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CHECKLIST OF THE SAVANNA INHABITING FROGS OF THE EL MANTECO REGION WITH NOTES ON THEIR ECOLOGY AND THE DESCRIPTION OF A NEW SPECIES OF TREEFROG (HYLIDAE, ANURA)

by

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With 4 text-figures and 3 plates

Summary

Three years of fieldwork in the El Manteco region by the junior author formed the basis for the checklist presented here. Among the frogs assembled is a small species of *Ololygon*, new to science, also found in Guyana and Surinam. The anuran succession in the temporary lagoons, formed during the rainy season, was studied during three years and a consistent pattern was found. Comparisons with the llanos fauna are made and it is concluded that the El Manteco region contains a relatively large percentage of Amazonian elements, absent from the llanos.

Resumen

Las observaciones que hizo el segundo autor durante tres años en la region de El Manteco forman la base de la lista presentada aquí. Entre las ranas coleccionadas hay una pequeña especie de *Ololygon*, tambien coleccionada en Guyana y Surinam, nueva para la ciencia. La sucesión de los anuros en las lagunas temporales que se forman durante la estación húmeda, se estudió durante tres años y se encontró un esquema constante. Se comparó la anurofauna de la region de El Manteco con la de los llanos y se sacó la conclusion de que la anurofauna de la region de El Manteco contiene un porcentaje relativamente alto de elementos amazónicos que no están presentes en los llanos.

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INTRODUCTION

The town of El Manteco is located at 7°25′ N 62°21′ W, at an altitude of 305 m, just inside the Yuruari basin in southeastern Venezuela, Estado Bolívar. The Rio Yuruari is a tributary of the Cuyuni, which drains off towards the Rio Essequibo in Guyana to the east, and not towards the Orinoco as do all the other river systems of the Venezuelan part of the Guiana Shield. To the north and east of the town extends the Yuruari savanna. The distribution of the forest around the Yuruari basin is shown in fig. 1. Accepting the classification of Ewell, Madriz & Tosi (1976), the forest bordering the savanna is premontane deciduous forest ("bosque humedo premontano"), which grades into tropical rain forest ("bosque humedo

Fig. 1. Map of the Yuruari basin with the localities mentioned in the text and reference localities. The grey area represents forest, the white area savanna, the stippled area is the artificial Caroni lake. Watersheds have been indicated with heavy interrupted lines.

tropical") within about ten kilometers from the savanna edge. The forests around El Pao, to the north of Upata, and in the north of the Serrania de Imataca, have been extensively cut back and cultivated. The forests to the

east and the south are largely untouched. The Yuruari savanna thus covers a block of land between El Manteco, Upata, El Palmar and Guasipati. To the south-east a narrow extension of this savanna runs southwards from El Callao to about 40 km north of El Dorado. To the west there is a connection with the Caroni savanna. The Yuruari savanna is an open savanna, criss-crossed by numerous gallery forests which follow river courses and border lagoons. There is a distinct dry season from January to May. Figure 2 shows the mean monthly and annual rainfall for the period 1958-1972, figure 3 the mean weekly maximum and minimum temperatures from 1974 to 1976. During 1975 air temperatures in shaded gallery forest reached as high as 44° C. Between March 1974 and July 1977 collections of the anurans of this area were made by SJG. In late October/early November 1976 the area was visited by MSH. The joint collection has been deposited in the Rijksmuseum van Natuurlijke Historie (RMNH). The present paper restricts itself to the anurans of the Yuruari savanna and of some inselbergs to the south of El Manteco.

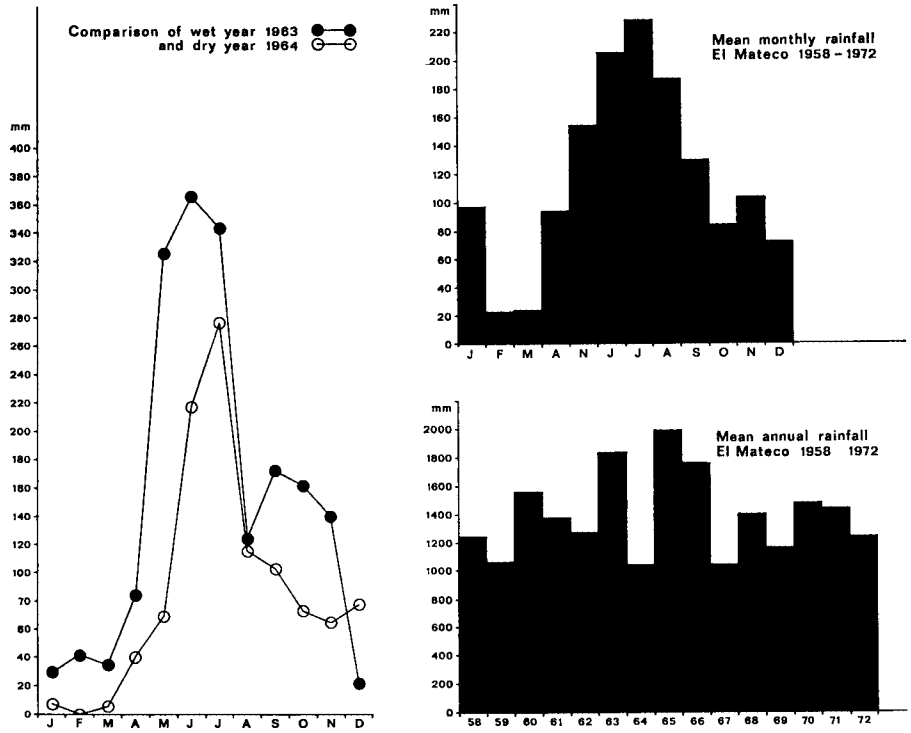

Fig. 2. Climatological data of El Manteco (Mateco: lapsus for Manteco).

History of investigation in the area

The anuran fauna of Venezuela has been studied now for nearly 125 years. A historical resumé has been published by Rivero (1961). A conspicuous omision in this resumé is the booklet of Gines (1959) which gives descriptions of all families and genera of anurans at that time known to occur in Venezuela. Most genera have been depicted quite adequately. Rivero (1961), after Lutz (1927), was the second author trying to present a complete picture of the Venezuelan frog fauna. Lutz's list mainly was based on literature records and on his own observations, both sets of data being based on collections made in the readily accessible coastal area. Rivero (1961) incorporated data on collections from the less accessible interior (Territorio Federal Amazonas and Estado Bolívar), the higher parts of which since the nineteen-twenties had received considerable attention from botanists, mammalogists and ornithologists. The anurans collected by several expeditions to some tepuis were dealt with in this paper. Rivero (1961) also included data on the poorly known frogs of the llanos. After his major work on the Venezuelan frogs, Rivero wrote a series of biogeographical papers (Rivero, 1963a, b, c; 1964a, b, c) in which he divided Venezuela into faunal regions (after Liddle, 1946) and considered the evidence presented by the frogs.

The region we are dealing with here is part of the "Venezuelan Guayana" area of Rivero (1964b), but also shows strong ties with the "Llanos" area (Rivero, 1964c). Frogs of Venezuelan Guiana have been dealt with by Rivero (1964b, 1966, 1967a, b; 1968a, b, c, d; 1970, 1971a, b, c) in a series of papers and by Hoogmoed (1979). In these papers there is much emphasis on the species inhabiting higher altitudes, as they evidently provide material for interesting zoogeographical arguments. Hardly any attention was paid to the frogs from the lower areas. Heatwole et al. (1965) reported on a collection of frogs which was obtained in two lowland localities in Venezuelan Guiana, one of which (Hacienda San Felipe) was lowland savanna, the other (km 38) being situated in damp tropical forest. Rivero (1971a) described a new hylid, the paratypes of which came from the area around the artificial lake in the Caroni River, south of Guri. Gorzula (1977b) dealt with the significance of foam-nesting in leptodactylids from the Yuruari basin.

Because of its situation just south of the Orinoco River and because of its vegetation, which apparently is a continuation of that of the llanos of Central Venezuela, it seems warranted to include here a short review of studies on llanos frogs as well. Again, credit should be given to Rivero (1964c) as having been the first to summarize data on frogs of the llanos region. Fouquette (1968) listed five frogs from two llanos localities. Among

the species mentioned by him was *Ololygon rubra* which previously had not been recorded from the llanos. Dixon & Staton (1976) reported on the biology of *Leptodactylus macrosternum*. Staton & Dixon (1977) summarized the available data from the literature and included their own field data, obtained during an 11 months stay in the llanos. They list 16 species of frogs as belonging to the llanos fauna.

Species accounts

Bufonidae

Bufo granulosus merianae Gallardo

Bufo granulosus granulosus, Rivero, 1961 : 23; Rivero, 1964b : 416.
Bufo granulosus merianae Gallardo, 1965 : 112.
Bufo granulosus, Gorzula, 1977a : 9, Gorzula, 1978 : 28.

Material. — El Manteco: 3 ♂♂, RMNH 18234-36, 3 km E., May 1974, 1 ex., RMNH 18237, May 1976, 2 ♂♂, RMNH 18243-44, 3 km E., 14-IV-1977, 1 ♀, RMNH 18245, 11-V-1977, 2 ♂♂, 2 ♀♀, RMNH 18246-49, 7-VI-1977, all leg. S. J. Gorzula; 1 ♂, RMNH 18250, 30-X-1976, 1 juv., RMNH 18251, 20 km S., 31-X-1976, both leg. M. S. Hoogmoed.

Habitat. — This species is an inhabitant of savannas and in forests only penetrates along roads, lumbertracks and other openings. It is absent from the real deep forest. In the savanna they make burrows, in which they hide during the day. They also may be found under wooden planks.

Natural history. — Specimens of this species were found in the stomach of the snake *Drymarchon corais corais* (Boie). During the breeding season the species is heavily preyed upon by *Caiman c. crocodilus* (L.) (Gorzula, 1977a, 1978). It is one of the first species to breed at the very beginning of the rainy season, and breeds mainly in variably sized temporary pools, though in smaller numbers it also occasionally may be found in permanent pools. Males call from the edge of the pools (pl. 2, fig. d). Later in the rainy season the aggregations tend to be composed mainly of males, females being definitely less frequently observed than in the early rainy season.

Discussion. — We identified the El Manteco specimens in our collection as belonging to the subspecies *merianae*, because they essentially agree with that subspecies in most characters. *B. g. beebei* Gallardo, the llanos subspecies (Cei, 1968) (erroneously reported as *B. g. granulosus* by Staton & Dixon (1977)), apparently does not reach the El Manteco area, probably because the savannas there are more or less isolated from the savannas on the right bank of the Orinoco River, which are in direct contact with the llanos. Therefore, we expect the Puerto Ordaz population of the species (not sampled) to belong to *beebei*.

Bufo guttatus guttatus Schneider

Bufo guttatus Schneider, 1799: 218.
Bufo guttatus guttatus, Rivero, 1961: 20; Rivero, 1964b: 416, 417.

