NUMBER 298
MAY 22, 1978

REPRODUCTION IN *MACROGENIOGLOTTUS ALIPIOI* CARVALHO (ANURA, LEPTODACTYLIDAE)

By J. PAUL ABRAVAYA AND JAMES F. JACKSON

NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

CONTRIBUTIONS IN SCIENCE

Published by the NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY
900 Exposition Boulevard, Los Angeles, California 90007

SERIAL PUBLICATIONS OF THE NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY

Prior to November 30, 1973, publications of the Natural History Museum have appeared under various formats—*Leaflet Series, Museum Graphic, Science Series, Study Guides, Contributions in Science, Contributions in History, Science Bulletins,* unnumbered catalogs of exhibitions, and other miscellaneous publications. The Museum now publishes the following serials at irregular intervals as CONTRIBUTIONS IN SCIENCE, HISTORY BULLETINS, SCIENCE BULLETINS, EDUCATION SERIES, HISTORY SERIES, and SCIENCE SERIES. The Contributions are short papers of octavo size. The Bulletins are longer, comprehensive papers of quarto size. The Series are papers of variable lengths of quarto or larger size. Papers in each serial are numbered separately and consecutively.

CONTRIBUTIONS IN SCIENCE contain articles in the earth and life sciences, presenting results of original research. Emphasis is intended principally for papers allied to biosystematic research, but other subjects and review-oriented ones will be considered. Number 1 was issued on January 23, 1957. Contributions must be not less than 8 nor exceed 72 printed pages.

INSTRUCTIONS FOR AUTHORS

Acceptance of manuscripts will be determined by the significance of new information. Priority will be given to manuscripts by staff members. All manuscripts must be recommended by the curator in charge of each discipline or by the Editorial Board. *Manuscripts must conform to the specifications listed below.* They will be examined for suitability by the Editorial Board and will include review by specialists outside the Museum.

Authors must adhere to the International Code of Nomenclature of Bacteria and Viruses, International Code of Botanical Nomenclature, and International Code of Zoological Nomenclature, including their respective recommendations. Further, authors proposing new taxa in a CONTRIBUTIONS IN SCIENCE must indicate that all primary types have been deposited in an appropriate scientific institution of their choice and must cite that institution by name.

MANUSCRIPT FORM.—(1) In preparation of copy follow the 1972 CBE Style Manual, third edition (AIBS), Chapters 5 and 6. (2) Footnotes should be avoided; acknowledgments as footnotes will not be accepted. (3) An informative abstract must be included for all papers. (4) A Spanish summary is required for all manuscripts dealing with Latin American subjects. Summaries in other languages are not required but are strongly recommended. (5) A differential diagnosis must accompany any newly proposed taxon. (6) Submit two copies of manuscript.

ILLUSTRATIONS.—All illustrations, including maps and photographs, will be referred to as figures. All illustrations should be of sufficient clarity and in proper proportions for reduction to CONTRIBUTIONS page size. In preparing illustrations and legends consult the 1972 CBE Style Manual, third edition (AIBS), Chapter 5. Submit only illustrations made with permanent ink and glossy photographic prints of good contrast. Submit duplicate copies of all illustrations. Original illustrations will be returned after the manuscript has been published.

PROOF.—Authors will be sent galley proofs which should be corrected and returned promptly. No changes or alterations, other than typesetting corrections, will be allowed unless paid by author. Requests for reprints may be placed through the Editor.

R. Edward Ostermeyer
Editor

All communications concerning manuscripts and exchange of or purchase of publications should be sent to the Editor, Museum Publications, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007.

