RESURRECTION OF HYLA ORNATISSIMA NOBLE (AMPHIBIA, HYLIDAE) AND REMARKS ON RELATED SPECIES OF GREEN TREE FROGS FROM THE GUIANA AREA NOTES ON THE HERPETOFAUNA OF SURINAM VI

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SUMMARY

In the present paper Hyla ornatissima Noble is removed from the synonymy of Hyla granosa Boulenger, and resurrected as a separate species on the basis of morphological, ecological and acoustical differences. Another relative of this group occurring in Guiana is Hyla sibleszi Rivero. Because of its superficial resemblance with these frogs Hyla punctata (Schneider), of another species-group, is also treated. All four species are extensively described, data on life history and distribution are given. H. sibleszi, so far only known from the type material and some associated specimens, is reported from several new localities in Venezuela and Guyana. It is suggested that the function of the intricate dorsal pattern of H. ornatissima serves to protect the animal from predation, camouflaging it on the leaves of the trees where the animals live. A key to discern the four species is presented.

RESUMEN

En el trabajo actual se ha observado que Hyla ornatissima Noble se está alejando de la sinonimía de Hyla granosa Boulenger y se está reestableciendo como un especie separata, a base de differencias morfológicas, ecológicas y acústicas. Otro pariente de este grupo que se encuentra en Guiana es Hyla sibleszi Rivero. La especie Hyla punctata (Schneider) ha sido estudiada por que en preservación es muy parecida a H. granosa. Se presenta una extensa descripción morfológica asi como datos sobre historia natural y distribución de las cuatro especies. Se señalada para H. sibleszi, especie de la que solo se conocia el material tipo y algunos ejemplares asociados, algunos nuevos localidades en Venezuela y Guyana. Para explicar el modelo dorsal intrincado de H. ornatissima se propone que este modelo probablemente sirve para proteger al animal de la predacion debido al parecido que presenta con las hojas de los árboles donde este rana vive. Se presenta una clave para la distinción de las cuatro especies.

Introduction

The small green treefrogs of the *granosa* and *punctata* groups occurring in the Guiana's are difficult to deal with, because in preservative they all are superficially very similar, with the exception of *Hyla ornatissima*, which in preservative still retains its conspicuous pattern. The reason for this

superficial similarity is that while the colour in life of all these frogs is green, with or without a pattern of some other colour, in preservative the animals become whitish and lose much of their pattern in life. This is caused by the fact that their colour originates from biliverdin, a green pigment resulting from the degradation of hemoglobin from hemolysed red blood cells and which cannot be excreted sufficiently by the liver (Jones, 1967, 1968a, b, 1969). The biliverdin is responsible for the green colour of the bones, the muscles and the lymph. In preservative biliverdin rapidly disintegrates, resulting in the pale, whitish specimens. As a consequence of this superficial resemblance there has been considerable confusion regarding frogs of these groups and some have been synonymised with others, or were only recently recognised as being separate species. However, when one knows the species alive, knows their colours, their habitat and their call, there is no problem at all in separating them. Personally I obtained

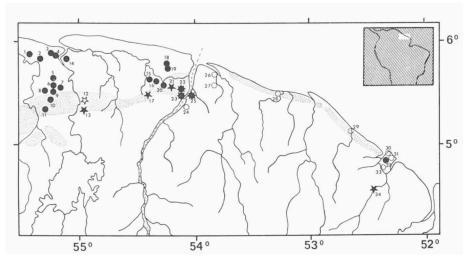


Fig. 1. Distribution of H. granosa (five-tipped asterisks) and Hyla punctata (dots) in north-eastern Surinam and northern French Guiana. Localities where both species occur (22, 23, 25; 77 in fig. 2) have been indicated with an eight-tipped asterisk. Solid symbols represent material examined; open symbols represent acoustical observations in Surinam, literature records in French Guiana (Lescure, 1976). I. 27 km W. Paramaribo; 2. Uitkijk road; 3. Paramaribo (Charlesberg); 4. Paramaribo; 5. Corner Meursweg/Kennedy Highway; 6. Onverwacht; 7. Overtoom; 8. Republiek; 9. Kennedy Highway, 36 km S. Paramaribo; 10. Zanderij; 11. Berlijn; 12. Encampment Blakawatra; 13. Encampment 8; 14. 5 km E. Meerzorg; 15. Moengo; 16. 2 km W. Ricanau Creek; 17. Patamacca; 18. Third swamp, km 19; 19. Djai or Jai Creek; 20. Moengo Tapoe; 21. 8 km E. Moengo Tapoe; 22. 10 km W. Albina + Mooi Wane Creek; 23. Between Albina and Papatam; 24. St. Jean du Maroni; 25. St. Laurent du Maroni; 26. Mana; 27. Acarouany; 28. Iracoubo; 29. Kourou; 30. Cayenne; 31. Montjoly; 32. Crique Cabassou; 33. Rochambeau; 34. River Comté.

data in the field on all four species treated here and I thought it useful to present extensive descriptions of preserved specimens and data on living specimens in order to end the confusion regarding the taxonomic status of these frogs.

Two other species of Hyla from the Guianas are green in life, whitish in preservative. They can be distinguished from the present species by their larger size (Hyla fuentei Goin & Goin) or by the presence of distinct tarsal and ulnar ridges and triangular dermal heel appendages (Hyla albomarqinata Spix). However, it should be mentioned here that both of these species are somewhat problematical. H. fuentei is only known from the holotype and two additional specimens from near the type-locality. One of these (RMNH 18614) was recently collected near the Marechals Creek in Surinam. H. albomarginata was reported from Surinam by Goin (1971), from French Guiana by Lescure (1976) and from Guyana by Boulenger (1900) and Parker (1935). The Surinam and French Guiana records are based on old material of which the locality is not very reliable, the Guyanese material (BMNH 99.3.25.20, specimen reported by Boulenger; BMNH 1930.10.10.53, specimen reported by Parker) actually consists of specimens of respectively H. sibleszi and H. granosa. As no recently collected material of H. albomarginata is available, I think that the records of this species from localities north of the equator either are based on misidentified material or on wrongly labelled specimens. The distribution Duellman (1977) gives for this species in my opinion is too extensive and I think that the distribution given by Lutz (1973) is closer to the actual situation.