Material. — El Manteco: 1 ♀, RMNH 18252, Hato Kamarapia,. 10 km E., 16-IX-1976, leg. S. J. Gorzula. Another specimen of this species was captured 200 m from the spot where 18252 was caught and was released again in 1974.

Habitat and natural history. — The only specimen in our collection was hiding in a drain on the premises of the ranch. As this species apparently is a forest-dweller (Hoogmoed field data in Surinam; Rivero, 1964b: 417) and the area around the ranch is pure savanna without any considerable gallery forest nearby, the presence of this species here is somewhat of an enigma to us. Its presence may be explained in two ways. It has either been accidentally introduced into the area and maintained itself, or it constitutes evidence of the retreat of the rainforest in the area in favour of the savanna. In the last case an isolated population of *B. g. guttatus* could have maintained itself in pockets of gallery forest. However, the mechanism causing this change of vegetation is not well understood, since in other comparable places it is known that at the present time the forest is gaining on the savanna (Teunissen & Wildschut, 1970). Of course man could have been instrumental in the disappearance of the forest in this area in favour of pastures for cattle and then the situation would be easier to understand.

Bufo marinus marinus (L.)

Rana marina Linnaeus, 1758: 211.
Bufo marinus marinus, Rivero, 1961: 25; Rivero, 1964b: 416; Heatwole, Solano & Heatwole, 1965: 352.

No material of this species was assembled for the collection, but it is undoubtedly one of the most abundant and widespread species in the area.

Habitat. — Very common in perianthropic environment (villages, ranches, in cesspits).

Natural history. — This species does not breed in all pools, but favours large, temporary ponds in the savanna. Breeding aggregations may be found anywhere between February and June, depending on the beginning of the rains. Breeding takes place exclusively during the first four weeks of heavy rains. Males call from the banks of pools, close to the water's edge.

Dendrobates leucomelas Steindachner

Dendrobates leucomelas Steindachner, 1864: 260; Rivero, 1961: 168; Rivero, 1964b: 416, 417; Heatwole, Solano & Heatwole, 1965: 350; Silverstone, 1975: 26; Paolillo, 1977: 36.

Material. — El Manteco: 1 ♀, RMNH 18253, 32 km S., 8-IV-1977, 1 ♂, RMNH 18254, 5 km E., 11-V-1977, 1 ♀, RMNH 18255, 10 km E., 30-V-1977, all leg. S. J. Gorzula; 1 ♀, RMNH 18256, 32 km S., 31-X-1976, leg. M. S. Hoogmoed.

Habitat. — This species is an inhabitant of gallery forest in savanna areas, of dry forest and of rainforest. It does not occur in the open savanna. Astonishingly it also occurs on top of the inselberg Piedra de los Lamentos, situated in rainforest 32 km south of El Manteco. The top of this inselberg is only sparsely covered with vegetation in the form of small scrubs (pl. 3, fig. e), but for the greater part it consists of bare granite, covered with boulders and flakes of granite. However, in a depression close by is a large, semi-permanent lagoon surrounded by a narrow strip of forest and bamboo thickets.

Natural history. — On two occasions (in April and November respectively) it was observed that *D. leucomelas* was rather common on top of the inselberg and active between 5.30 a.m. and 6.30 a.m. (around sunrise). Afterwards the animals disappeared from view. In daytime one specimen (RMNH 18256) was found hiding under a boulder, thus implying that in daytime the frogs hide under rocks and in crevices. In gallery forest the species is frequently seen during daytime, sometimes in pairs. In July a pair of adults was found in gallery forest at the base of a tree. About 30 cm up the tree forked and in this fork was a small rain-filled hollow containing a tadpole. Whether or not the tadpole belonged to this species could not be established. The female RMNH 18256, collected on October 31, 1976 contained small ovarian eggs. This probably means that reproduction is restricted to the wet season.

Notes on nomenclature. — Silverstone (1975) cites as author of the name *Dendrobates leucomelas* "Fitzinger in Steindachner" and says that it is "a Fitzinger label name first published by Steindachner as a synonym of *D. tinctorius* (Schneider)". This is correct, but the subsequent citation of authorship is not. Fitzinger did not participate in Steindachner's publication, neither did he himself ever publish the name with a valid description of the taxon. He only wrote it on some labels added to this taxon. Steindachner (1864) cited the name in the synonymy of *D. tinctorius*, but in the discussion provided a valid description. This case has further been ably discussed by Silverstone (1975). Thus, the only conclusion can be that Steindachner is the author of *D. leucomelas*.

Hylidae

Hyla crepitans Wied

Hyla crepitans Wied, 1824: pl. 51, fig. 1; Rivero, 1961: 103; Rivero, 1964b: 416; Heatwole, Solano & Heatwole, 1965: 353; Duelmann, 1977: 48.

Material. — El Manteco: 1 ♂, RMNH 18267, 2 km E., May 1974, 1 ♂, RMNH 18270, 3 km E., 27-VI-1974, 1 ♂, RMNH 18268, June 1974, 1 ♂, RMNH 18269, 30-IX-

1974, 1 ♀, RMNH 18275, 18-XI-1976, 1 ♀, RMNH 18280, 12 km SE., 21-IV-1977, 1 ♀, RMNH 18281, 28-III-1977, 1 ♂, 2 ♀♀, RMNH 18282-83, 18286, 4 km E., 11-V-1977, 1 ♂, RMNH 18284, 7-VI-1977, 1 ♀, RMNH 18285, 20 km S., 9-VIII-1976, all leg. S. J. Gorzula; 1 ♂, RMNH 18288, 12 km SE., 30-X-1976, leg. M. S. Hoogmoed.
El Plomo: 1 ♀, 3 ♂♂, RMNH 18276-79, 16-IV-1977, leg. S. J. Gorzula.

Habitat. — This species mainly inhabits savanna, but it may enter houses and also is present in gallery forest. It can be found near lagoons and rivers.

Natural history. — Examination of the material revealed the presence of females with small ovarian eggs in March, April and May (RMNH 18276, 18281, 18283), with small oviducal eggs in May (RMNH 18286) and with large oviducal eggs in August (RMNH 18285). The mature oviducal eggs have a brownish-black and a creamish pole. Only few data on calling are available. A male was found on October 30, 1976 calling from a shrub in a *Mauritia*-swamp, about 1 m above the ground. During the rainy season specimens were often found sitting on the banks of lagoons or rivers. From field experience in Surinam it is known that this species calls while sitting in the shallow water of pools with a sandy bottom. All males found in the El Manteco area had vocal slits, well developed vocal pouches and prepollical spines. These data indicate that breeding is restricted to the rainy season, the eggs probably starting to develop only well after the rains have started and reaching maturity in the mid rainy season, the period when *H. crepitans* is present at its breeding sites (see Anuran succession in temporary lagoons).

Hyla geographica Spix

Hyla geographica Spix, 1824: 39; Duellman, 1973: 526; Duellman, 1977: 60.
Hyla geographica geographica, Rivero, 1961: 101.

Material. — El Manteco: 5 ♂♂, RMNH 18261-65, 6 km E., 7-XI-1976, 1 ♀, RMNH 18266, 20 km S., 9-VIII-1976, all leg. S. J. Gorzula.

Habitat. — Gallery forest in savannas and clearings in rainforest.

Natural history. — In November 1976 males were calling in bushes over a riverside flood-pool at about 1.5 m above the surface of the water. A female with mature oviducal eggs (very dark, with a black and a dark-brown pole) was found in early August 1976 2 m above the ground in a tree at the edge of an artificial dam along a road in a clearing in rainforest. These scant data could mean that reproduction at least covers the mid rainy season and maybe lasts till the end of the rains.

Hyla microcephala misera Werner

Hyla misera Werner, 1903: 252; Rivero, 1961: 135; Heatwole, Solano & Heatwole, 1965: 353.
Hylo microcephala misera Fouquette, 1968: 324; Duellman, 1977: 73.

Material. — El Manteco: 1 ♀, 2 ♂♂, RMNH 18297-99, 2 km E., 24-VII-1974, 1 ♂, RMNH 18300, 2 km E., 8-VII-1974, all leg. S. J. Gorzula; 5 ♂♂, RMNH 18301-05, 3 km E., 31-X-1976, leg. M. S. Hoogmoed.

Habitat. — Marginal vegetation near permanent and temporary lagoons in open savanna.

Natural history. — Males start calling at the beginning of the mid rainy season and continue for the rest of the rainy season during wet nights and after rainy days. They generally call from bushes and trees along the margins of the pools, sitting on leaves 1-3 m above the ground. They often form mixed choruses with *Hyla minuscula* Rivero, but the latter species is always much more abundant. A female (RMNH 18298) with ovarian eggs in different stages of development, from small to nearly mature (a dark-brown and a white pole) and well developed oviducts was collected in July. The total number of eggs in one complement is about 400.

Remarks. — *Hyla microcephala misera* of Goin (1971) is nothing but *H. minuscula* Rivero (see below).

Hyla minuscula Rivero

Hyla minuscula Rivero, 1971a: 1; Duellman, 1977: 75.

Material. — El Manteco: 2 ♂♂, RMNH 18306-07, 5 km E., 7-XI-1976, 1 hgr., RMNH 18309, 24-XI-1976, 2 ♂♂, RMNH 18310-11, 1 km E., 8-VI-1977, all leg. S. J. Gorzula; 7 ♂♂, RMNH 18312-18, 14 km SE., 30-X-1976, 1 ♀, 3 ♂♂, RMNH 18219-22, 3 km E., 31-X-1976, all leg. M. S. Hoogmoed.

Habitat. — Low bushes and cyperaceous vegetation along edges of permanent and temporary lagoons in open savanna.

Natural history. — Males call on rainy nights from the beginning of the mid rainy season right to the end of the rains. They generally call from within 30-150 cm above the ground or the surface of the water. They may sit on leaves of bushes or straddle the vertical blades of the cyperaceous vegetation. An amplexing pair (RMNH 18219-22) was found in late October, the female having mature, oviducal eggs (with a black and a creamish pole). These data indicate that breeding lasts till the very end of the rainy season.

Remarks. — Goin (1971), in his paper on the Surinam treefrogs, lists *Hyla microcephala misera* Werner as being an inhabitant of this country. Now that fieldwork has been done, both in Surinam and in the Venezuelan part of Guiana by one of us (MSH), it has become clear that the taxon Goin (1971) named *H. microcephala misera* actually is conspecific with *H. minuscula* Rivero and that *H. microcephala misera* is absent from the eastern part of Guiana (Hoogmoed, 1979). Apparently *H. minuscula* is a member of the *H. nana* group, of which it represents the northernmost representative. It

even may turn out to be a subspecies of *H. nana* Boulenger. *H. minuscula* in Surinam apparently does not reach further east than Bigisanti, from where *H. nana* has been reported by Lescure (1977), who also stated that further west its place in the coastal swamps was taken by *H. minuscula* (which Lescure indicates as *H. microcephala misera*). From French Guiana only *H. nana* is known (Lescure, 1976) and according to this author the specimens are identical with those from Paraguay and Argentina. As no localities are known in Surinam where both taxa occur sympatrically, the hypothesis of *minuscula* being a subspecies of *nana* does not seem too far-fetched.