Printed in the United States of America by Chapman's Phototypesetting on 70# Patina Book

REPRODUCTION IN *MACROGENIOGLOTTUS ALIPIOI* CARVALHO (ANURA, LEPTODACTYLIDAE)[1]

By J. PAUL ABRAVAYA[2] AND JAMES F. JACKSON[3]

ABSTRACT: Mating behavior, mating call, and larval morphology are described for the leptodactylid frog *Macrogenioglottus alipioi* Carvalho. The mating behavior is conducted in a way that would be advantageous in a species in which the number of eggs oviposited per female is great but the number of ovipositing females per pond is small. Feeding behavior is modified for the capture of slow moving prey such as snails and earthworms. The sonogram of the mating call of *M. alipioi* is similar to that of *Odontophrynus americanus*. The tadpoles of *Macrogenioglottus* are similar to those of *Odontophrynus*, having the same tooth row formula and similar arrangement of labial papillae. They differ, however, in the position of the spiracle and the vent. A review of the taxonomic history of *M. alipioi* combined with new data suggests a close relationship between *Macrogenioglottus* and *Odontophrynus*.

INTRODUCTION

Although *Macrogenioglottus alipioi* Carvalho was described 30 years ago (Carvalho 1946) and has been considered of no small interest to anuran phylogeny (Reig 1972; Duellman 1975), little on its biology has been published. We report our observations on reproduction of the species made in 1974 at the Reserva Biologica Nova Lombardia, Município de Santa Teresa, Espírito Santo, Brazil. The vegetation of the area was classified as Subtropical Lower Montane Moist Forest by the Holdridge (1967) system. Because of the extremely dissected topography, the only lentic water (other than that in tank bromeliads) is found in oxbow ponds along the valley streams. These ponds are empty much of the year and receive significant amounts of water only when their progenitory streams overflow after heavy rains characteristic of the wet season. Choruses of *Macrogenioglottus alipioi* were heard only after extremely heavy rains which resulted in such flooding.

Our observations were made at an oxbow pond 30 by 6 m and less than a meter deep. The water was stained by tannic acids and on the pond bottom was a deep layer of organic mud and decaying plant material. The elevation of the pond is 810 m.

The pond was visited several times a month between June 1973 and November 1974. No reproductive activity was noted on rainless days or nights, but activity was

---

[1]REVIEW COMMITTEE FOR THIS CONTRIBUTION
ROBERT L. BEZY
W. RONALD HEYER
ROY W. MC DIARMID
JOHN W. WRIGHT

[2]Research Associate in Mammalogy, Natural History Museum of Los Angeles County, and Department of Biology, California State University, Northridge, California 91234.
[3]Department of Biology, University of Southwestern Louisiana, Lafayette, Louisiana 70504.

noted on the two visits we made during nights of substantial rain, and during one day after a heavy rain.

Specimens of adult *Macrogenioglottus alipioi* were deposited in the Museu de Biologia "Prof. Mello Leitão," Santa Teresa, Brazil. Eighteen tadpoles were deposited in the Natural History Museum of Los Angeles County (LACM 121739).

REPRODUCTIVE BEHAVIOR

On the night of 4 January 1974 a chorus of 6 male *M. alipioi* was heard. All males were stationed on the bank within a meter of the water. No females were found at the pond, but a female was watched for an hour as she walked several hundred meters along a dirt road toward the chorus. When she reached the point on the road nearest the pond, she turned uphill and proceeded in the opposite direction from the pond.

On 10 February 1974 observations were made at the pond from 19:30 until 01:30 (local time) of the next day. Three calling males were stationed on the bank at the water's edge. One male once moved into the pond and called while standing in water 2-3 cm deep. An amplexed pair was located in the pond at 20:30. Amplexus is axillary, the male's forelegs clasped around the female one-third to one-fourth the distance between her fore- and hindlegs, and his forefeet placed in her axillae. Initially the pair floated quietly and moved only every five minutes; later they moved once or more each minute. The female initiated changes of location by swimming or walking one to several meters dragging the male behind. When they reached a new site, oviposition usually occurred. When she stopped, the male flexed his forelegs and pulled himself forward on top of the female. While in this position, he flexed his hindlegs and brought his hindfeet together at the female's vent. The hindfeet were then pushed directly backward in a single stroke that started slowly and then accelerated, as if the male were conducting eggs or sperm posteriorly. During or after this movement, the male slid backwards off the female. Then the male kicked several times rapidly; these kicks were sometimes between the female's hindlegs but usually lateral to them. Whether the male is distributing sperm over the eggs or whether he is distributing the eggs through the water, or both, was impossible to determine. The number of eggs oviposited at each site was not determined but probably is small, perhaps less than 20. Eggs were laid in short strands and small clusters, 2-eggs thick. They adhered to vegetable debris and did not float. The amplexed pair was collected at 23:30 and laid fertilized eggs in the plastic collecting bag. A second female that presumably had not oviposited was found walking toward the pond. She was collected and found to contain approximately 3650 eggs.