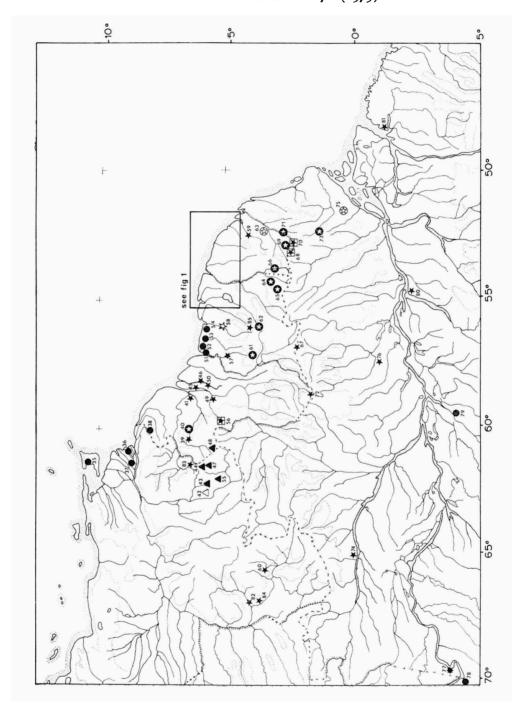
Hyla granosa Boulenger

Hyla granosa Boulenger, 1882: 358; Beebe, 1919: 208; Nieden, 1923: 301; Crawford, 1931: 33; Crawford & Jones, 1933: 90 (partly); Parker, 1935: 512; Lutz, 1951: 326; Rivero, 1961: 99 (partly); Bokermann, 1966: 51; Cochran & Goin, 1970: 231; Rivero, 1972: 181 (partly); Lutz, 1973: 70; Duellman, 1974: 8 (partly); Lescure, 1975: 77; Lescure, 1976: 495; Duellman, 1977: 62 (partly); Lescure, 1977: 93.

Hyla albomarginata, Parker, 1935: 511.

Hyla inornata Lutz, 1951: 328 (nomen nudum); Lutz, 1973: 70 (nomen nudum).

Material. — Surinam. Distr. Nickerie. BWKW-camp Kabalebo: 1 9, 3 \$ \$, RMNH 17888, 22-VII-1975, leg. M. S. Hoogmoed & W. N. Polder. Upper Kutari River ("New River, 750 ft"): 1 \$, BMNH 1939.1.1.60, leg. C. A. Hudson. Distr. Suriname. Encampment 8: 1 \$, RMNH 15077, 12-V-1968, leg. M. S. Hoogmoed. Distr. Marowijne. Patamacca: 2 \$ \$, RMNH 17887, 25-II-1975, leg. M. S. Hoogmoed. 8 km E. of Moengo Tapoe: 1 \$, RMNH 15099, 8-VI-1968, leg. M. S. Hoogmoed. 10 km W. of Albina: 2 \$ \$, RMNH 17884, 14-I-1975, I \$, RMNH 17885, 15-I-1975, all leg. M. S. Hoogmoed. Between Albina and Papatam: 1 9, 1 \$, RMNH 17886, 17-I-1975, leg. M. S. Hoogmoed. Distr. Brokopondo. Airstrip Rudi Kappel (Tafelberg): 1 \$, MSH field no. 1979-2774, 13-VII-1979, leg. M. S. Hoogmoed & W. N. Polder.



French Guiana. River Comté: 1 9, 2 8 8, MNHNP 1977.644-46, 14-II-1970, leg. J. Lescure. Pierrette, Approuague River: 1 9, 4 8 8, MNHNP 1977.647-651, 17-II-1971, leg. J. Lescure. Environs of Saint Laurent du Maroni: 1 8, MNHNP 1977.652, January 1970. Haut Oyapock. Creek Euleupousing: 1 hgr., MNHNP 1977.637, 13-III-1976, leg. J. Lescure. Between Village Zidock and Trois Sauts: 1 9, 12 8 8, MNHNP 1977.653-665, leg. J. Lescure.

Guyana. Mazaruni - Potaro Distr. Kaieteur top: 1 9, BMNH 1938.10.3.21, leg. J. Smart; Machreba Falls, Kurupung River: 1 ex., UMMZ 85183, 22-II-1939, leg. A. L. Pinkus. Kartabo: 1 ex., AMNH 39734, 1 ex., CM 5436, 2-VIII-1925, leg. E. P. Jones. Potaro Road, 82 miles S. of Bartica: 1 9, BMNH 1934.11.1.41, 1 8, WCAB 2244, 1 8, MZUSP 10861, all leg. G. S. Carter. East Demerara-West Coast Berbice Distr. Moraballi Creek: 1 9, BMNH 1930.10.10.53, leg. Buckland (Oxf. Univ. Brit. Guyana Exp.); 1 ex., OUM (Oxford University Museum) 3157 B 218, 6-XI-1959. Demerara Falls: 1 9, BMNH 1947.2.12.93 (72.10.16.45) (paralectotype). Wismar: 1 ex., AMNH 45752. Marudi Creek: 1 ex., AMNH 46234. Rupununi Distr. Upper Essequibo River, between Camp 2 and Onoro: 2 hgr., BMNH 1936.4.2.37-38, 22-XI-1935, leg. J. G. Myers. Essequibo River: 2 ex., AMNH 49260, 49262. No further data: 2 ex., AMNH 10400, 39085.

VENEZUELA. Territorio Amazonas. La Culebra, Upper Cunucunuma River: 7 & & , UPRM 119-125, 31-V-1950, leg. J. A. Rivero. Canaripo: 1 & , 2 & & , RMNH 18704-06, 28-V-1978, leg. M. S. Hoogmoed & J. Cerda. Between Caño Cotua and Cerro Yapacana: 1 & , RMNH 18706, 3-VI-1978, leg. M. S. Hoogmoed & J. Cerda. Estado Bolívar. 85 km S. of El Dorado: 2 & & , RMNH 18708-09, 9-VI-1978, leg. M. S. Hoogmoed.