Hyla multifasciata Günther

Hyla multifasciata Günther, 1858: 101; Duellman, 1977: 78.
Hyla albopunctata multifasciata, Rivero, 1961: 105.

Material. — El Manteco: 1 ♂, RMNH 18290, 16 km SE., 2-VI-1976, 2 ♂♂, RMNH 18291-92, 5 km E., 10-XI-1976, 1 ♂, RMNH 18293, 4-IX-1976, 1 ♂, RMNH 18294, 4 km E., 14-IV-1977, all leg. S. J. Gorzula; 1 ♂, RMNH 18296, 12 km SE., 30-X-1976, leg. M. S. Hoogmoed.

Habitat. — Gallery forest and cyperaceous vegetation around permanent lagoons in open savanna.

Natural history. — Males were heard calling from the mid rainy season through to the end of the rainy season. They start calling at sunset, emitting their call with long intervals. During calling the males may sit on the ground, but mostly they are up in the vegetation to a maximum height of about 2 m. They straddle branches or sit in the forks of branches. No females were collected in the El Manteco region.

Remarks. — Although Rivero (1961) reports this species from Venezuelan Guiana and from the Coastal Range, for unknown reasons he omitted it in his paper dealing with Guiana (Rivero, 1964b), though again including it in his paper dealing with the Coastal Range (Rivero, 1964a).

Ololygon rubra (Laurenti)

Hyla rubra Laurenti, 1768: 5; Rivero, 1961: 120; Rivero, 1964b: 416; Heatwole, Solano & Heatwole, 1965: 353; Rivero, 1969a: 109; Duellman, 1977: 96.
Ololygon rubra, Fouquette & Delahoussaye, 1977: 392.

Material. — El Manteco: 2 hgr., RMNH 18324-25, 1 ♂, RMNH 18326, 4-IX-1976, 1 ♀, RMNH 18327, 2-VIII-1976, 2 ♀♀, 1 ex., RMNH 18328-30, 25-II-1977, 2 ♀♀, RMNH 18331-32, 8-IV-1977, 32 km S., 1 ♀, RMNH 18333, 7-VI-1977, all leg. S. J. Gorzula.

Habitat. — In the savanna only known from perianthropic environments (toilets, showers, etc.). On the Piedra de los Lamentos, a granite inselberg

isolated in rainforest 32 km S. of El Manteco, this species occurs in terrestrial bromelias.

Natural history. — No calling males were observed. Females with small oviducts are known from February and August, a female with small ovarian eggs from April, females with mature oviducal eggs from April and June. In the same batch of specimens both females with mature oviducal eggs and females with immature ovarian eggs (RMNH 18331-32) may be present, indicating that breeding lasts for an extensive period, probably throughout the rainy season.

Ololygon trilineata nov. spec. (pl. 1)

Holotype. — 1 ♀, RMNH 18257, 12 km SE. El Manteco, Estado Bolívar, Venezuela, 31-X-1976, leg. M. S. Hoogmoed & S. J. Gorzula.

Paratypes. — Venezuela. Estado Bolívar, El Manteco: 2 ♂♂, RMNH 18258-59, 12 km SE., leg. S. J. Gorzula.

Guyana, 1 ♂, AMNH 97949, 1937-1938, leg. R. Snedigar. Isheartun: 1 ♂, AMNH 43637, 5/15-XI-1973, leg. R. Snedigar. Rupununi River, near Moro, E. of Tirke: 1 hgr., AMNH 46248, 7-X-1937, leg. R. Snedigar. Parabam: 1 ♂, AMNH 97944, 12-IV-1938, 4 ♂♂, AMNH 97945-48, April 1938, all leg. R. Snedigar.

Surinam. Distr. Nickerie, Sipaliwini: 1 hgr., RMNH 18260, base of Vier Gebroeders Mountain, 24-IX-1968, leg. M. S. Hoogmoed.

Diagnosis. — A small (snout-vent length in males 19-22.5 mm, in the female 20 mm) species of the *squalirostris* species group, with pointed snout. Male without a prepollex. Prevomerine teeth in short, widely separated, transverse to slightly oblique (converging posteriorly) rows. Skin of dorsum shagreened to slightly pustulous, that of the belly coarsely granular. Tympanum small, round, 1/4-1/3 of the horizontal diameter of the eye, separated from the eye by a distance equal to or slightly larger than its diameter. A feeble supratympanic fold. Interorbital distance 1.1-1.8 times the width of an upper eyelid. Discs on fingers equal to or slightly larger than the tympanum. Webbing of hands very reduced, feet with moderately well developed webbing. When the hind limbs are folded and flexed at right angles to the sagittal plane of the body the heels show considerable overlap. Colour in preservative light brown to greyish brown with a pattern of dark brown longitudinal stripes: a narrow vertebral stripe, wider dorsolateral bands. Flanks either uniform dark brown or with a dark lateral band along the lower part. A dark brown canthal stripe. Ventral parts immaculate, white to pale brown.

Description. — Head distinctly longer than wide, as wide as the adjacent part of the body, flat, depth just over one third of the head length. Snout pointed in dorsal and lateral view, protruding distinctly over the mouth,

1.3-1.8 times as long as the horizontal diameter of the eye. Distance between eye and nostril equal to or slightly longer than the horizontal diameter of the eye, 2.0-2.5 times the distance between nostril and tip of snout. Canthus rostralis indistinct, rounded, straight; loreal region flat to slightly concave, sloping steeply to the lips. Lips not flaring. Nostrils hardly protuberant, situated just below the canthus rostralis, directed laterally and dorsally. Distance between the nostrils 0.7-0.9 times the interorbital width, equal to or slightly wider than the width of an upper eyelid, about 1.5 times the distance between nostril and tip of snout, area between the nostrils flat. Interorbital space slightly convex, 1.1-1.8 times as wide as an upper eyelid. Temporal region nearly vertical. Tympanum distinct, round to vertically oval, ½-¼ times the horizontal diameter of the eye; separated from the eye by a distance equal to or slightly longer than its diameter. A feeble, sharply curved supratympanic fold from the posterior corner of the eye to the insertion of the forelimb, obscuring the upper margin of the tympanum.

Choanae small, oval. Prevomerine processes small, bearing two short, transverse to slightly oblique rows of teeth, 2-5 (mostly 4) teeth per row; situated just anterior to the line connecting the posterior margins of the choanae. Tongue oval to cordiform, attached to the floor of the mouth, only its lateral and posterior margins free. Males with large subgular vocal sacs, opening into the mouth via short slits, one on each side of the tongue, from its midlateral base extending posteriorly, not close to the median edge of the mandible.

Pupil horizontally oval. Palpebral membrane not reticulated, with a narrow pigmented zone along its rim.

Skin of dorsum, top of head and legs shagreened to slightly pustulous, pustules widely separated. Upper eyelid with concentration of small pustules. Skin of throat in males thick, with longitudinal folds, in the female shagreened. Skin around corners of the mouth coarsely granular. Skin of belly and under thighs coarsely granular. Skin in groins and axils and under remainder of limbs smooth. No axillary membrane. Males and females without a mental gland.

Males without prepollex. Inner metacarpal tubercle distinct, oval. Outer metacarpal tubercle distinct, oval, as large as the inner one. Subarticular tubercles present, round, low, undivided. A row of supernumerary tubercles present under the basal part of each finger, that of the fourth finger starting laterally of the outer metacarpal tubercle. A feeble, fleshy ridge along the outer edge of the fourth finger. First finger shorter than second, second shorter than fourth, third longest. Web between first and second fingers absent, between other fingers rudimentary; webbing formula: 1(3), 2i(3),

2e(2-2¼), 3i(3½), 3e(3), 4(2¾). Discs on fingers transversely oval, large, equal to or slightly larger than the tympanum, except the disc on the inner finger which is smaller.

A distinct, small, oval inner metatarsal tubercle. Outer metatarsal tubercle indistinct, small, round. Subarticular tubercles round, low, undivided. Indistinct low supernumerary tubercles present. Third toe equal to, slightly longer or slightly shorter than the fifth toe. Web between toes present, webbing formula: 1(2), 2i(2¼-2½), 2e(1½), 3i(2½-2¾), 3e(1½), 4i(2½-3), 4e(2½-2¾), 5(1). Toes with well developed, round to transversely oval discs, those of first and second toe distinctly smaller than those on the other toes, which are as large as those on the three outer fingers. When the hind limbs are folded and flexed at right angles to the sagittal plane, the heels show a considerable overlap.

In preservative the back is light brown to greyish brown. Dark brown vertebral stripe from tip of snout to vent. A dark brown to black canthal stripe. A dark dorsolateral line starting at the upper eyelid and continued to the groin, a lateral line starting at the posterior corner of the eye, following the supratympanic fold and from the insertion of the forelimb following the border between flank and belly to the groin. Below the lateral line a white line, starting on the upper lip below the eye and continued to the groin, inferior border only indicated. In some specimens this line even is not apparent. The area between dorsolateral and lateral dark lines darker than the back, sometimes even so dark that the bordering lines are hardly evident. An indistinct paravertebral line, starting at the upper eyelid, may be present on each side of the vertebral stripe. On each side of the posterior part of the urostyl a dark brown to black, elongate, triangular to semicircular subcutaneous spot is formed by blood vessels. Ventral parts immaculate, white to pale brown.

Measurements. — Snout-vent length in males 19.0-22.5 mm ($\bar{x}$ = 20.7 mm, N = 9), in the female holotype 20.0 mm. Tibiae in males 44.7-51.0% ($\bar{x}$ = 47.3%, N = 18) of the snout-vent length, in the female holotype 49.0-49.5% ($\bar{x}$ = 49.3%, N = 2). Head length in males 31.6-34.7% ($\bar{x}$ = 33.6%, N = 8) of the snout-vent length, in the female holotype 34.5%. Diameter of the eye in males 2.2-4.2 times ($\bar{x}$ = 3.0, N = 16) the diameter of the tympanum, in the female holotype 2.8-2.9 times ($\bar{x}$ = 2.9, N = 2).

Habitat. — In the El Manteco region this species was present in the floating cyperaceous vegetation mat along the margin of a permanent lagoon with *Mauritia flexuosa*, in open, white sand savanna. The Sipaliwini specimen was found on grass beside a creek in open savanna near a forest-island.

Natural history. — Males in El Manteco were calling from the cyperaceous

vegetation about one meter above the surface of the water in early November. Visits to the same spot in late January, early April and late July 1977 did not reveal any calling males. The Guyana males, collected in April and November, had distended vocal sacs.