Although we have no data on tadpole vagility or survivorship, for heuristic purposes we hypothesize three possible adaptive functions of the multiple oviposition. The frequent changes of oviposition sites and the deposition of eggs in small batches could function to reduce the probability that all the eggs would be lost due to predation or desiccation. Spreading the tadpoles around the pond could possibly also function to minimize competition between siblings. Such a function would be advantageous in a species where the number of eggs oviposited per female is great but the

number of ovipositing females per pond is small, as it appears to be in *M. alipioi* judging from our observations and the fact that the type specimens were a single pair collected in amplexus (Carvalho 1946). In a species with numerous amplexing pairs per pond, there would be little advantage to such egg dispersal because tadpoles produced by other pairs would be hatching throughout the pond.

MATING CALL

The call of *M. alipioi* sounds most like a fog horn. Figure 1 illustrates the sonogram of calls recorded on a Uher model 4000 at an ambient temperature of 17°-20°C on 10 February. The call is a series of pulsed notes, each note lasting 0.24-0.27 seconds. The number of notes in the call varies from one to several dozen. When repeated, the notes are separated by intervals of 0.54-0.58 seconds. Maximum sound energy of the moderately well-tuned note is spread over the frequency range 230-800 hz. In the frequency range 800-1180 hz exists a component of weaker intensity with a pulse rate of 195-230 pulses per second. The beginning and end of the note on the sonogram are slightly less dark than the middle, indicating weak intensity modulation. The low frequency-low intensity "echo" that appears between notes on the sonogram (Fig. 1) probably originated from another individual in the chorus. The males alternate their calls to form duets and triplets.

NATURAL HISTORY

Fertilized eggs with their gelatinous envelopes averaged 2.2 mm in diameter. The tadpoles hatched 48–70 hours after fertilization. In the laboratory, tadpoles grew even when the only nutrient provided was organic muck from a pond bottom. They refused to eat meat but readily accepted fruit of avocado and papaya. The tadpoles stayed near the bottom of the aquarium and did not swim much. This inactivity may serve a protective function, since the pond had a high density of predaceous *Ceratophrys* tadpoles. Three tadpoles transformed at ages of 86, 95, and 127 days. This rate of development is consistent with apparent ecological necessities, since the oxbow ponds are nearly dry by May. The snout-vent lengths of the transformed frogs were 19.9, 19.8, and 21.0 mm.

Stomachs of 5 adult *M. alipioi* were examined. Two were empty; one contained 2 earthworms; one contained a small snail shell; and one contained the central spiral of a snail shell and part of an earthworm. An adult maintained in the laboratory ate snails and earthworms, appearing to prefer the former. It attempted to eat roaches but was not often successful in picking them up. When a *M. alipioi* recognized a potential food item, presumably by its movement, it would walk close, open its mouth, and pick up the item through a slow extrusion of the tongue. Neither the very deliberate feeding movements nor the dentition and lingual morphology of *M. alipioi* appear adapted for capturing fast-moving prey. Consequently, we believe that our sample of stomach contents, although limited, accurately reflects the dietary habits of the species.