Brazil. 2 9 9, BMNH 1947.2.12.97-98 (74.7.16.5-6) (paralectotypes). Estado Pará. Santarem: 2 9 9, BMNH 1947.2.12.94-95 (75.10.22.7-8), leg. H. Wickham (paralectotypes). Belém: 1 3, MNRJ 3336, Utinga, 31-VIII-1944, leg. B. Lutz; 1 3 MNRJ 1640, Aura, leg. A. Carvalho. [Igapo] Cachimbo: 3 3 3, MZUSP 21828-30, 18/X-19/XI-1955, leg. F. S. Perreira et al. Estado Amazonas. Igarapé Belém, Rio Solimões: 10 ex., MZUSP 26532, 26534-37, 26539-43, 8/28-IV-1966, leg. B. Malkin. Taparucuara, Rio Negro: 1 hgr., RMNH 17890, leg. P. J. M. Maas. Estado Mato Grosso. Aldeia Tapirapé: 1 3, MNRJ 3143, leg. A. L. de Carvalho. Estado Acre. Porangaba, Rio Jurúa-Mirim: 1 9, RMNH 17889, leg. P. J. M. Maas. Feijo: 2 ex., WCAB 1251, 1254. Tarauacá: 2 ex., WCAB 1364-65. Serra da Moa: 1 3, RMNH 17921, leg. P. J. M. Maas.

Fig. 2. Distribution of Hyla granosa, H. ornatissima (circles wtih asterisk inside), H. punctata and H. sibleszi (triangles) in the Guiana area. Localities where H. granosa and H. ornatissima occur together (56, 68, 70) have been indicated with a square with a solid asterisk inside. For further explanation of symbols see legend of fig. 1. 35. Port of Spain; 36. Guayo; 37. Araguaimojo; 38. Yarakita River; 39. Kurupung River; 40. Meamu River; 41. Kartabo; 42. Guayaraca + Auyántepui; 43. Camarata; 44. Paso del Danto, km 112-120; 45. Moraballi Creek; 46. Wismar; 47. km 126-132 road between El Dorado and Sta. Elena de Uairén; 48. Roraima; 49. 82 miles S. of Bartica; 50. Demerara Falls; 51. 10 km SW. Nieuw Nickerie; 52. SE. Nieuw Nickerie; 53. Wageningen; 54. East-West road, 93 km W. Paramaribo; 55. Acopántepuí; 56. Kaieteur Falls; 57. BWKW Camp, Kabalebo; 58. Witagron; 59. Pierrette; 60. La Culebra; 61. Rechter Kabalebo River, 7 km S. Camp Keyser; 62. Gran Rio; 63. Yanioué; 64. Loë Creek, Camp Hofwijks II; 65. Loë Creek, Camp Hofwijks VII; 66. Tanpoc River; 67. "New River, 750 feet"; 68. Creek Euleupousing; 69. Montagne St. Marcel; 70. Village Zidock + Village Pina + Trois Sauts; 71. Creek Yengalu; 72. Upper Essequibo River, between Camp 2 and Onoro; 73. Serra do Navio; 74. Taparucuara; 75. Rio Camaipí; 76. Igapo Cachimbo; 77. Igarapé Belem; 78. Benjamin Constant; 79. Borba; 80. Santarem; 81. Belém; 82. Canaripo; 83. 85 km S. of El Dorado; 84. Between Caño Cotua and Cerro Yapacana; 85. Airstrip Rudi Kappel (Tafelberg).

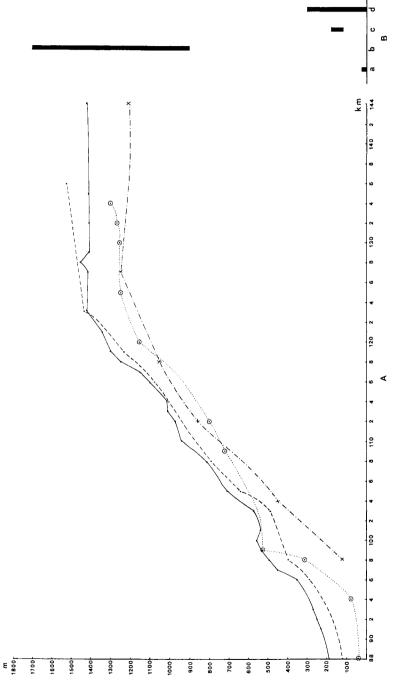


Fig. 3. A. Profile of northern slope of Serra de Lema, showing the altitude of localities on the El Dorado — Sta. Elena de Uairén road, between km 88 and 144. Observations made by Hoogmoed in 1978 (drawn line: sunny weather, 15/16 May 1978; stippled line: rainy weather, 9/10 June 1978), by Duellman in July 1974 (dots and dashes) and by Anonymus (line of dashes). B. Altitudinal distribution of a. Hyla punctata (Schneider), b. H. siblessi Rivero, c. H. ornatissima Noble, d. H. granosa Boulenger.

COLOMBIA. Caquetá. Tres Esquinas: 3 ex., WCAB 40529-31. Rio Arteguaza: 5 ex., WCAB 40591-93, 4601-02.

Peru. Estiron. Rio Ampyiacu: 131 ex., MZUSP unnumbered, 15/22-V-1966, leg. B. Malkin.

ECUADOR. Pastaza. Canelos: 1 &, BMNH 1947.2.12.99 (80.12.5.181), leg. Buckley (lectotype).

Diagnosis. — A medium-sized (snout-vent length of males 30-43 mm, of females 33-38 mm) Hyla of the granosa species group. Male with a small prepollex and a non-protruding prepollical spine. Prevomerine teeth in fairly short, angular to arched rows. Skin of dorsum and belly coarsely granular. Tympanum round, distinct, approximately half the horizontal diameter of the eye, separated from the eye by a distance half its diameter to slightly less than its diameter. A feeble, curved supratympanic fold. Interorbital distance 1.8-3.3 times the width of an upper eyelid. Discs on fingers smaller than the tympanum. Subarticular tubercles 3rd and 4th finger single. When the hindlimbs are folded and flexed at right angles to the sagittal plane, the heels do touch or are narrowly separated. Colour in preservative pale yellowish grey or pink, with purple, pinkish or cream-coloured upper eyelids, a transverse brown band or row of spots on top of the head between the eyes. Short brown canthal stripes, starting from the nostrils, and some scattered brown spots on the back, the shanks and the forearm may be present.