Etymology. — From Latin tres, meaning three, and linea, meaning line. In reference to the three distinct lines on the dorsum.

Ololygon x-signata x-signata (Spix)

Hyla x-signata Spix, 1824: 40; Rivero, 1969a: 112; Duellman, 1977: 111.
Hyla rubra (partly), Rivero, 1961: 121; Rivero, 1964b: 416.
Ololygon x-signata, Fouquette & Delahoussaye, 1977: 393.

Material. — El Manteco: 1 ♂, RMNH 18334, 2 km E., 8-VII-1974, 2 ♂♂, RMNH 18335-36, 2 km E., 24-VII-1974, 5 ♂♂, RMNH 18337-41, 7-VI-1977, all leg. S. J. Gorzula.

Habitat. — Inhabits the margins of lagoons in the savanna.

Natural history. — Males start calling in the mid rainy season and continue through to the late rainy season. They call from low bushes and from the ground around permanent and temporary lagoons. No data on breeding conditions of females are available.

Phrynohyas venulosa (Laurenti)

Rana venulosa Laurenti, 1768: 31.
Phrynohyas zonata, Duellman, 1956: 35.
Hyla tibiatrix tibiatrix, Rivero, 1961: 127.
Hyla v. venulosa, Rivero, 1964b: 416, 418.
Phrynohyas venulosa, Duellman, 1977: 154.

Material. — El Manteco: 1 ♂, RMNH 18342, 28-VI-1974, 4 ♂♂, RMNH 18343-46, 8-VI-1977, all leg. S. J. Gorzula.

Habitat. — Inhabits savanna, also in perianthropic environment.

Natural history. — Males start calling at the beginning of the mid rainy season. Calling males float in the centre of large temporary pools in the savanna. Calling only lasts a few days. In Surinam it was also observed that breeding in this species only lasted a few days and was correlated with heavy rainfall.

The local name "Rana lechera" is due to the fact that upon capture specimens exude a white, sticky, latex-like secretion, which is painful when getting into cuts or eyes.

Phyllomedusa hypocondrialis (Daudin)

Hyla hypocondrialis Daudin, 1802: 20.
Phyllomedusa hypocondrialis hypocondrialis, Rivero, 1961: 150; Rivero, 1964b: 416; Heatwole, Solano & Heatwole, 1965: 355.
Phyllomedusa hypocondrialis, Duellman, 1977: 161.

Material. — El Manteco: 1 ♂, 1 ♀, RMNH 18347-48, 20 km S., 9-VIII-1976, 1 ♂, 1 ♀, RMNH 18349-50, 2 km E., 27-VI-1974, 1 ♂, RMNH 18353, 8-VI-1977, all leg. S. J. Gorzula.

Habitat. — An inhabitant of savannas and comparable open vegetations.

Natural history. — Breeding starts about three weeks after the onset of the rains. Copulating pairs and freshly constructed nests may then be found, while males will call sporadically till the end of the rainy season. The eggs are deposited in nests in bushes about 1 m above the water. The nests are constructed by glueing together two leaves (Pyburn & Glidewell, 1971). After capture in June, an amplexing pair (RMNH 18349-50) deposited 62 fertile and 9 infertile eggs. A female with mature, white, oviducal eggs was found in August. Nearly metamorphosed tadpoles were found in the lagoon on top of the Piedra de los Lamentos in October. These data indicate that breeding lasts from very early in the rainy season to the end of it.

During the rainy season specimens are found in trees and bushes overhanging water, 1-3 m above the surface. During the dry season this species disappears from view.

Sphaenorhynchus eurhostus Rivero

Hyla orophila planicola, Rivero, 1961: 136; Rivero, 1964b: 416.
Sphaenorhynchus eurhostus Rivero, 1969b: 701; Duellman, 1977: 179.

Material. — El Manteco: 1 ♂, RMNH 18354, 3 km E., 21-XI-1976, leg. S. J. Gorzula; 1 ♂, RMNH 18355, 3 km E., 31-X-1976, leg. M. S. Hoogmoed.

Habitat. — An inhabitant of open vegetations like swamps and savanna lagoons with a well developed vegetation.

Natural history. — As this species is only known from the El Manteco area by the two males listed above, hardly anything is known about the breeding strategy of this species. Males call from bushes at the edge of lagoons, sitting 5-50 cm above the surface of the water.

Remarks. — This species was originally reported from Venezuela by Rivero (1961) after a single specimen (MCZ 19917) from the Orinoco River below Barrancas, which supposedly is situated in the Delta Amacuro region. Rivero (1964b) treats this species as a member of the fauna of Venezuelan Guiana and not as belonging to that of the Delta. Apparently the specimens reported here are the first additional material of the species from Venezuelan Guiana. Further east, in Guyana, Surinam and French Guiana, the species is an inhabitant of the coastal marshes, in Amazonia it inhabits floating meadows (Hödl, 1977). In Venezuela it can be expected to occur in the Delta Amacuro, in the northern part of the Estado Bolívar and possibly also in the eastern part of the llanos, bordering on the Orinoco.

Recent fieldwork (1978) by both authors showed its presence on the Paria peninsula (Guaraunos and San Juan de las Galdonas); Duellman obtained it near El Dorado (13 km S., 1 km E. of Puente Cuyuni (Kansas University 167220)).

Leptodactylidae

Leptodactylus bolivianus Boulenger

Leptodactylus bolivianus Boulenger, 1898: 131; Rivero, 1961: 38; Rivero, 1964b: 416; Heatwole, Solano & Heatwole, 1965: 360; Gorham, 1966: 126.

Material. — El Manteco: 1 ♀, 1 hgr., RMNH 18356-57, 20 km S., 9-VIII-1976, 1 hgr., RMNH 18358, 14 km WSW., 4-IX-1976, 1 juv., 1 hgr., RMNH 18359-60, 4 km E., 15-II-1977, 1 hgr., RMNH 18361, 15-III-1977, 1 hgr., RMNH 18363, November 1975, all leg. S. J. Gorzula.

El Plomo: 1 ♂, RMNH 18362, 3-IV-1977, leg. S. J. Gorzula.

Habitat. — An inhabitant of both forest and savanna. In the savanna it occurs along the banks of large ponds and lagoons. In the forest near ponds and creeks. Where it occurs together with *L. macrosternum*, *L. bolivianus* is the rarer species.

Natural history. — A male was observed calling at the edge of a road-side pond in rainforest in April. No calling males were observed in the savanna, but an adult male with a well developed copulation spine on each thumb (RMNH 18362) also was collected in April. A female with mature oviducal eggs (with a brown and a creamish pole (RMNH 18356)) was collected in a clearing in rainforest in August. These scant data seem to indicate an extended breeding period, covering the early and mid rainy season, though the available data do not exclude breeding in the late rainy season as well.

Leptodactylus fuscus (Schneider)

Rana fusca Schneider, 1799: 130.

Leptodactylus sibilatrix, Rivero, 1961: 44; Rivero, 1964b: 416; Heatwole, Solano & Heatwole, 1965: 361.

Leptodactylus sibilator, Gorham, 1966: 139.

Material. — El Manteco: 1 ♂, RMNH 18377, 3 km E., 25-V-1974, 1 ♀, RMNH 18378, 2 km E., June 1974, 1 ♂, RMNH 18379, 13 km S., 5-IV-1976, 1 ♀, 2 ♂♂, RMNH 18380-82, 3 km E., 14-IV-1977, 1 ♀, 1 ad., RMNH 18384-85, 5 km E., 11-V-1977, 1 ♂, RMNH 18386, 8-VI-1977, all leg. S. J. Gorzula.

Habitat. — A savanna species that may be found associated with large temporary and permanent lagoons.

Natural history. — Males start calling, or better whistling, with the very first rains and continue through to the mid rainy season. The males excavate small caves (cf. pl. 3, fig. 6) from the mouth of which they call. The caves are made in depressions which are liable to flood shortly after the rains start. Thus, calling aggregations invariably occur in lagoons that are just

beginning to flood or at the water's edge of permanent lagoons. Inside the caves the eggs are laid in a foamy mass. After the cave has been flooded the larvae swarm into the water of the lagoon. An extensive description of the breeding strategy of this species has been given by Lescure (1972) and by Lamotte & Lescure (1977). Males have a well developed edge on the snout, possibly used in digging the small caves. Females with mature, completely white, oviducal eggs were found in April (RMNH 18380), May (RMNH 18385) and June (RMNH 18378), at the height of the rainy season.

Remarks. — Only this species was encountered in the Yuruari savanna, and in the Gran Sabana only *L. longirostris* Boulenger, which might indicate that these species are vicariants. Rivero (1971) also reports that *L. fuscus* and *L. longirostris* do not occur sympatrically in the La Escalera region, but they are sympatric in other regions (table 1).

Leptodactylus macrosternum Miranda Ribeiro

Leptodactylus ocellatus macrosternum Miranda Ribeiro, 1926: 147.

Leptodactylus ocellatus, Rivero, 1961: 45; Rivero, 1964b: 416; Heatwole, Solano & Heatwole, 1965: 360.

Leptodactylus macrosternum, Gallardo, 1964: 379; Gorham, 1966: 130; Rivero, 1967: 6; Gorzula, 1978: 28.

Material. — El Manteco: 1 ♂, 2 ♀♀, RMNH 18365-67, 15-III-1977, 1 ♂, 1 ♀, RMNH 18368-69, 14-IV-1977, all leg. S. J. Gorzula; 1 ♂, 4 ♀♀, RMNH 18370-74, 12 km SE., 30-X-1976, 1 ♀, RMNH 18375, 1 km E., 31-X-1976, 1 ♀, RMNH 18376, 3 km E., 30-X-1976, all leg. M. S. Hoogmoed.

Yuruari river, 6 km E. of El Manteco: 1 hgr., RMNH 18364, 7-XI-1976, leg. S. J. Gorzula.

Habitat. — This species seems to be characteristic for open savannas, where it can be found among the vegetation along the margins of large lagoons.

Natural history. — Although a fairly common species, data on breeding are very limited. Males never were observed calling. Breeding males with two large, black prepollical spines on each inner finger (RMNH 18365, 18369) and females (RMNH 18366-68) with mature (a grey and a black pole) oviducal eggs were collected in March and April. A halfgrown male, collected in October, has two very small, unpigmented prepollical spines. Newly metamorphosed froglets were found in August. Dixon & Staton (1976) studied a population of this species in the savannas near San Fernando de Apure and found that breeding there took place early in the wet season (May-September/October). Specimens seem to reach sexual maturity within six months and to reproduce the next year. At the height of the dry season individuals aestivate.

Leptodactylus rugosus Noble

Leptodactylus rugosus Noble, 1923: 297; Rivero, 1961: 50; Rivero, 1964b: 416, 417; Heatwole, Solano & Heatwole, 1965: 360; Gorham, 1966: 138.