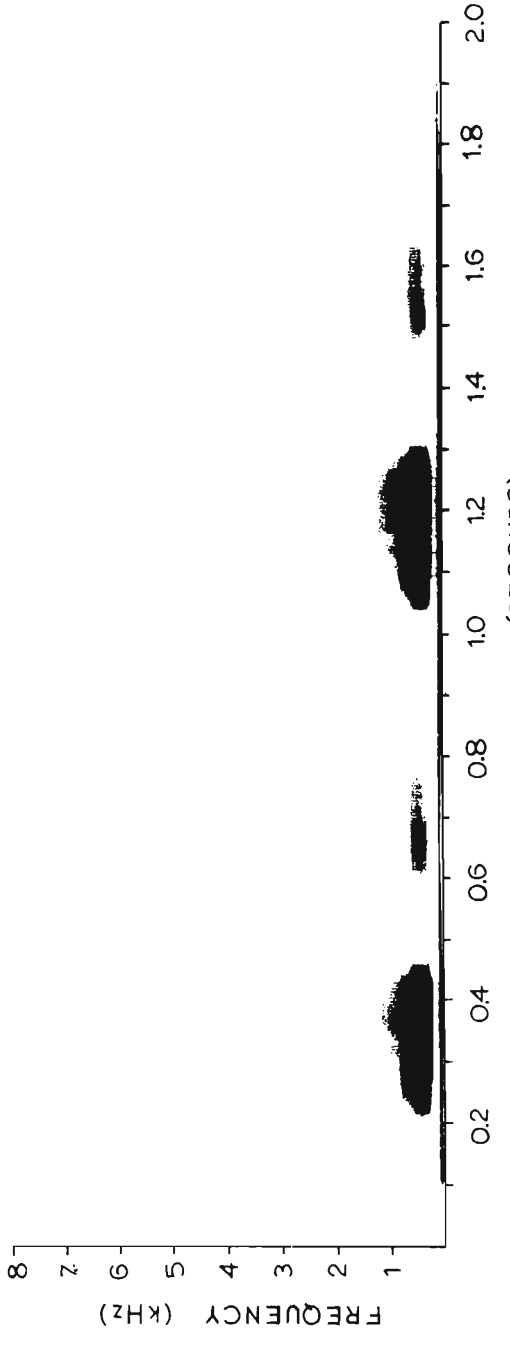

FIGURE 1. Sonogram of mating call of *Macrogenioglottus alipioi* Carvalho. 10 February 1974; Santa Teresa, Espírito, Santo, Brazil; ambient temperature 17–20 C.

DESCRIPTION OF TADPOLE

The tadpole of *M. alipioi* is illustrated in figure 2. The tadpole is characterized as follows (terminology of Altig 1970): sinistral spiracle; dextral anus; complex mouthparts; labial papillae well developed laterally and complete along posterior labium, absent on median portion of anterior labium; labia strongly emarginate laterally; tooth rows 2/3; second anterior tooth row with a broad A-2 gap; first posterior tooth row with narrow P-1 gap; denticles fine and short; upper jaw narrow and smooth; lower jaw narrow and toothed laterally; eyes and nostrils dorsal, eyes directed dorsally; body elliptical in dorsal view; somewhat depressed dorso-ventrally, greatest depth .35-.43 of standard length; dorsal and lateral surface of body brownish-grey, reticulated with non-pigmented areas; venter transparent; tail musculature pigmented with a series of dark grey spots or bars along dorsal portion and with irregular dark grey reticulation on ventral portion; margins of tail fin spotted irregularly with dark grey; standard length 12-18 mm; tail relatively short, 1.24-1.40 of standard length. The tadpole in Figure 2 is at stage 30 (Gosner 1960); standard length 13.9 mm, tail 21.5 mm, body width 9.8 mm. Tadpoles at stage 25 show considerable variation in growth; four specimens examined ranged from 4.5 mm to 11.5 mm in standard length.