Description. — Head as long as wide, narrower than body, flat, depth 1/3 of the head length. Snout round in dorsal, truncate in lateral profile, not projecting over the mouth; fairly long, up to 1.5 times the horizontal diameter of the eye. Distance between eye and nostril approximately as long as the diameter of the eye $(74.5\text{-}102.4\% \ (\bar{x} = 88.0, N = 20))$ in females, 76.7-104.9% ($\bar{x} = 94.2$, N = 98) in males), much more than twice the distance between nostril and tip of snout. Canthus rostralis indistinct, rounded, concave; loreal region weakly concave, sloping gradually to the lips. Lips not flaring. Nostrils laterally and ventrally of the canthus rostralis, distinctly protuberant, directed laterally. Distance between the nostrils at least half the interorbital distance, wider than an upper eyelid. Interorbital space flat to slightly convex, 1.8-3.1 ($\bar{x} = 2.3$, N = 19) times as wide as an upper eyelid in females, 1.8-3.3 ($\bar{x} = 2.4$, N = 83) times in males. No cranial crests. Temporal region sloping steeply. Tympanum large, round, approximately half the horizontal diameter of the eye, separated from the eye by a distance approximately half its diameter; situated just anteriorly of the insertion of the forelimb. Supratympanic fold feeble, obscuring the upper edge of the tympanum, sharply curved, from posterior corner of eye to insertion of forelimb.

Choanae large, oval. Prevomerine processes present, medium-sized, bearing two angular to arched rows of teeth, 5-15 teeth per row; situated between the posterior parts of the choanae. Tongue round to cordiform, attached to the floor of the mouth, only its lateral and posterior margins free. Male with paired vocal slits, one on each side of the tongue, extending from the midlateral base of the tongue to near the corner of the mouth, 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, including top of head, flanks and belly coarsely granular; skin of throat finely granular. Anterior and ventral aspects of limbs smooth, all other surfaces of limbs coarsely granular. Skin in groins and axils smooth. No axillary membrane. Males with a distinct, large mental gland of variable shape, from elongate kidney-shaped to oval.

Males with a small prepollex and a non-protruding, small prepollical spine. Inner metacarpal tubercle oblong, merging into the prepollical swelling. Outer metacarpal tubercle hardly distinguishable, small, round. Subarticular tubercles present, single, hardly larger than the granules of the skin covering the palms. First finger shorter than second, second shorter than fourth, third longest. Web between fingers present, between first and second rudimentary, webbing formula: 1 (3), 2i (3), 2e (1¾), 3i (3), 3e (2¼), 4 (2). Discs on fingers round, with a groove around the edge, large, subequal, distinctly smaller than the tympanum.

An indistinct, large, oval inner metatarsal tubercle. No outer metatarsal tubercle. Subarticular tubercles present, round, flat, single, not very distinct. Third toe slightly shorter than fifth. Web between toes present, webbing formula: $I(I^{1/2})$, I(I), I(I),

In living specimens the back in daytime is grass-green with yellow-green fingers and toes. Upper eyelids yellow. Back with red spots. A transverse series of red spots between the eyes, red canthal stripes extending from the nostrils backwards. Throat green, belly flesh-coloured with green to bluish-green hue, lower surface of limbs green. Entrails enclosed by chalky white integument. Bones green. Iris orange-, reddish- to chestnut-brown. At night the animal changes colour and the back becomes more or less orange.

In preservative the back is cream-coloured to yellowish-grey in specimens preserved during several years, pink in recently (two years) preserved speci-

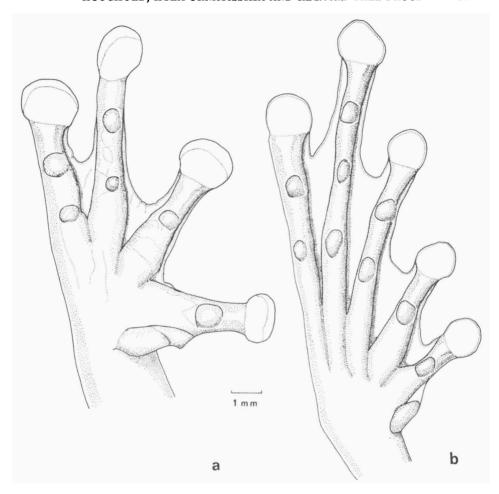


Fig. 4. Hyla granosa (3, RMNH 17884a). a. ventral view of right hand; b. ventral view of right foot.

mens. Upper eyelids yellowish. Back with a highly variable pattern. In some specimens from Venezuela, Guyana, southern Surinam, Brazil and in nearly all from French Guiana, there is a conspicuous, transverse, brown (white in juveniles) band between the eyes and a short brown canthal stripe, extending backwards from the nostrils. On the back several large, brown spots, with a white margin are present. Similar spots are present on the lower arm (one, rarely two), on the shanks, where they form a row of three or four, starting on the knee and ending at the heel, and on the tarsi (three to five), extending on to the fifth toe. A good drawing of a specimen showing this pattern (BMNH 1947.2.12.97) has been published by Boulenger (1882), whereas

Lutz (1951) and Rivero (1972) published photographs of this specimen. See also pl. 1 fig. b.

In most specimens from Venezuela, Guyana, Surinam and Brazil examined by me, the pattern (brown or purple) is very reduced: the interorbital bar has been broken into several small spots or even has disappeared completely. The canthal stripes still may be present, often reduced to small clusters of melanophores around the nostril, sometimes absent. The spots on the back are reduced to small dots, either several or just a few, scattered randomly, sometimes the back is immaculate. There seems to be a tendency in females from Surinam and Guyana to be more extensively patterned. Belly immaculate, creamish, with a central white spot, caused by a white area in the abdominal muscle layer. All internal organs covered by white integuments.

Measurements. — Snout-vent length in males 30-43 mm ($\bar{x}=37.6$, N = 50), in females 33-38 mm ($\bar{x}=35.3$, N = 10). It is of interest to note that the males tend to be larger than the females, an unusual occurrence in frogs. Tibiae in males 45.0-53.2% ($\bar{x}=49.2$, N = 99) of the snout-vent length, in females 49.1-53.5% ($\bar{x}=51.6$, N = 20). Head length in males 33.2-38.6% ($\bar{x}=35.3$, N = 49) of snout-vent length, in females 32.3-38.8% ($\bar{x}=35.4$, N = 10). Diameter of eye in males 1.4-2.3 times ($\bar{x}=1.7$, N = 98) the diameter of the tympanum, in females 1.3-2.3 times ($\bar{x}=1.8$, N = 20). For a comparison with the other species see fig. 11.