Material. — Piedra de los Lamentos, 32 km S. of El Manteco: 3 hgr., RMNH 18392-94, 31-X-1976, leg. M. S. Hoogmoed & S. J. Gorzula; 1 hgr., RMNH 18395, 31-X-1976, foot of "Piedra", leg. M. S. Hoogmoed.

Habitat. — In open, rocky places, under logs and rocks.

Natural history. — In the El Manteco area this species is only known from the Piedra de los Lamentos, a large, granite inselberg, isolated in the forest south of El Manteco, still within the Yuruari drainage. The inselberg, projecting about 200 m above the surrounding terrain, consists mainly of bare rock with bamboo-thickets and scrub in several places. On top of the inselberg there is a large lagoon, which may dry up during severe droughts. The frogs were found at the base of the rock under logs at the forest edge, but also under flakes and boulders of granite on top of the mountain (pl. 3, fig. e). No data on breeding are available.

Remarks. — Although not a typical savanna inhabitant, this species is included here because it occurs in comparable open habitats. Data from other areas in Venezuelan Guiana suggest that the species is strictly rupicolous, without having a predelection for a particular substrate, occurring both on sandstone and on granite.

Leptodactylus wagneri (W. Peters)

Plectromantis wagneri W. Peters, 1862: 232.
Leptodactylus podicipinus petersii, Rivero, 1961: 47; Gorham, 1966: 136.
Leptodactylus podicipinus petersi, Rivero, 1964b: 416.
Leptodactylus wagneri, Heyer, 1970: 17.

Material. — El Manteco: 1 ♀, RMNH 18398, 23 km S., 9-III-1975, 2 hgrs., 1 ♂, 1 ♀, RMNH 18399-402, 3 km E., 28-II-1975, 1 ♀, RMNH 18403, 15-III-1977, 1 hgr., RMNH 18404, 13 km S., 5-IV-1977, 1 ♀, RMNH 18405, 3 km E., 14-IV-1977, all leg. S. J. Gorzula; 1 hgr., 1 ♂, RMNH 18396-97, 3 km E., 31-X-1976, leg. M. S. Hoogmoed.

Habitat. — This species is not present in the open savanna, but may be found in gallery forest and on the banks of large, permanent lagoons, surrounded by a belt of more or less closed high vegetation. It is also present in rainforest.

Natural history. — Males never were observed calling. Females with small, white oviducal eggs were collected in February (RMNH 18401), March (RMNH 18403) and April (RMNH 18405). Another female, collected in March (RMNH 18398), only had small oviducts. A male with well developed prepollical spines (two per thumb), was collected in October (RMNH 18396), another male, captured in February (RMNH 18399), had

two small prepollical spines. These data indicate that breeding takes place early in the rainy season, probably starting immediately after the onset of the first rains.

Physalaemus enesefae Heatwole, Solano & Heatwole

Physalaemus enesefae Heatwole, Solano & Heatwole, 1965: 355; Lynch, 1970: 489; Gorzula, 1977b: 657.

Material. — El Manteco: 1 ♀, RMNH 18409, June 1974, 9 ♂♂, RMNH 18410-18, 4 km E., 8-VI-1977, leg. S. J. Gorzula.

Habitat. — In the El Manteco region this species is only known from the savanna and it apparently does not penetrate into the forest. However, the type locality of this species is recorded as being in forest, though it is not stated which kind of forest. According to Ewell, Madriz & Tosi (1976), the type locality is situated in an area of damp tropical forest (bosque humedo tropical). They also report the presence in this life zone on several places in Estado Bolívar of edaphic savannas. As this species probably also has been reported from the central llanos by Staton & Dixon (1977), the observation of the species in forest seems rather strange. We therefore suppose that a more or less extensive savanna area is present in the immediate surroundings of the type locality, and that the type specimens entered the forest along trails. This supposition was reinforced in June 1978 when the first author during fieldwork in the Las Claritas area (85 km south of El Dorado) also found the species in rainforest along trails, branching off from the main road and from clearings.

Natural history. — Calling and breeding start in the mid rainy season (mostly June/July) and only last for a maximum of two weeks. Males invariably call from small, water-filled depressions (imprints of cow hoofs in soft mud) several metres away from the edge of the water. Within a week after the start of the rains the depressions are flooded and connected to the main body of water of the lagoon. The location may be either permanent or temporary lagoons in open savanna. Foam nests are produced which float on the surface of the water where it is a few (one to two) centimetres deep, invariably in the small depressions. The nests disintegrate and the larvae enter the water within three days after the nests were constructed. The temperature of the nests is significantly lower than that of the water on which they float. Gorzula (1977b) suggested that the function of these foam nests initially is to protect the larvae in them against excessive heat and that during their disintegration over a period of three days the larvae would be offered the opportunity to acclimatize to the higher temperature of their new environment. Before calling and breeding start and after they

end, this species virtually disappears (Gorzula, 1977b), which might mean that it aestivates.

The single available female, which was captured in June, contains mature, white, oviducal eggs. The males all have distended vocal sacs and brown nuptial pads on the inner side of the thumbs.

Remarks. — The El Manteco specimens were directly compared with the holotype (MCZ 51770) and agreed in all characters.

Calling males have a brick to salmon pink back, which colour may disappear in daytime. Apart from the localities in the Yuruari savanna, this species was also observed by Gorzula in San Pedro de las Bocas and by Hoogmoed in El Dorado and near Las Claritas.

Physalaemus pustulosus ruthveni (Netting)

Eupemphix ruthveni Netting, 1913: 167.
Eupemphix pustulosus ruthveni: Rivero, 1961: 90; Gorham, 1966: 114.
Physalaemus pustulosus: Lynch, 1970: 489.
Engystomops pustulosus: Gorzula, 1977b: 657.

Material. — El Manteco: 1 ♂, RMNH 18419, 31-X-1976, leg. M. S. Hoogmoed; 1 ♂, RMNH 18420, 7-XI-1976, 1 ♀, 1 ♂, RMNH 18421-22, 20 km S., 9-VIII-1976, 1 ♀, 8 ♂ ♂, RMNH 18426-34, 7-VI-1977, all leg. S. J. Gorzula.
Upata: 1 ♂, RMNH 18423, 25 km S., 3-VII-1974, leg. S. J. Gorzula.

Habitat. — This species seems to be an inhabitant of savannas. It enters the forest along roads and logging tracks and establishes breeding populations in clearings.

Natural history. — Calling and breeding start in the mid rainy season and last through to the end of the rainy season. As in *P. enesefae*, males call from small, flooded depressions, but usually they are hidden under a leaf or something similar. Their breeding strategy roughly appears to be the same as in *P. enesefae*. Females with mature, white oviducal eggs were found in June (RMNH 18433) and in August (RMNH 18422). Foam nests are generally made in small temporary pools and in shaded, shallow ditches ('quebradas' and 'morichales'). A detailed account of the construction of the foam nest by this species is provided by Heyer & Rand (1977). Generally *P. pustulosus* and *P. enesefae* are not found in the same pond, but occasionally they may occur mixed. As is the case with *P. enesefae*, this species virtually disappears during the dry season.

Pleurodema brachyops (Cope)

Lystris brachyops Cope, 1868: 312.
Pleurodema brachyops: Rivero, 1961: 88; Rivero, 1964b: 416; Gorham, 1966: 155.
Pleuroderma brachyops: Gorzula, 1977a: 9; Gorzula, 1977b: 657; Gorzula, 1978: 28.

Material. — El Manteco: 9 ♂ ♂, RMNH 18435-43, 7-XI-1976, leg. S. J. Gorzula.

Habitat. — Around permanent and temporary lagoons in the savanna.

Natural history. — During the dry season these frogs virtually disappear, but at the onset of the rains they may be found in any unshaded body of water larger than 0.1 m². This is one of the first frogs to breed after the very first rains. Thereafter they call on any rainy night for the rest of the rainy season. Towards the end the aggregations seem to consist only of males. The species appears to favour any temporary body of water. Only at the beginning of the rainy season it may be found in small numbers in large permanent lagoons. Later on it seems to be absent from these sites. It breeds in water bodies as small as flooded ruts made by cars. Calling occurs in the water itself and if the pool is small the calling males are in the centre. This species constructs a foam nest which floats free on the surface of the water. Amplexus is axillar. The male seems to stimulate the female to spawn by rapidly squeezing her several times with his forelimbs. About three seconds later he reaches under her with his hindlimbs and picks up a small quantity of spawn. This is held behind the male on the surface of the water by the hindlimbs. The male then whisks the eggs to a foam by a rapid criss-cross movement of the feet (pl. 2, fig. a). The pair subsequently rests for about 30 seconds (pl. 2, fig. b) before again adding to the foam nest. When the nest is partially complete the male shapes it by a spreading action of the hindlimbs after each addition of new foam (pl. 2, fig. c).

This is another species which during the rainy season is heavily preyed upon by *Caiman crocodilus* (Gorzula, 1977a, 1978). Specimens may also fall prey to waterscorpions (Hemiptera).

Remarks. — The variation in size in apparently sexually adult males with well developed vocal sacs is striking: the largest male (RMNH 18438) has a snout-vent length of 46 mm, the smallest male (RMNH 18436) only measures 34 mm. Whether these differences in size reflect age differences or differences in food availability is not clear. If the size differences do reflect differences in age, this would mean that males propagate at least in two consecutive years.

Microhylidae

Elachistocleis ovalis (Schneider)

Rana ovalis Schneider, 1799: 131.
Elachistocleis ovalis: Rivero, 1961: 177; Rivero, 1964b: 416; Gorzula, 1977a: 9.
Elachistocleis: Gorzula, 1978: 28.

Material. — El Manteco: 3 ♀♀, 9 ♂♂, 1 ad., RMNH 18455-67, 4 km E., 15-II-1977, 1 ex., RMNH 18453, 13 km S., 5-IV-1977, 1 ♂, RMNH 18454, 1 km E., 8-VI-1977, leg. S. J. Gorzula.

Habitat. — An inhabitant of savannas, where it is found both in permanent and in temporary waters, without preference.

Natural history. — Males start calling in the mid rainy season (two weeks after the rains begin) and continue for about 12-16 weeks. They call from shallow water at the very edge of ponds. Two females with small oviducts (RMNH 18455, 18467) and one with small oviducal eggs (RMNH 18456) were collected in February. The available data seem to suggest that breeding continues for the greater part of the rainy season.

During the dry season specimens were found in groups at the edge of lagoons under planks and buried in a sandy hollow about 4 cm underneath the surface.

This species too is heavily preyed upon during the breeding season by *Caiman crocodilus* (Gorzula, 1977a, 1978).

Remarks. — We tentatively identified this species as *Elachistocleis ovalis*, though completely aware of the taxonomic problems relating to this taxon. However, these problems only can be solved within the framework of a revision of the entire group and the present paper is not a proper place to pursue the matter too far. It should suffice to state that the El Manteco population differs markedly from populations in the llanos and in the Paria peninsula, but agrees with the populations in coastal Surinam. Therefore we prefer to restrict ourselves to giving here a diagnosis.