EVOLUTIONARY RELATIONSHIPS

In the description of *Macrogenioglottus*, Carvalho (1946) assigned the genus to the Ceratophryidae (=Ceratophrydidae) and considered *Odontophrynus* its closest relative. Since then the relationship of *Macrogenioglottus* to *Odontophrynus* has been a subject of considerable disagreement. Lynch (1971) synonymized *Macrogenioglottus* with *Odontophrynus* in the leptodactylid subfamily Telmatobiinae which was separated from the subfamily Ceratophryinae. From the appendix of his paper one would assume that this synonymy was made without examination of specimens of *Macrogenioglottus*. This presumably is the reason that some of the characters in his diagnostic definition of *Odontophrynus* (sensu lato) actually exclude *Macrogenioglottus*. For example, *Macrogenioglottus* is considerably larger (Carvalho 1946) and falls outside Lynch's size range for *Odontophrynus*, and the inner metatarsal tubercle of *Macrogenioglottus*, though enlarged, is not spade-like. Reig (1972) on the other hand made a detailed anatomical comparison of *Macrogenioglottus*, *Odontophrynus*, *Ceratophrys*, and *Bufo*. He concluded that similarities between *Macrogenioglottus* and *Odontophrynus* are convergent and that *Macrogenioglottus* resembles a hypothetical taxon representing the ancestral bufonoid stock. He proposed elevating *Macrogenioglottus* to familial rank placing it together with the Bufonidae, Atelopodidae and Ceratophrynidae in the superfamily Bufonoidea, retaining *Odontophrynus* in the Leptodactyloidea.

Martin (1972) used evidence from laryngeal anatomy and function, and from karyotypes (Bogart 1967) to suggest that *Odontophrynus*, as well as *Macrogenioglottus*, are close to the base of the bufonid-*Atelopus* radiation. He felt that anatomical evidence (Reig 1972) actually supported this conclusion and that Reig's suggestion of convergence between *Macrogenioglottus* and *Odontophrynus* was untenable.

