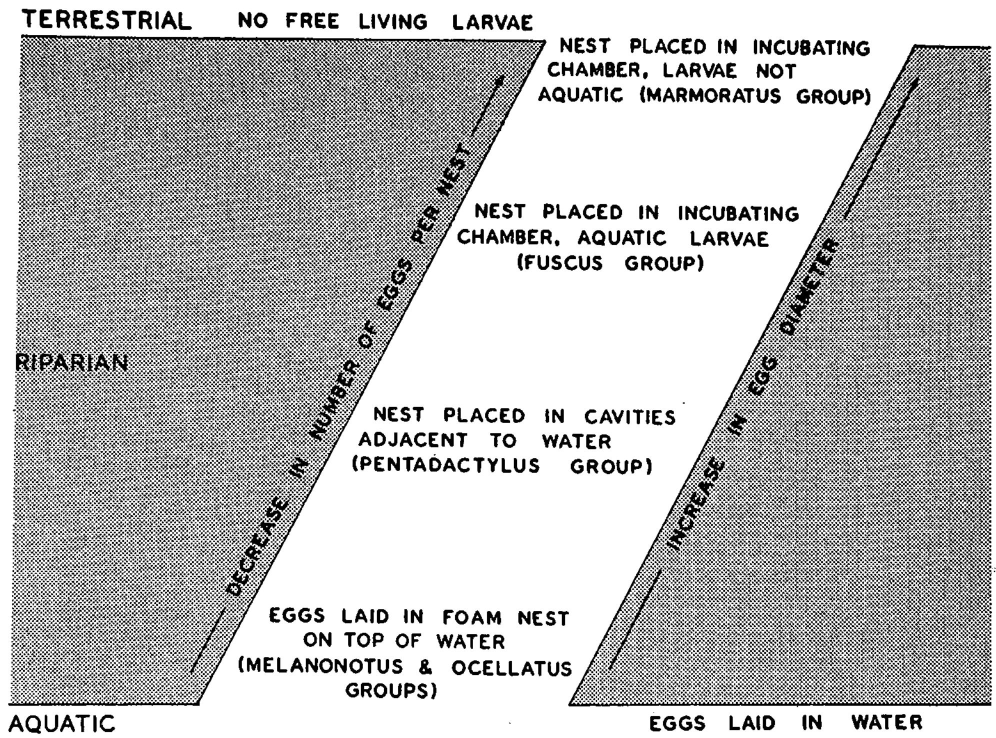

FIG. 2. The adaptive shift demonstrated by the species groups of the genus *Leptodactylus*. The large terrestrial and aquatic zones are above and below the transitional riparian zone. Riparian in this context means any fresh water-dry land interface. See text for further explanation.

morphological characters. Most of the specialized characters have been derived in parallel in the Fuscus, Melanonotus, Ocellatus, and Pentadactylus groups on the one hand, and the Marmoratus group on the other. The trend toward a more terrestrial life has apparently occurred twice within the genus *Leptodactylus*.

Male thumb spines apparently facilitate amplexus. Males of certain species of the Melanonotus and Ocellatus groups have thumb spines. Mating pairs of these species are quite active, as the male beats up the foam nest while the pair is in amplexus. Thumb spines would seem to help anchor the male to the female in an aquatic situation. Males of the large-sized Pentadactylus group also have thumb spines. Presence of thumb spines (and chest spines) would appear to be necessary in anchoring a mating pair due to the large adult size. The species do not undergo amplexus in an aquatic situation. Thumb spines are absent in males of the more terrestrial species of the Fuscus and Marmoratus groups.

Toe fringes in adults are characteristic of members of the Melanonotus and Ocellatus groups. Extensive toe ridges are present in juveniles of the Pentadactylus group, but are lost during ontogeny. Toe fringes or ridges are absent in both juvenile and adult members of the Fuscus and Marmoratus groups. Toe fringes give a larger surface area to the foot, which is important to species associated with water, such as members of the Melanonotus and Ocellatus groups are. Toe fringes allow members of the Melanonotus and Ocellatus groups to be effective swimmers when in the water. The fringes adhere to the sides of the toes when the frogs are out of water, and do not impede terrestrial locomotion as a membranous web might.

In the Melanonotus, Ocellatus, and Pentadactylus groups in which member species deposit the foam nest in an exposed situation, the eggs have melanophores apparently in order to act as a shield to ultraviolet light. Egg melanophores are absent in members of the Fuscus and Marmoratus groups.

A trend of decreasing numbers of eggs together with an increase of individual egg diameter correlated with terrestriality is evident. Members of the Melanonotus and Ocellatus groups lay from 1000–2000 eggs of 1.0–1.5 mm diameter per nest. (No Pentadactylus group nests were available for analysis.) Members of the Fuscus group lay from 50–850 eggs of 1.6–2.5 mm diameter per nest. Members of the Marmoratus group lay from 4–25 eggs of 2.1–3.0 mm diameter per nest.

Larvae of members of the Fuscus, Melanonotus, Ocellatus, and Pentadactylus groups are all quite generalized, having a 2/3 tooth row formula, and a sinistral spiracle. The terrestrial larvae of the Marmoratus group lack tooth row denticles and a spiracle.