Diagnosis. — A small species, the males of which reach snout-vent lengths of 24-27 mm, the females 29-30 mm. Snout pointed, twice as long as the horizontal diameter of the eye. A transverse dermal fold across the head just behind the eyes. When flexed and placed at a right angle to the sagittal plane of the body, the heels just touch. Back dark grey with minute light grey spots. Light spots in axils, groins, hollow of the knee, on back of thigh light stripe. Ventral parts marbled creamish and dark brown, with a tendency to form a transverse band of large light spots across the chest. Light spots on throat smaller than those on belly. Breeding males with black gular sac.

In life the spots in axils, groins, hollow of the knee and on the back of the thigh orange; belly marbled lemon yellow and grey.

Pseudidae

Pseudis paradoxus caribensis Gallardo

Pseudis paradoxus: Rivero, 1961: 91; Heatwole, Solano & Heatwole, 1965: 352.
Pseudis paradoxus caribensis Gallardo, 1961: 116; Duellman, 1977: 200.

Material. — El Manteco: 8 juvs., RMNH 18444-51, 1 km N., 26-XI-1976, 1 juv., RMNH 18452, 15-III-1977, all leg. S. J. Gorzula.

Habitat. — Inhabits open watery situations, like marshes, ponds in savannas and other comparable open habitats (e.g., lagoon on top of inselberg). In the El Manteco area it is found in large permanent lagoons, but during the rainy season migration of this aquatic species to ponds and large temporary lagoons takes place on rainy nights.

Natural history. — Males start calling within two weeks after the first rains and soon after amplexing pairs can be observed. Heatwole et al. (1965) observed an amplexing pair early in August near Miamo. Amplexus is axillar. The males carry on calling till the end of the rainy season and during that period may be heard in daytime: e.g. on October 31, 1976 this species was heard calling in the lagoon on top of the inselberg south of El Manteco. All specimens collected are recently metamorphosed juveniles. RMNH 18444-51 were found in a temporary lagoon in late November, which implies that metamorphosis is completed within six months. RMNH 18452, which is also recently metamorphosed was collected in March in a permanent lagoon and might be a specimen that hatched late in the previous wet season.

Remarks. — Rivero (1961) reported this species from Venezuela on the basis of literature records. In 1964 (b) he did not mention it for Guiana. Gallardo (1961) reports the present subspecies only from Estado Cojedes. Heatwole et al. (1965) were the first to report the species for Venezuelan Guiana. The present record extends the known distribution in Guiana to the west.

Ranidae

Rana palmipes Spix

Rana palmipes Spix, 1824: 29; Rivero, 1961: 176; Rivero 1964b: 416.

Material. — El Manteco: 1 hgr., RMNH 18472, 13 km S., 5-IV-1977, leg. S. J. Gorzula. Paviche, 28 km W. of El Manteco: 4 juvs., RMNH 18468-71, 24-VI-1974, 1 ♀, 8 juvs., RMNH 18473-81, 10-IV-1977, all leg. S. J. Gorzula; 1 hgr., RMNH 18482, 1-XI-1976, leg. M. S. Hoogmoed & S. J. Gorzula.

Habitat. — Although occasionally encountered in pools, this species essentially occurs along river banks covered with mature gallery forest. It is generally absent from standing water, but very common along the banks of the artificial Caroni lake.

Natural history. — The only available data about breeding are that in the single adult female (RMNH 18473) the oviducts are well developed and that recently metamorphosed (RMNH 18468-71, 18474-81) or metamorphosing juveniles (field data Gorzula) were found from mid April to July.

Remarks. — It appears that this species is absent from the Yuruari basin. So far, in the El Manteco region it only has been recorded from the Caroni

drainage. A similar restricted distribution is known for this species in Surinam. Thus far this species only is known in that country from two creeks in rainforest (Van Amskreek and Mozeskreek), both belonging to the Nickerie River basin (field data Hoogmoed, 1975). What might cause this localised distribution is not clear. There is no reason to suspect ecological exclusion, because apparently there is no frog species replacing *Rana palmipes* in the Yuruari basin. Neither is a species failing in the Caroni basin which is present in the Yuruari basin.

Anuran succession in temporary lagoons

As has been pointed out above, in the south-eastern Venezuelan savanna there are two distinct seasons per year: the dry season and the rainy season. The dry season generally lasts from January to May, but can vary as shown by fig. 3. Over the years 1974 through to 1976 the rainfall followed the expected pattern up till May 1975. From then on rain fell fairly well spread but in (comparatively) low quantities. The expected dry season between January and May 1976 never came.

The lagoon level (fig. 3, pl. 3) is that of a small permanent lagoon about

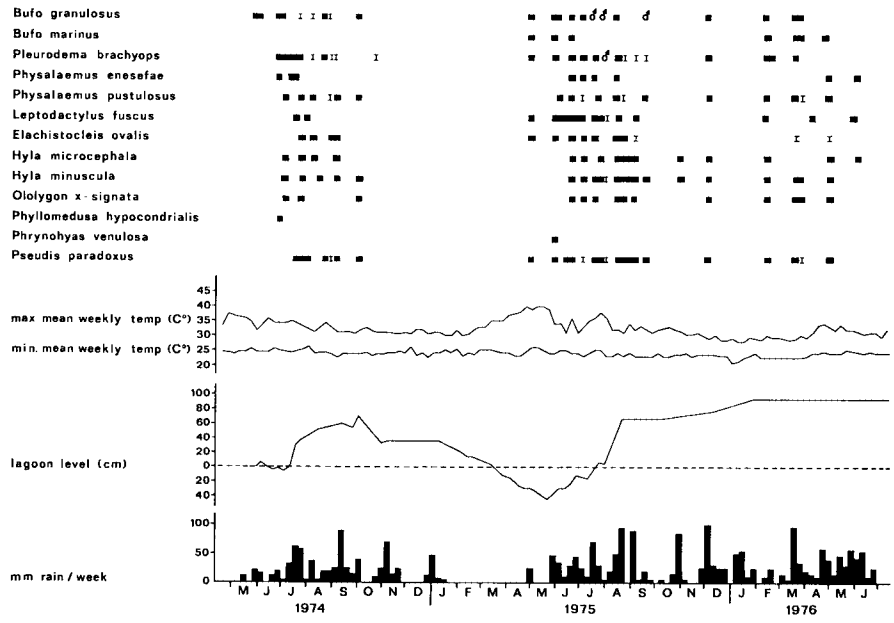

Fig. 3. Climatological data of El Manteco for the period May 1974-June 1976 combined with data of calling frogs. In the upper part of the figure solid squares or rectangles indicate large choruses, I indicates the calling of scattered individuals, and ♂ indicates times when aggregations were all males. For further explanation see text.

2 km east of El Manteco in the savanna, where at an arbitrary datum zero level was designated on May 25, 1974. Thus all subsequent fluctuations in lagoon level refer to the differences from the zero level at the end of the 1974 dry season. Fig. 3 also indicates the weeks in which choruses of 13 of the commoner species of frogs were heard. The data are pooled from studies of two permanent lagoons, and about ten temporary lagoons and ponds. It can be seen from the data for 1974 and 1975 that breeding occurred when the lagoons were filling up and extending. The 1975 data show that bufonids and leptodactylids both begin to breed earlier and cease breeding earlier than hylids. In 1976, when there was no dry season, mating was apparently less concentrated, but it may merely have been more spaced out. Although in the general area the breeding seasons of the anurans are fairly extended, in any one lagoon there is a distinct succession of species present. The rate of succession depends on the individual topography and size of a lagoon as well as on the amount of rainfall at any one time. In a large lagoon, at a given time different stages of succession may be reached in different parts of the lagoon. In a year of sporadic rain a lagoon may reach an advanced stage in the succession, dry out, and then with the next rains begin again at stage I. The succession in temporary lagoons may be divided into four stages:

Stage I. — The lagoon represented in fig. 4 and pl. 3, figs. a-c is bordered to the left by gallery forest, to the right there is a bed of cyperaceous vegetation, and further up is a belt of mimosa shrubs. In this stage, which begins with the very first rain, the lagoon is virtually dry with only a few shallow puddles. Large numbers of *Pleurodema brachyops* are calling and constructing foam nests in these puddles and at the edges are choruses of *Bufo granulosus* (pl. 2, fig. d). In the dry bed of the lagoon male *Leptodactylus fuscus* make small caves from the mouths of which they call (cf. pl. 3, fig. d). The foam nest is made inside the cave, and the tadpoles on hatching stay there until the lagoon level rises and floods the nests.

Stage II. — The Bufonidae and Leptodactylidae predominate in this stage. *Pleurodema brachyops* is still mating and calling in the centre of the lagoon. In the shallows, along the water margin, are large numbers of *Elachistocleis ovalis*. On the bank, beside but not in the water, are aggregations of *Bufo granulosus* together with *B. marinus*. *Leptodactylus fuscus* is calling from the now reduced dry lagoon bed. In the cyperaceous vegetation mat water-filled hoof prints have been made by animals that have begun to use the lagoon again. In these small hollows two species of *Physalaemus* may be found. Both *P. enesefae* and *P. pustulosus* make foam nests. Their tadpoles are released into the water of the hollows when the nests disintegrate after two or three days. When the lagoon floods, the tadpoles join the main body