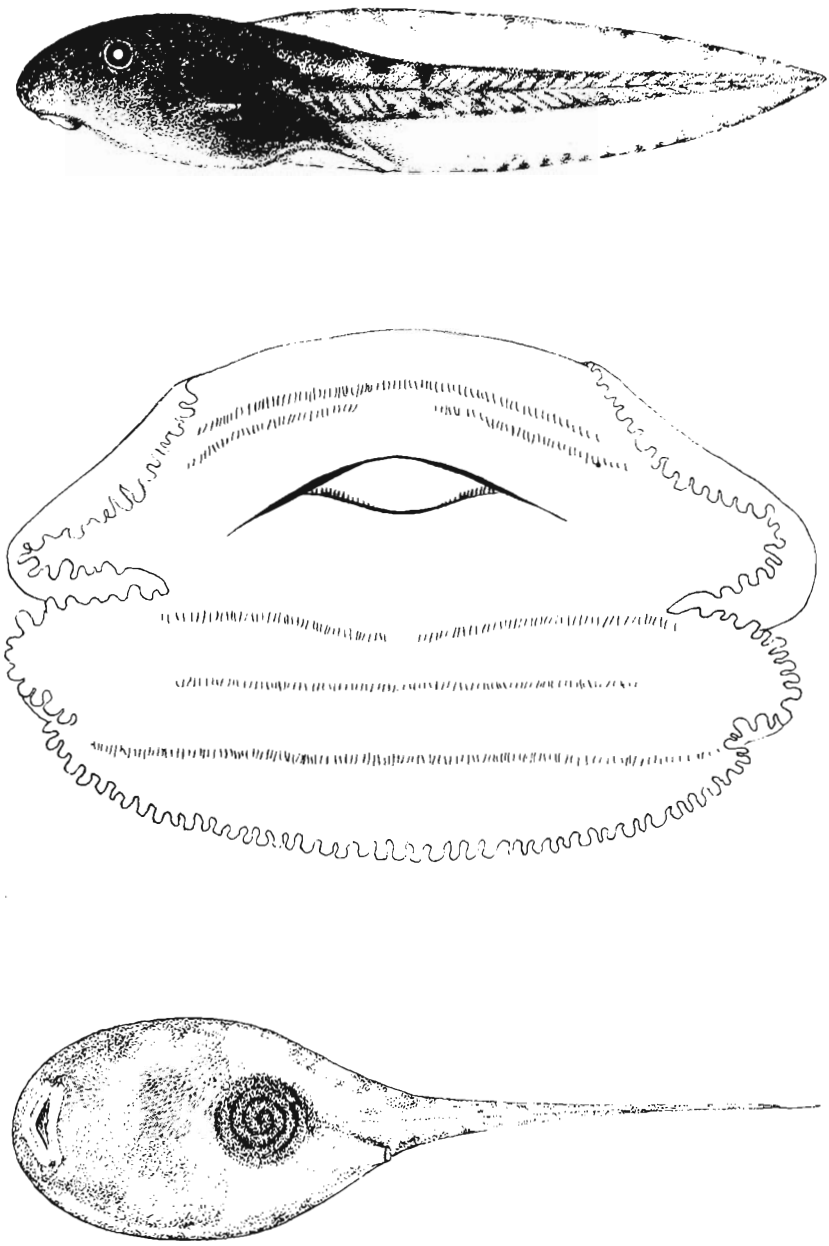

FIGURE 2. Stage 30 larva of *Macrogenioglottus alipioi* Carvalho (LACM 121739).

Heyer (1975) did not examine specimens of *Macrogenioglottus* but using the data provided by Reig (1972) suggested that within the New World Leptodactylidae *Macrogenioglottus* has affinities with *Ceratophrys, Lepidobatrachus, Odontophrynus* and *Proceratophrys*. He did not consider *Macrogenioglottus* and *Odontophrynus* to be congeneric.

The tadpole of *Macrogenioglottus* is quite similar to those of *Odontophrynus* examined by us and described by Savage and Cei (1965). It has the same tooth row formula, a similar arrangement of labial papillae and the labia are emarginate as in *O. occidentalis* and *O. americanus*.

It differs principally by having a shorter tail (1.24-1.40 standard length in *Macrogenioglottus* versus 1.30-2.15 in *Odontophrynus*) and finer denticles. Viewed laterally, the spiracle opening of *Macrogenioglottus* is clearly at a level dorsal to the mouth, whereas in *Odontophrynus* the spiracle opening is at the same level as the mouth. There appears to be confusion regarding the position of the vent in *Odontophrynus*. Savage and Cei (1965) stated that it is median. Lynch (1971:26) called the vent dextral for the genus *Odontophrynus* but gave a median vent as a character diagnostic for the tribe Odontophrynini (Lynch 1971:131). After examining tadpoles of *Odontophrynus americanus* (LACM 28060), *O. cultripes* (LACM 28059), and *O. occidentalis* (LACM 28068), we consider all to be weakly dextral. Regardless of whether the vent of *Odontophrynus* is considered median or dextral, it is clearly less extremely dextral than the vent of *Macrogenioglottus*.

The mating calls of *Odontophrynus americanus* and *O. occidentalis* have been described by Barrio (1964). These calls have similarities to that of *Macrogenioglottus* in consisting of several unmodulated notes repeated at regular intervals and in having a dominant frequency between 400-1200 hz. The call of *O. occidentalis* is least similar since it has a very short interval between the notes (about .04 seconds) and is thus a trill. The inter-note interval of *O. americanus* (about 0.4 seconds) is closer to that of *Macrogenioglottus*. Both *Odontophrynus* species differ from *Macrogenioglottus* in producing calls with complex harmonics. Of the two, *O. americanus* is again the closer to *Macrogenioglottus* by having a less accentuated harmonic structure, suggesting that the pulse rate is similar to that of *Macrogenioglottus*.

In summary, we feel that the weight of taxonomic evidence indicates a close relationship between *Macrogenioglottus* and *Odontophrynus* and that new evidence from larval morphology and mating call support this conclusion. However, to include *Macrogenioglottus* in the genus *Odontophrynus*, as presently known, would seem to violate the homogeneity traditionally expected of a genus of four or five species.