Natural history. — A nocturnal species. Specimens were caught in the months January-August, October and November. Data from Surinam cover the months January, February, April-July and October-November, which coincide with the short and the long rainy season and (October-November) with the long dry season (Hoogmoed, 1969). In all these months calling males were collected or heard. Lescure (1976) found calling males and females with nearly mature oviducal eggs (MNHNP 1977.651 in French Guiana in February. In July a female (RMNH 17888a) with large, oviducal eggs was captured in the midst of a chorus of calling males, in January a female (RMNH 17886b) with well developed oviducts was collected, and another female (RMNH 17889) collected in Acre, Brazil in May had small ovarian eggs. During recent field work in Venezuela calling males and a female with mature oviducal eggs (RMNH 18704) were obtained in early June. From these data it might be concluded that this species breeds during the short and the long rainy season. The acoustical observations of calling males in October 1975 (Blakawatra) and November 1975 (airstrip Rudi Kappel (Tafelberg)) in Surinam still remain puzzling, because breeding of

this species during the long dry period seems unlikely. Unfortunately no specimens could be collected on those occasions, though the occurrence of the species there is now substantiated for both localities by voucher specimens (RMNH 15077 and MSH field no. 1979-2774). Calling males were collected between 19.15 and 23.40 hours. Females were collected during the same period. The males were calling from trees, bushes and herbaceous vegetation 20-250 cm above the ground. Sometimes the specimens were on branches, most of them, however, were sitting on slightly inclined leaves, with stretched arms leaning on the lower part of the leaf, thus causing the body to attain a more or less horizontally position. The leaves the frogs were sitting on were fairly large to large, with a smooth surface. The call emitted is very loud, clear, musical and can be heard over fairly large distances (several hundreds of meters). Once heard it cannot be easily mistaken for the call of any other Surinam frog (pl. 5 figs. a, b). Crawford & Jones (1933) describe the call of this species as being a medium-pitched "pink", which certainly is not the case. This description much more reminds me of the call of Hyla punctata. Crawford & Jones (1933) say they have three specimens from near Kartabo. Of these I saw one (CM 5436), which unmistakably is Hyla granosa. I therefore come to the conclusion that either the authors by some lapse attached the field data to the wrong specimens or that their material consisted of both H. granosa and H. punctata.

Habitat. — In Surinam the species is known from a number of localities in or near the coastal savanna belt (figs. 1, 2), all with a white sand type of soil. The frogs were found in rather open situations, either small swampy areas in forest or in restricted open areas adjacent to forest, like eroded creek valleys and wet clearings. Anyway, in my experience this frog ranks in Surinam as an inhabitant of forest on sandy soil, not of extensive open vegetations like swamps or savannas.

In Canaripo, this species was only collected in forest edges bordering on flooded savanna-areas. Both savanna and forest were on coarse riversand. At the foot of Cerro Yapacana the species occurred in inundated caatinga forest, which is relatively open and on sandy soil. Near Las Claritas (85 km south of El Dorado) specimens were calling from the forest edge along road-side pools in rain forest areas with lateritic soils.

Combining these data from Venezuela with those from Surinam I think we can state that *Hyla granosa* is an inhabitant of rather open forests and prefers edge situations. The apparent correlation with sandy soils probably is due to the fact that the vegetation on that type of soil is rather more open than on loamy soil.

Range and distribution. — The species ranges over the greater part of the Amazon region and the Guianas, from Colombia, Ecuador and Peru to Brazil, Venezuela and the three Guianas. In Surinam the species is only known from the coastal savanna belt, from one locality in Central Surinam and from one in the extreme south. The French Guianese (Saint Laurent du Maroni) and Guyanese localities at least partly coincide with the continuations to respectively the east and the west of the Surinam coastal savanna belt in the neighbouring countries. Some other localities are situated in the interior of both countries (Pierrette, River Comté, Haut Oyapock, Machreba Falls, Upper Essequibo River). The Surinam coastal savanna belt specimens occur from 0-40 m above sea level, the specimen from the south was collected at 750 feet, the one from Central Surinam at 300 m. The recently collected Venezuelan specimens (RMNH 18704-09) all are from elevations between 90 and 200 m. No data are available on the altitudes of other localities where this frog was collected (figs. 1, 2, 3). On the basis of data I communicated to him, Lescure (1975: 77, map 6) was the first to mention this species from Surinam, without indicating his source.

Discussion. — The presence of two pattern morphs in the type-series of Hyla granosa Boulenger led Lutz (1951, 1973) to suppose that Boulenger's material was not monospecific, but could contain two species, an ornamented one and a plain one. This opinion was shared by Bokermann (1966). Lutz expressed as her opinion that the name granosa should remain attached to the ornamented specimens and for the plain ones she suggested the name inornata. The proposition was purely speculative and not accompanied by a valid description and thus the name Hyla inornata Lutz, 1951 constitutes a nomen nudum under the rules of the International Code for Zoological Nomenclature. Duellman (1974), discussing the synonymy of Hyla granosa, quite correctly considered Hyla inornata Lutz as such, but apparently was not aware of the fact that Lutz proposed the name for the first time in 1951, not in 1973.

Cochran & Goin (1970) restricted the type-locality to "British Guiana, Demerara Falls", but they did not select a lectotype. Duellman (1974) selected BMNH 1947.2.12.99 from Canelos, Provincia Pastaza, Ecuador as lectotype. Consequently the type-locality now is Canelos, Ecuador, which invalidates Cochran & Goin's (1970) type-locality restriction.