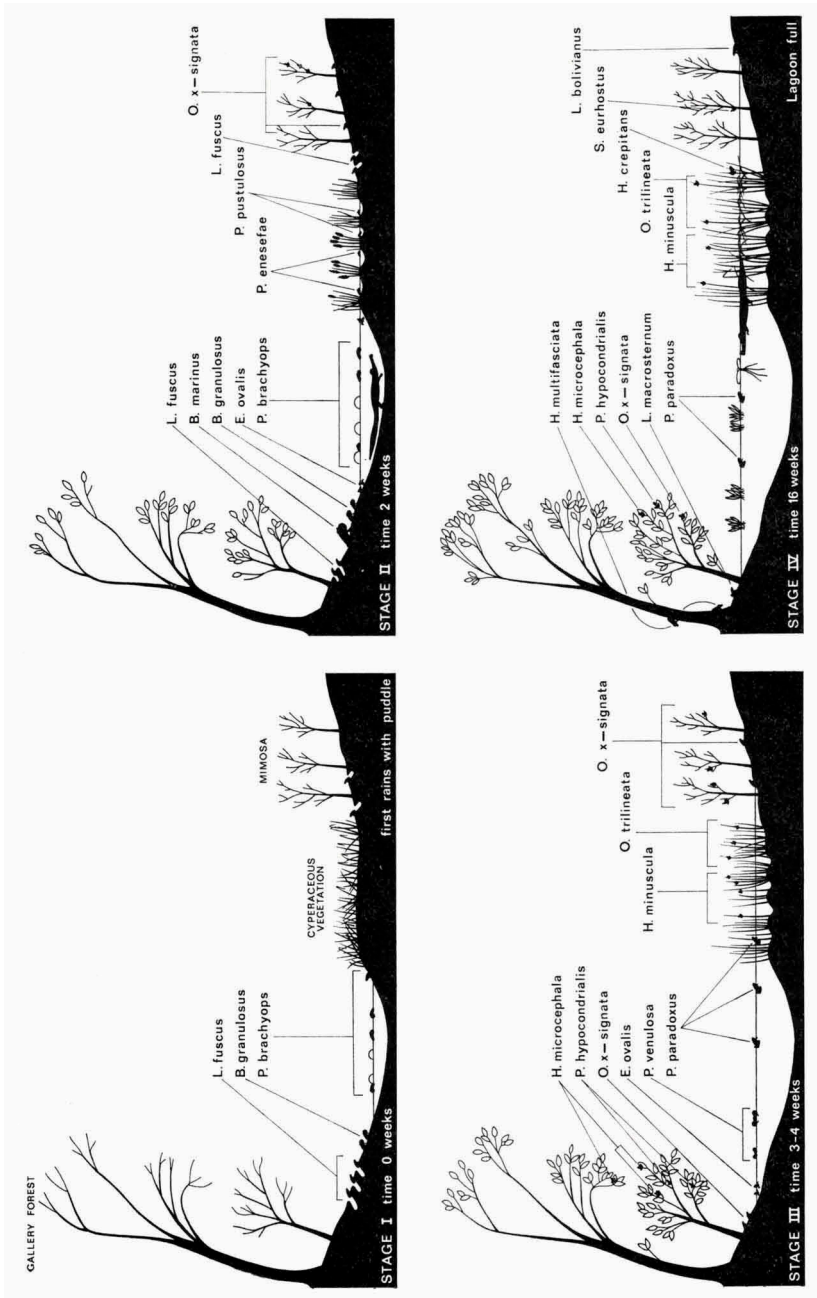

Fig. 4. Schematic representation of the four stages of anuran succession in temporary lagoons. For further explanation see text.

of water. The first hylid to appear is *Ololygon x-signata,* which calls from the shore and from low bushes. During this period on rainy nights specimens of *Caiman crocodilus* make short-term migrations to the temporary lagoons to feed, specifically, on *Bufo granulosus, Pleurodema brachyops,* and *Elachistocleis ovalis.*

Stage III. — Towards the end of the second stage *Phrynohyas venulosa* comes to the lagoon to breed. The reproductive period of this species is short and lasts only three or four nights. With further flooding of the lagoon the leptodactylids and bufonids are no longer in evidence. *Pseudis paradoxus* specimens migrate from nearby permanent lagoons, where they passed the dry season, to temporary lagoons. One such migration was observed during the night after a day of heavy rain. In the late afternoon a large chorus of *Pseudis* was heard in the permanent lagoon at the corner nearest to the temporary one, but the significance of this is not known. Migrations such as these are known to occur over distances of up to at least 500 m. Along the margins of the water *Elachistocleis ovalis* is still present in large numbers. *Ololygon x-signata* is still calling from the shore and from low bushes. In such bushes besides the water *Phyllomedusa hypocondrialis* uses leaves to make nests for its eggs, the tadpoles hatching from the eggs later fall into the lagoon. Two species of *Hyla* and one of *Ololygon* are also present: *H. minuscula* and *O. trilineata* are present in the now flooded cyperaceous vegetation, *H. microcephala misera* in water-side trees and bushes of the gallery forest.

Stage IV. — By the time the lagoon is full, mating generally has stopped. However, various species are still present at the lagoon and some of these are still calling, either as individuals, or forming small choruses when it rains. The floating vegetation is well developed. In the water itself only *Pseudis paradoxus* is present. The two species of *Hyla,* the two of *Ololygon,* and *Phyllomedusa hypocondrialis* from stage III are present in their respective locations. In addition small numbers of *Hyla multifasciata* are calling from the ground and from bushes up to 2 m above the ground in the gallery forest. Also in the gallery forest and in mimosa shrubs at the border of the lagoon are isolated *Sphaenorhynchus eurhostus.* On the now matted cyperaceous vegetation some *Hyla crepitans* are present. Depending on the size of the lagoon several *Caiman crocodilus* live in the main body of the lagoon until it begins to dry out again, when they return to a permanent lagoon. Occasional *Leptodactylus macrosternum* and *L. bolivianus* also occur along the banks. These are typically permanent lagoon species which are generally found only at temporary lagoons when there is a permanent lagoon nearby.

When the lagoon dries out some species (*Pseudis paradoxus, Leptodactylus macrosternum* and *L. bolivianus*) return to the permanent lagoons, others (hylids, bufonids) enter gallery forest, and still others (*L. fuscus, Elachistocleis ovalis*) bury themselves in and around the dry lagoon bed to aestivate.

It is notable that the leptodactylid frogs, which all make foam nests, apparently can exploit the temporary lagoons much earlier than the hylids, whose eggs are more water dependent. In the case of the bufonids and leptodactylids, the lagoon is used only for reproduction, whereas many hylids stay, probably for periods long after reproduction has been accomplished.

Discussion

Recently, Staton & Dixon (1977) published an account of the herpetofauna of the central llanos of Venezuela. They investigated three localities, but only in two of these (Hato Masaguaral and Hato La Guanota) representative samples of the anurofauna were obtained. Also in Surinam representative samples from two localities are available (field data Hoogmoed). One of the Surinam localities (Zanderij) is situated in the belt of coastal savannas, the other (Sipaliwini) is an extensive, isolated savanna in the interior on the watershed with Brazil. Enough data are available to allow comparison of the savanna anurofaunas of these four localities with the locality studied here.

When comparing these five anurofaunas the most striking fact is the richness of the El Manteco anurofauna, in contrast with that of either of the other localities. All species, except one (*Leptodactylus labialis*), occurring in Masaguaral and La Guanota also occur in El Manteco, thus giving the impression of an essentially identical fauna with a number of species added. Some of these species, like *Ololygon x-signata*, still may be expected to be found in the llanos localities. A few either are endemic to Guiana (*Ololygon trilineata, Dendrobates leucomelas*) or are restricted to special habitats (*Leptodactylus rugosus*). The remaining species are Amazonian elements that apparently reach their limit of distribution at or near the Orinoco River. The proportion of Amazonian and endemic Guianan elements in the Surinam localities is even greater than in El Manteco.

Table 1 presents a list of the species playing a part in these considerations, in table 2 the faunal resemblance factors for the five localities, considered here, have been compiled. From these data it is clear that the anurofauna of both llanos localities is virtually identical. There is a very high resemblance between the two llanos localities and El Manteco on the one hand and a high

TABLE 1. Checklist of anurans occurring in five savanna localities in northern South America

	Masaguaral	La Guanota	El Manteco	Zanderij	Sipaliwini
Bufo granulosus	x	x	x	x	-
guttatus	-	-	x	-	-
marinus	x	x	x	x	x
Dendrobates leucomelas	-	-	x	-	-
Hyla boans	-	-	-	x	x
crepitans	x	x	x	x	-
geographica	-	-	x	-	x
leucophyllata	-	-	-	x	-
marmorata	-	-	-	x	-
microcephala misera	x	x	x	-	-
minuscula	-	-	x	-	-
multifasciata	-	-	x	x	x
Ololygon boesemani	-	-	-	x	-
egleri	-	-	-	x	x
rubra	x	x	x	x	-
trilineata	-	-	x	-	x
x - signata	-	-	x	x	x
spec. D	-	-	-	-	x
Osteocephalus taurinus	-	-	-	x	-
Phrynohyas venulosa	x	x	x	-	-
Phyllomedusa bicolor	-	-	-	x	-
hypocondrialis	-	-	x	x	x
Sphaenorhynchus eurhostus	-	-	x	-	-
Adenomera hylaedactylus	-	-	-	x	-
Leptodactylus bolivianus	x	x	x	x	x
fuscus	x	x	x	x	x
labialis	x	x	-	-	-
longirostris	-	-	-	-	x
macrosternum	x	x	x	-	x
pentadactylus	-	-	-	x	-
rugosus	-	-	x	-	-
wagneri	x	x	x	x	x
Physalaemus enesefae	x	-	x	-	-
pustulosus ruthveni	x	x	x	-	-
Pleurodema brachyops	x	x	x	-	-
Pseudopaludicola pusilla	-	-	-	-	x
Elachistocleis ovalis	x	x	x	x	-
Pseudis paradoxus	x	x	x	-	-
Rana palmipes	-	-	x	-	-
Total	16	15	26	20	15

TABLE 2. Comparison of savanna anurofaunas of five localities in northern South America. The faunal resemblance factors (FRF) were computed with the formula $\frac{2C}{N^1 + N^2}$ (Duellman, 1966) in which C is the number of species common to both localities compared, N^1 and N^2 the total numbers of species known from localities 1 and 2

	Species in Common				
FRF	Masaguaral	La Guanota	El Manteco	Zanderij	Sipaliwini
Masaguaral	16	15	15	8	5
La Guanota	0.96	15	14	8	5
El Manteco	0.71	0.66	26	11	10
Zanderij	0.44	0.45	0.47	20	9
Sipaliwini	0.32	0.33	0.48	0.51	15

resemblance between the two Surinam localities and El Manteco on the other hand. The resemblance between Sipaliwini and the two llanos localities is low, that between Zanderij and the three Venezuelan localities is high. The resemblance between Zanderij and Sipaliwini is of the same magnitude as that between Zanderij and the Venezuelan localities, but it is caused by the presence of different species. From these data it can be concluded that El Manteco is situated in an area which still has a nearly complete llanos anuran complement but in addition also has a good number of Amazonian and endemic species. This is clearly demonstrated by its relatively high number of species. The Amazonian species and the Guiana endemics are the main cause for the high resemblance of the El Manteco anurofauna with that of the two Surinam localities. The resemblance between Zanderij and the Venezuelan localities is completely due to the presence of widespread species. A number of these are absent in Sipaliwini, where the influence of the Amazonian species and the Guiana endemics is greater.

Thus, the relative richness of the anurofauna of the El Manteco region is due to the mingling of two faunas, viz., a western llanos one and an eastern/southern Guiana/Amazonian one. The fact that collecting in the area has been performed during a very long, continuous period no doubt also has been of some influence. In neither of the other localities collecting has been

performed for comparable periods and in each of them some additional species may be expected to occur.

