

Papéis Avulsos de Zoologia

DIVERGENCE RATE IN SOUTH AMERICAN LIZARDS OF THE GENUS *LIOLAEMUS* (SAURIA, IGUANIDAE)

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ABSTRACT

Liolaemus lutzae and *occipitalis* are allopatric, closely related species, both restricted to sand dune and sand bar environments. Geomorphic data permit dating the spread of the ancestral population and the isolation of peripheral populations at some time between 3,700 and 2,500 B.P.

A handicap in the study of the evolution of complex biotas in the tropics is the lack of data on rates of differentiation. The iguanid lizard, *Liolaemus lutzae*, has a very restricted distribution, disjunct from the remainder of the genus, and strict ecological preferences, which permit an attempt at an interpretation of its history.

The genus *Liolaemus* is large (about 70 forms) and complex. Its distribution is typically Andino-Patagonian, comprising (i) the mountains, plateaus and coast of western South America south of Ecuador, (ii) all of Patagonia, (iii) Argentina north of Patagonia, coastal Uruguay and Rio Grande do Sul in Brasil and (iv) the disjunct range of *L. lutzae*.

Liolaemus lutzae Mertens, 1938, is known from a few localities on the coast of the Brazilian states of Rio de Janeiro and Guanabara, being especially abundant on the long sand bar (restinga) of Marambaia and in the dunes of Cabo Frio, some 180 km further east. It is found only in a narrow strip of sand at most some tens of meters wide, next to the sea (Dansereau, 1947).

Closest to *lutzae*, taxonomically, ecologically (Gliesch, 1923) and geographically is *L. occipitalis* Boulenger, 1885, which occurs in the sandy littoral regions of Uruguay and Rio Grande do Sul, Brasil, the northern limit as presently known being Torres, about 1,000 km along the coast line from the nearest *lutzae* locality. In the intervening regions there are at least two areas which would seem ecologically favorable to either species, one in southern Santa Catarina and the other in southern S. Paulo. No specimens

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are known from those areas; on the other hand, there has been no oriented search for them.

L. occipitalis and *lutzae* are very close, but there are several very obvious differences:

1. The head scales of *occipitalis* are small, swollen; those of *lutzae* are larger, flat, more regular. The former has 8-9 scales between the upper canthals, and the latter only 4-5. The enlarged supraorbitals of *lutzae* are separated from the superciliaries by only one row of small scales, while there are two rows in *occipitalis*. Mertens (1938) refers to the presence of a frontal in *lutzae*, but this is not constant.
2. The keels on the dorsal scales of *occipitalis* are blunt, somewhat irregular; those of *lutzae* are sharp and regular.
3. The mid-dorsal region of *lutzae* is always brown, as dark as or only a little lighter than the unbroken para-vertebral dark bands; in *occipitalis* the vertebral region is light gray, and the para-vertebral bands almost always interrupted.
4. The throat of *lutzae* is immaculate; that of *occipitalis* shows numerous distinct dark spots.
5. *L. occipitalis* is a larger form, specimens 65 mm long (snout to vent) being common; *lutzae* hardly reaches 50 mm.

These differences are quite at the level usual for what are considered "good" species in *Liolaemus* and other iguanid genera. Given the distribution of the two species, it is reasonable to accept the hypothesis that they are offshoots of a single ancestral species, formerly widespread, whose range has been broken up by disappearance in the intervening region of the suitable ecology. Since both species are narrowly restricted to sand dunes and sand bars, their evolution must be closely linked to the history of land forms in the coast of southern Brasil.

Bigarella (1965) presents a good summary of the evolution of the coast in the area of interest, correlating changes of absolute and relative sea level with local climate and geomorphic events in general, and providing several C14 datings.

From his fig. 1 it is easy to see that optimal conditions for the existence of a continuous coastal belt of sand bars and dunes obtained during a dry phase which followed the Cananéia submergence, whose earlier half is synchronous with Fairbridge's (1961, 1962) Younger Perón. This dry phase contained: (i) the Crane Key and Pelham Bay emergences of Fairbridge, separated by a short-lived minor ascension (not reaching the general mean) of the sea level, called by Bigarella (1965) "Ilha do Mel"; (ii) the deposition of the southern Brazilian stone-lines (Ab'Saber, 1962); (iii) a strong reactivation of a previous generation of dunes (Ab'Saber, 1965).

The beginning of this phase is dated by the Sambaqui (shell mound) do Macedo, for which Hurt (1964) gives ages varying between $3,513 \pm 56$ and $3,284 \pm 48$ years B. P. The end of the period is dated, also by Hurt, cited by Bigarella (1965), at $2,680 \pm 150$ years B. P.; this is the C₁₄ age for the hanging beach

of Saco da Tamburutaca (Paranaguá submergence of Bigarella).

We consider it most probable that the spread of *Liolaemus* happened during this Crane Key-Pelham Bay interval, and that its range was broken up by the Paranaguá submergence.

However the possibility must be faced that the migration route of *Liolaemus* was the previous generation of dunes cited above (Ab'Saber, 1965). This would imply that during the later episode there may have been contact, but that the species were already too differentiated to mix, that neither was able to gain a foothold in the other's territory, and that no traces of these events remain in the present distribution.

The dating of the older generation of dunes is still uncertain. Some (Tricart, Vogt & Gomes, 1960; Pimienta, 1958) would place it into the Flandrian, 8 to 10,000 years ago. This would imply into epeirogenetic phenomena to explain the raised position of the relevant wavebuilt terraces, which are 3 to 4 m higher than Fairbridge's Older Perón. Those (Delaney, 1963) who do not believe in epeirogenetic movements would place these dunes in Tyrrhenian times, 25 to 60,000 years ago. Bigarella (1965) tentatively refers them to the Older Perón, 5,000 to 5,500 B. P.

Even if we accept the oldest, and, to us, less probable date, the rate of divergence observed is still very fast. This indicates that no interpretation of present patterns of differentiation should be undertaken without close attention being paid to the very drastic and rapid late Quaternary changes of climate and to their influence on local topography and ecology.

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