When starting my studies on this group of frogs, I was inclined to give Lutz's suggestion that there might be two species in the type-series of *Hyla granosa* serious consideration. One of the reasons that prompted me to investigate the matter was that among 'recently' (about 35 years ago)

collected material there were both a male and three halfgrowns, showing the well-defined pattern. Originally, and I must admit, till recently, it was thought that the well-defined pattern only occurred in females, the males were supposed to be plain. This new material, however, showed that the theory of sexual dimorphism in pattern in this species no longer could be maintained. After examining the entire type-series and numerous other specimens from different parts of the range, I came to the conclusion that the type-series just contains the extremes of pattern which may occur in this species and between which all possible transitions exist. From the above it is clear that the well-defined pattern is not restricted to females, but also occurs in males, although it should be pointed out that the percentage of females showing a distinct and complete pattern is much higher than that in males in Surinam and Guyana, though not in French Guiana. The series of males from La Culebra (UPRM 119-125) illustrates best the enormous variation there may be in pattern. Four specimens have no pattern whatsoever, two specimens have the basic headpattern and several spots on the back, whereas the most extreme pattern I am acquainted with in this species is exhibited by UPRM 119, which has a large triangular figure on the back (pl. 1 fig. a). Seeing such specimens might easily lead to confusion with H. ornatissima, when anatomical details are not properly considered.

Rivero (1961, 1972) and Duellman (1974, 1977) synonymised Hyla ornatissima Noble with H. granosa Boulenger. As will be pointed out under H. ornatissima this opinion should be rejected.

Hyla ornatissima Noble

Hyla ornatissima Noble, 1923: 291; Crawford, 1931: 33; Lutz, 1951: 328; Goin, 1971: 14; Lutz, 1973: 72; Lescure, 1975: 76; Lescure, 1976: 498; Lescure, 1977: 93.

Hyla granosa (partly), ? Rivero, 1961: 101; Rivero, 1972: 182; Duellman, 1974; 8; Duellman, 1977: 62.

Material. — Surinam. Distr. Nickerie. Rechter Kabalebo River: 1 &, RMNH 17883, 7 km S. Camp Keyser, 24-V-1975, leg. M. S. Hoogmoed & A. Deel. Distr. Brokopondo. Gran Rio: 1 ex., RMNH 4859, 23-VIII-1910, leg. J. F. Hulk. Distr. Marowijne. Loë Creek, Camp Hofwijks II: 1 &, RMNH 17882, 31-VII-1975, leg. M. S. Hoogmoed. Loë Creek, Camp Hofwijks VII: 1 &, RMNH 17879, 6-VIII-1975, 6 & &, RMNH 17880, 3/4-VIII-1975, 3 & &, RMNH 17881, 1-VIII-1975, all leg. M. S. Hoogmoed; 1 &, AMNH 90790, 1/4-VIII-1975, leg. C. W. Myers.

French Guiana. Tanpoc River. Koumakou Rapids: 1 & MNHNP 1977.643, March 1977, leg. Moretti. Haut Oyapock: 1 & MNHNP 1977.641-42, 1976, 1 & MNHNP 1977.639, 9-V-1976, all leg. P. Grenand. Haut Oyapock. Creek Euleupousing: 1hgr., MNHNP 1977.635, 12-III-1976, leg. M. Descamps. Montagne Saint Marcel: 1 & MNHNP 1977.636, July 1975, leg. J. J. de Granville. Between Village Pina and Village Zidock: 1 & MNHNP 1977.638, 22-IV-1976, leg. P. Grenand. Village Zidock: 1 & MNHNP 1977.640, 1976, leg. P. Grenand.

GUYANA. Potaro-Mazaruni Distr. Upper Potaro River (formely Tung Distr.): 2 & &, BMNH 1905.11.1.41-42. Meamu, Mazaruni River: 1 Q, AMNH 13491, 10-VI-1920, leg. W. Beebe (holotype).

Brazil. Territorio Amapá. Rio Amapari, km 180: 1 9, 3 8 8, WCAB 5692-95. Creek Yengalu (border Brazil/French Guiana): 1 8, MNHNP 1977.666, 22-IV-1976, leg. P. Grenand.

Diagnosis. — A medium-sized (snout-vent length of males 29-31 mm, of females 40-42 mm) Hyla of the granosa species group. Male with a distinct prepollex and a projecting prepollical spine. Prevomerine teeth in long, straight to slightly convex, oblique (converging anteriorly) rows. Skin of dorsum smooth, that of belly coarsely granular. Tympanum round, 1/4-1/3 of the horizontal diameter of the eye, separated from the eye by a distance slightly less than its diameter. A feeble supratympanic fold. Interorbital distance 1.1-1.8 times the width of an upper eyelid. Discs on fingers larger than the tympanum. Subarticular tubercles of 3rd and 4th finger bifid. Eyes every large, bulging. When the hindlimbs are folded and flexed at right angles to the sagittal plane the heels show considerable overlap. Colour in preservative creamish with a dark reddish pattern consisting of short canthal stripes, a transverse, halter-shaped band between the eyes and a longitudinal stripe on the back, widening into a rhomboid halfway. Legs with series of spots.

Description. — Head as long as wide, distinctly wider than the adjacent part of the body, very flat, depth one third of the head length in males, one fourth in females. Snout round in dorsal, truncate in lateral profile, projecting slightly over the mouth; short, slightly longer than the horizontal diameter of the eye. Distance between eye and nostril mostly shorter than the horizontal eye diameter (81.1-117.1% ($\bar{x} = 94.5$, N = 8) in females, 63.3-97.5% $(\bar{x} = 73.9, N = 46)$ in males), 2.5-3 times the distance between nostril and tip of snout. Canthus rostralis indistinct, rounded, concave; loreal region distinctly concave, gradually sloping to the lips. Lips not flaring. Nostrils very protuberant, situated in swollen areas laterally and ventrally of the canthus rostralis, directed laterally. Distance between the nostrils at least half the interorbital distance, less than the width of an upper eyelid, about twice as much as the distance between nostril and tip of snout; area between the nostrils concave. Interorbital space slightly convex, in males 1.1-2.1 times $(\bar{x} = 1.3, N = 47)$ as wide as an upper eyelid, 1.6-2.6 times $(\bar{x} = 1.9,$ N = 7) in females. No cranial crests. Temporal region sloping steeply. Tympanum distinct, small, round, approximately 1/3-1/4 the horizontal diameter of the eye; separated from the eye by a distance slightly less than its diameter; situated just anterior of the insertion of the forelimbs. A feeble,

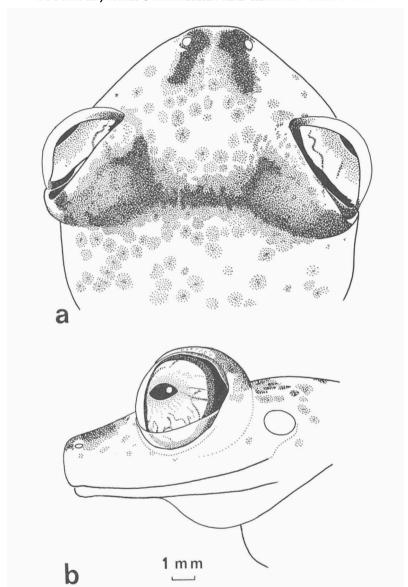


Fig. 5. Hyla ornatissima Noble (3, RMNH 17880a). a. dorsal and b. lateral view of head.

sharply curved supratympanic fold from the posterior corner of eye to insertion of forelimb, not obscuring the upper margin of the tympanum.