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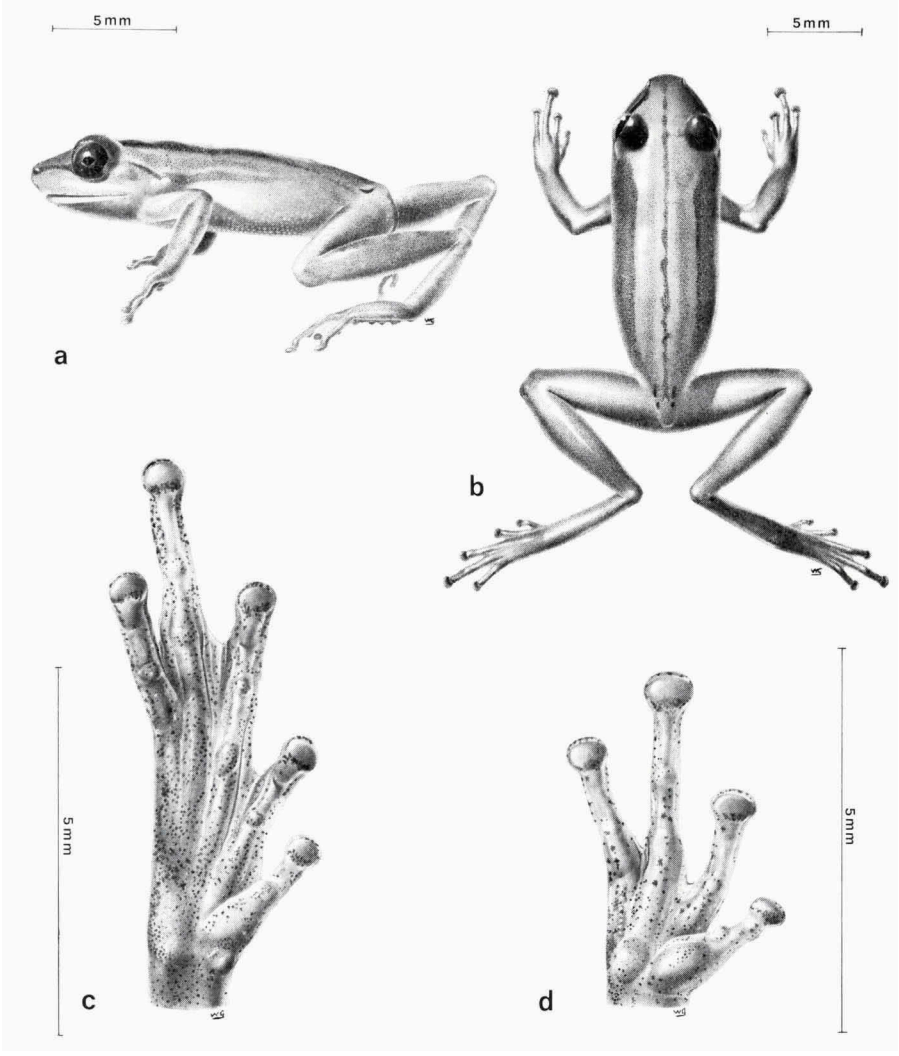

Ololygon trilineata nov. spec.: a. lateral view of halfgrown, paratype, RMNH 18260, snout-vent length 14.7 mm; b. dorsal view of ♂ paratype, RMNH 18258, snout-vent length 19.0 mm; c. plantar view of right foot of ♂ paratype, RMNH 18259 (length of foot 7 mm); d. palmar view of right hand of ♂ paratype, RMNH 18259 (length of hand 4 mm). All del. W. C. G. Gertenaar.

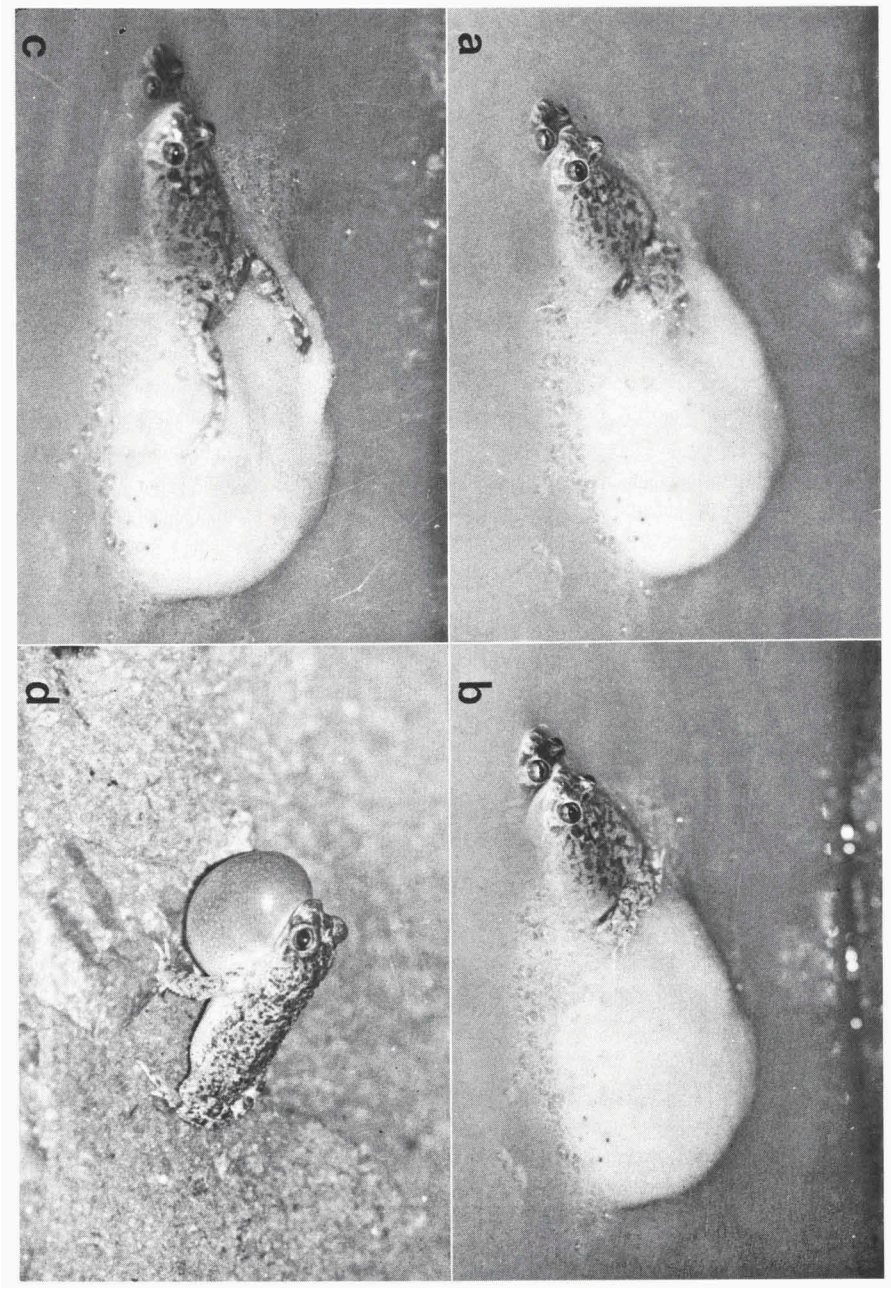

Fig. a-c. Foam nest construction by *Pleurodema brachyops*: a. male whisking egg-mass; b. male and female in resting position; c. male shaping newly added foam; d. calling male of *Bufo granulosus merianae*. Photographs S. J. Gorzula.

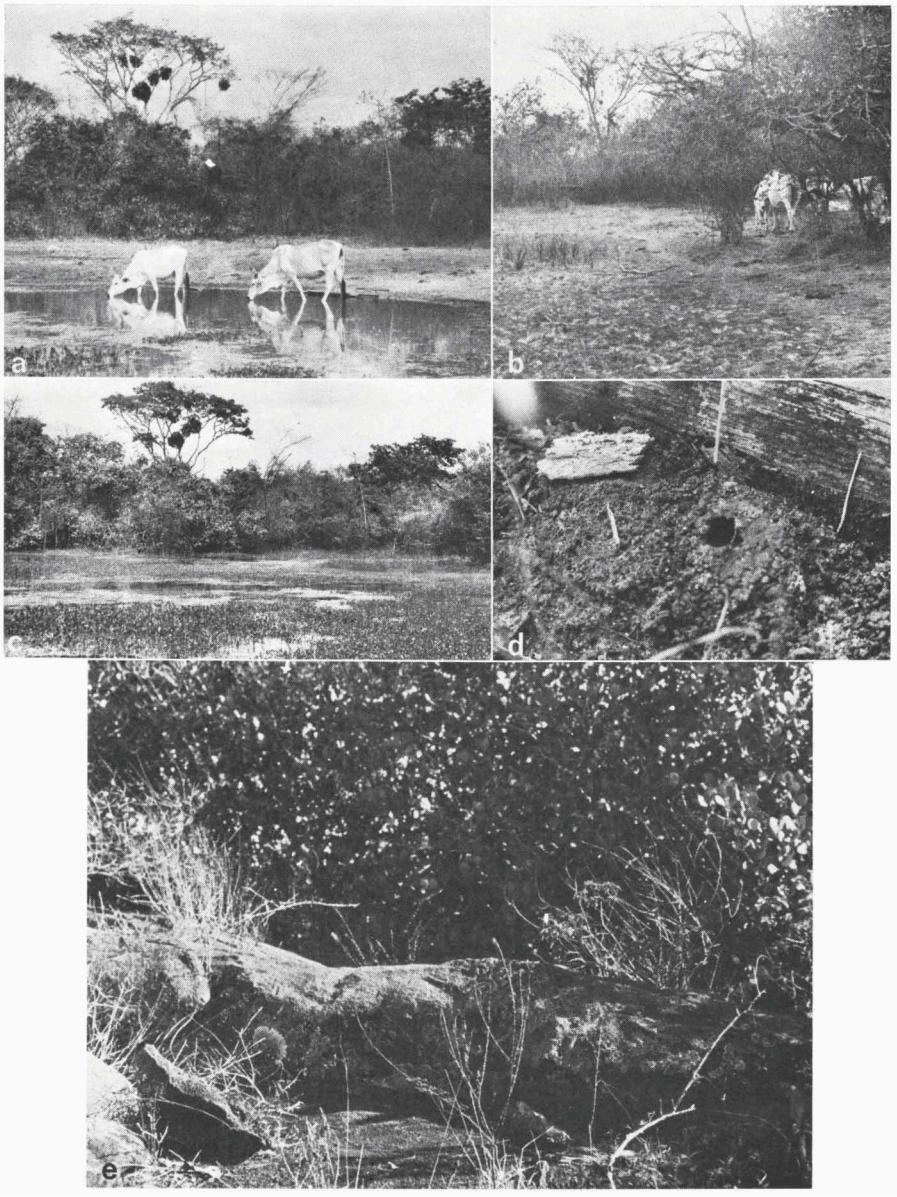

Fig. a-c. Temporary lagoon near El Manteco: a-b. during the dry season; c. during the wet season; d. nest of *Leptodactylus longirostris*, near Nieuw Koffiekamp, Surinam, 11 December 1974; e. habitat of *Dendrobates leucomelas* on top of the Piedra de los Lamentos, 32 km S. of El Manteco. Photographs a-c by S. J. Gorzula, d-e by M. S. Hoogmoed.