ACKNOWLEDGMENTS

We are grateful to Dr. Jacques Vielliard, Laboratoire de Zoologie, École Normale Supérieure, Paris, for recording the mating call and furnishing the sonogram. We thank Andrew Starrett, Anthony Gaudin, W. Ron Heyer and John Wright for useful criticisms of the paper. To Robert Bezy we owe special thanks for his critiques

and help in preparing the manuscript. Field work was supported by a grant from Instituto Brasileiro de Desenvolvimento Florestal to Museu de Biologia Mello-Leitão, Santa Teresa, Espírito Santo. We thank Augusto Ruschi for aid during our stay at Museu Mello-Leitão, Mary Butler for preparing drawings of tadpoles, Marianne Hata and Terri Togiai for typing the manuscript.

RESUMO

O comportamento nupcial, o grito nupcial e a morfologia larval são descritos para o anuro *Macrogenioglottus alipioi* Carvalho (Leptodactylidae). Na Reserva Nova Lombardia, Santa Teresa, Espírito Santo, Brazil, o cruzamento ocorre em pequenas lagoas formadas pelo transbordamento dos corregos durante a estação chuvosa. O numero de pares que cruzam em cada lagoinha é baixo. Amplexus é axilário. Cada fêmea põe mais do que tres mil ovos, mas esses são distribuidos pela lagoinha em pequenas porções em lugares distintos. O grito nupcial é baixo (frequência 230-800 hz tem força sonora máxima) e é repetido várias vezes. A duração do grito é de .24-.27 segundos e o intervalo entre os gritos é de .54-.58 segundos. O girino é semelhante ao girino de *Odontophrynus*, mas existem diferenças na localização do espiráculo e do anus. Observações no laboratório e o exame de conteúdos estomacais indicam que os adultos alimentam-se de caracois e minhocas. Tanto o grito nupcial como a morfologia do girino de *Macrogenioglottus* são semelhantes aos de *Odontophrynus*, mas diferenças na morfologia adulta exigem que se os mantenham em gêneros separados.

LITERATURE CITED

ALTIG, R. 1970. A key to the tadpoles of the continental United States and Canada. Herpetologica, 26:180–207.

BARRIO, A. 1964. Characteres eto-ecologicos diverenciales entre *Odontophrynus americanus* (Dumeril et Bibron) y *O. occidentalis* (Berg) (Anura, Leptodactylidae). Physis, 24:385–390.

BOGART, J. P. 1967. Chromosomes of the South American amphibian family Ceratophridae with a reconsideration of the taxonomic status of *Odontophrynus americanus*. Canadian Jour. Genet. Cytol., 9:531–542.

CARVALHO, A. L. DE. 1946. Um novo género de Ceratofridídeo do sudeste baiano. Bol. Museu Nac., N. S. Zool., Rio de Janeiro, 73:1–5.

DUELLMAN, W. E. 1975. On the classification of frogs. Occas. Papers Mus. Nat. Hist. Univ. Kansas, 42:1–14.

GOSNER, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica, 16:183–190.

HEYER, W. R. 1975. A preliminary analysis of the intergeneric relationships of the frog family Leptodactylidae. Smithsonian Contr. Zool., 199:1–55.

HOLDRIDGE, L. R. 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica.

LYNCH, J.D. 1971. Evolutionary relationships, osteology, and zoogeography of leptodactylid frogs. Misc. Publ. Mus. Nat. Hist. Univ. Kansas, 53:1–238.

MARTIN, W. F. 1972. Evolution of vocalization in the genus *Bufo*; pp. 279–309 *in* Evolution in the genus *Bufo* (W. F. Blair, ed.), Univ. of Texas Press, Austin and London, 460 pp.

REIG, O. A. 1972. *Macrogenioglottus* and the South American bufonid toads; pp. 14–36 *in* Evolution in the genus *Bufo* (W. F. Blair, ed.), Univ. of Texas Press, Austin and London, 460 pp.

SAVAGE, J. M. AND J. M. CEI. 1965. A review of the leptodactylid frog genus, *Odontophrynus*. Herpetologica, 21:178–195.

Accepted for publication February 18, 1977.