Choanae large, oval. Prevomerine processes present, medium-sized, bearing two oblique, long rows of teeth, straight or with the ends curved in opposite directions, the median end curved backwards, the lateral end forwards, 8-16 teeth per row; situated at the level of the line connecting the posterior margins of the choanae. Tongue small, round to cordiform, attached to the floor of the mouth, only its lateral and posterior margins free. Males with subgular vocal sacs, opening into the mouth via long slits, one on each side of the tongue, from its midlateral base to near the corner of the mouth, 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 smooth. Skin of throat finely shagreened, skin of belly and under the thighs coarsely granular. Skin in groins and axils smooth. No axillary membrane. Males without a mental gland.

Males with a well developed prepollex and a projecting prepollical spine. Inner metacarpal tubercle indistinct, oval, merging with the area around the

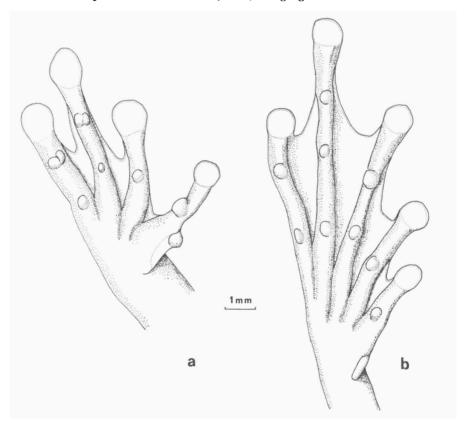


Fig. 6. Hyla ornatissima Noble (3, RMNH 17884a). a. ventral view of right hand; b. ventral view of right foot.

prepollical spine. Outer metacarpal tubercle indistinct, round, smaller. Subarticular tubercles present, the ones under the penultimate articulation of third and fourth fingers bifid. First finger shorter than second, second shorter than fourth, third longest. Web between fingers present, between first and second rudimentary, webbing formula: I (3), 2i (3), 2e (1¾), 3i (3), 3e (2½), 4 (2¼). Discs on fingers round, with a groove around the edge, large, subequal, larger than the tympanum.

An indistinct, oval inner metatarsal tubercle. A small, oval, very indistinct outer metatarsal tubercle. Subarticular tubercles distinct, round, single. Third toe slightly shorter than or as long as fifth. Web between toes present, webbing formula: I(1), 2i(1), 3i(1), 3e(1), $4i(1\frac{1}{2})$, $4e(1\frac{1}{2}-2)$, 5(1). Web thin, with smooth margin. Toes with well developed round discs, slightly smaller than those on fingers, as large as the tympanum, with a groove around the edge. When the hindlimbs are folded and flexed at right angles to the sagittal plane the heels show a considerable overlap.

In living specimens the back is transparent yellow-green with reddish-brown small spots. A band between the eyes, spots on the canthus rostralis extending backwards from the nostrils, a longitudinal stripe down the middle of the back, widening into a rhomb halfway down its length. The larger spots show a grey centre, surrounded by reddish-brown lines, which in turn are surrounded by a yellow zone. The centre of the rhomb on the back also may show yellow. Limbs with black spots. Palms and soles ochre-yellow. Outer margin of upper eyelids silver-coloured. Belly transparent yellow-green to flesh-coloured, throat pale green, entrails and heart enclosed by chalky-white integument. Bones green. Iris pale reddish-brown to gold-brown around pupil, peripheral area silver to grey-green, colours not separated by a sharp boundary.

In preservative the back is whitish with two short, black, canthal spots, extending backwards from the nostrils, a black halter-shaped figure between the eyes and a black line down the middle of the back from the back of the skull to the vent, widening into a rhomb halfway down its length. Centre of the rhomb light- to dark-brown. In females this rhomb tends to be larger than in males. Lower arm with two black spots, sometimes a third one is present on the base of the fourth finger. Shanks with a row of four to seven black spots from knee to heel, tarsus and fifth toe with a row of four to five black spots. All black spots surrounded by a purple to pinkish area. The larger spots on head and dorsum surrounded by white areas, most extensive around the central dorsal rhomb, more so in females than in males. Dorsum and dorsal surfaces of limbs with brown to purple spots, concentrated around the larger spots. Belly immaculate, white, transparent.

Chalky-white integument well visible, divided into two distinct parts, an anterior part enclosing the heart, the liver and associated organs and a posterior part covering the bladder and the posterior part of the intestine. Stomach and large intestine without chalky-white integument.

Measurements. — Snout-vent length in males 23-31 mm ($\bar{x}=29.6$, N = 24), in females 40-42 mm ($\bar{x}=40.8$, N = 4). There is a distinct sexual dimorphism in size, the females being considerably larger than the males. Tibiae in males 53.9-70.0% ($\bar{x}=57.3$, N = 48) of the snout-vent length, in females 55.2-60.2% ($\bar{x}=57.2$, N = 8). Head length in males 32.6-39.3% ($\bar{x}=35.5$, N = 24) of snout-vent length, in females 33.8-35.5% ($\bar{x}=34.6$, N = 4). Diameter of eye in males 2.2-3.9 times ($\bar{x}=3.2$, N = 46) the diameter of the tympanum, in females 2.1-2.9 times ($\bar{x}=2.6$, N = 8). For a comparison with the other species see fig. 11.