Large egg size, reduction of larval tooth rows, and absence of a spiracle do not necessarily indicate that a frog larva is terrestrial, or *vice versa*. *Kalophrynus pleurostigma*, a microhylid, has large eggs (diameter at mid-gastrulation, including envelope, 5 mm), has a spiracle (microhylid larvae lack tooth denticles), and depends solely upon yolk stores for nourishment until metamorphosis (Inger, 1956). The larvae are aquatic, however, inhabiting small water filled depressions in the forest (Inger, 1956). *Pelophryne brevipes*, a bufonid, has large yolked eggs (egg size not available for *P. brevipes*, diameter 2.0–2.5 mm in *P. albotaeniata* and *P. lighti*), a reduction of tooth rows, no spiracle, and probably does not feed; yet the larva is aquatic, inhabiting very small water-filled depressions, such as broken bottles in the forest (Inger, 1960). Members of the Australian leptodactylid genus *Kyarranus* which have terrestrial larvae have large yolked eggs (diameter 3.2 mm at gastrulation), no tooth denticles, but do have a spiracle (Moore, 1961). *Zachaenus parvulus*, a South American leptodactylid with terrestrial larvae, has a large egg (6 mm including jelly envelope), tooth denticles present (but the total number is reduced in comparison with an aquatic, feeding tadpole), and no spiracle (Lutz, 1943). Reduction of tooth row denticles in a larva with large yolk stores is doubtless a result of the larva not having to utilize its mouthparts for feeding. The loss of a spiracle may be imposed by the physical problems associated with large yolk stores. Large egg size appears to be the important determinant in allowing any shift towards terrestriality in anuran larvae; tooth row reduction and loss of the spiracle may or may not follow as a consequence of increasing the yolk stores.

A change apparently correlated with a fossorial life is a strengthening of the bones of the nasal region. Members of both the Fuscus and Marmoratus groups have a more rigid bony structure of the anterior region of the head than do members of the other species groups. The snout may actually be used in the construction of the incubating chamber, but this has not been observed. In the Fuscus group, the snout is strengthened by a calcification of the anterior sphenethmoid region, and in the Marmoratus group the snout is strengthened by an enlargement of the nasal bones (nasal 10.6% of the skull area in a 26 mm specimen of *L. marmoratus*, only 8.6% in a 32 mm specimen of *L. latinasus*, the next smallest species of *Leptodactylus* examined).

The family Leptodactylidae includes members showing every stage in a continuum from an aquatic to a terrestrial life history. Several of the intermediate forms have foam nests. The routes to terrestriality in the family may have been as shown within the genus *Leptodactylus*, through evolution of a foam nest.

The genus *Leptodactylus* provides an example of an almost complete transition from the aquatic to the terrestrial adaptive zones. Its example lends support to the adaptive zone concept, particularly with respect to four aspects of the transition zone: (1) Each of the individual steps along the transition is small; (2) Each species in the transition zone is adapted to its environment; (3) Each of the species groups has certain characters which serve as adaptations in themselves. These same characters probably served as the base for further adaptation, allowing a more terrestrial life. The most striking example is the placement of the foam nest; and (4) The most notable features of the shift pertain to the ecologies of the species groups.

The *Leptodactylus* example clarifies certain details of the adaptive zone concept which might have not been predicted from the fossil record alone. The group undergoing transition between two major adaptive zones has usually been thought of as a small-sized group. Usually, however, it is fossil genera that are given as examples for groups going through the transition. The *Leptodactylus* example emphasizes that a small group, below the generic level, may pass through the transition between two major adaptive zones. More importantly, however, the *Leptodactylus* example indicates that the transition zone may be stable. Simpson's model indicates that a transition zone exists for a short period of time only. The argument for a short lived transition zone is that once a transition zone has been passed through, it should never reopen. Members of the genus *Leptodactylus* have re-entered a transition zone, and are presently exploiting a transition zone. Goin (1960) indicated that there are numerous amphibian life histories intermediate between a completely aquatic and a completely terrestrial life cycle. Amphibians, the first vertebrate group to enter the transition between the aquatic and the terrestrial adaptive zones, still occupy the transition zone. The stable transition zone for Amphibia suggests that selection for a terrestrial way of life has continued intensely throughout geologic history.

Summary

Five species groups within the frog genus *Leptodactylus* are recognized; the advanced Fuscus and Marmoratus groups, the primitive Melanonotus and Ocellatus groups, and the intermediate Pentadactylus group.

The species groups form a series of stages bridging the transition between the major aquatic and terrestrial habitats. The example of evolution in *Leptodactylus* emphasizes that: (1) the adaptive transition from water to land occurs by microevolutionary means, (2) the forms in the transition have certain characters that likely served as preadaptations in the ancestral stocks of the more terrestrial species, and (3) the transition between major habitats is closely associated with the reproductive biology and behavior of the forms in the transition zone. The *Leptodactylus* example demonstrates that selection pressures have continually operated on anurans to move towards terrestriality, resulting in multiple entries into the terrestrial adaptive zone.

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