Natural history. — As all other treefrogs this species is nocturnal. Specimens were collected from March through August, that is during the long rainy season in the Guiana's. Two females (WCAB 5693, MNHNP 1977.638) have large, well developed oviducal eggs, unfortunately only of MNHNP 1977.638 the collecting date is known: April 22, 1976, which is at the beginning of the long wet season. The holotype, with well developed oviducts, was collected on the 10th of June, at the height of the long wet season. Most males recently collected in Surinam were collected at night between 19.45 and 00.30 hours in late July and early August. They were calling from branches of small trees and shrubs on the banks of creeks, from one to three meters above the ground. The area they were found in is completely covered with rainforest. Most specimens were collected during or after light showers. The call they emitted was not very loud and hardly could be distinguished over the noise made by falling raindrops or other species calling (pl. 6 fig. c). Thus, it appears that reproduction occurs during the long wet season. One specimen (RMNH 17883) was collected in daytime; when the labourers were clearing an area for a camping-ground it jumped from the stem of a small tree on the arm of one of them. The area being cleared was situated on the bank of a creek in thick rainforest.

Range and distribution. — The species only is known from a few localities in Guyana, Surinam, French Guiana and Amapá (fig. 2). Lescure (1975) mentions a locality "Río Camaipí", based on a specimen in the collection of the Museu Goeldi in Belém (personnal comm. 1977). In Surinam Hyla ornatissima is known from localities between 120 and 180 m above see level (fig. 3). No further details are available for the other known localities.

Habitat. — In Surinam it is an inhabitant of rainforest near creeks in the interior, south of the coastal savanna belt with white sand bottom.

Discussion. — The conspicuous pattern of this frog has been the source of much discussion whether this species should be considered as a mere, extensively patterned variant of Hyla granosa or not. As I have probably seen all except two (Camaipí and Yanioué) of the hitherto known specimens of H. ornatissima, I am convinced that in this species there is hardly any variation in pattern. The confusion arose because of the variation in the pattern occurring in H. granosa (more or less reminiscent of that in H. ornatissima) and the extreme scarcety of specimens of H. ornatissima, of which till a few years ago only eight specimens were known (Goin, 1971; Lutz, 1973). During fieldwork carried out in Surinam and French Guiana by respectively the present author and Lescure in the years 1973-1977 an additional 21 specimens became available, together with data on habitat, natural history and colour of living specimens. These data were of considerable help in solving the problem of the identity of H. ornatissima. As will be pointed out below, in a table, there are enough differences between the two to consider them as distinct species and not as extremes and intergrades of one single species. I think it useful to present a historical review before discussing the differences.

Since its description in 1923 by Noble, on the basis of a single adult female specimen, this species has been treated with some mistrust by taxonomists. The first to use the name after the original description was Crawford (1931), but he did not have material at his disposal and only based himself on the literature. The next author was Lutz (1951), who neither possessed material, did not see the type-specimen, but republished its original description together with a photograph and recognised it as a good species. But, in the same paper, in the discussion of H. granosa, she made the suggestion that "The ornamented females [of H. granosa, M.S.H.] might be akin to Hyla ornatissima Noble". This probably was the source of all trouble. Possibly embroidering on this suggestion, Rivero (1961), in his discussion of H. granosa, says: "Hyla ornatissima Noble is, I believe, a synonym". In 1972, the same author says about his 1961 statement: "El material adicional [of H. granosa, M.S.H.] que he podido examinar desde entonces tiende a confirmar esta opinión aunque hay que admitir que la coloración "ornatissima" es más común en el oeste [here is meant east, M.S.H.] del área de distribución de la especie". He continues saying that in the western ("el este (sic!) (Ecuador y las regiones circunvecinas)") part of the range of granosa specimens with dorsal markings appear, but that these markings are small and with regular margins, whereas in Venezuela and the Guianas they are larger and with irregular margins. Lutz (1973) reports some new specimens of *H. ornatissima* (Bokermann collection), of which she says that their pattern completely agrees with that of the holotype. At the same time she repeats her 1951 suggestion of a possible synonymy with *H. granosa*, but does not take a clear stand in this matter. Duellman (1974) agrees with Rivero and says: "Noble's (1923: 291) type of *Hyla ornatissima* is a patterned juvenile" [of *H. granosa*, M.S.H.]. From his remark it is evident that he did not examine the type, because on closer examination it is immediately clear that the specimen is an adult female (as was said in the original description) with well developed oviducts.

Goin (1971) was the first to report additional specimens from Guyana and Surinam. He mentions Lutz's (1951) opinion on the species, but does not comment on it. As he treats the species separately he apparently is of the opinion that *ornatissima* is a good species. Lescure (1975) compiled the known distribution in a map and considered *ornatissima* a good species. In 1976 the same author mentions the opinion held by Rivero and Duellman, but says he prefers to treat *ornatissima* and *granosa* as two distinct species. In a footnote he adds that he is convinced the two species are distinct after having seen a recently collected male. As differences between the species he mentioned body-size and pattern.

Considering the confusion around granosa and ornatissima I deemed it useful besides giving extensive descriptions of both species, to tabulate the differences between them.

Hyla granosa Boulenger

- 1. Back plain to patterned, pattern mostly not very extensive.
- 2. Skin of dorsum granular.
- 3. Body-form robust.
- 4. Tympanum large, 1/2 the diameter of the eye.
- 5. Vomerine teeth in medium-sized angular or arched rows.
- 6. All internal organs enclosed by white integument.
- 7. One white, central area on the belly.
- 8. Prepollical spine in males not projecting.
- Hand and foot less extensively webbed than in ornatissima.

Hyla ornatissima Noble

- Pattern on back extensive, without much variation.
- 2. Skin of dorsum smooth.
- 3. Body-form slender.
- 4. Tympanum small, 1/4-1/3 the diameter of the eye.
- 5. Vomerine teeth in long, more or less straight rows.
- Stomach and large intestine not enclosed by white integument, rest of internal organs surrounded by white integument.
- 7. An anterior and a posterior white area on the belly.
- 8. Prepollical spine in males projecting.
- Hand and foot more extensively webbed than in granosa,

- 10. When folded and flexed at right angles to the sagittal plane the heels do touch or are narrowly separated.
- 11. Mental gland present in males.
- 12. Eyes rather small.
- 13. Snout-vent length & & 34-42 mm. Snout-vent length ♀ ♀ 33-38 mm.
- 14. Interorbital distance 1.8-3.3 times the width of an upper eyelid.
- 15. Tibia 46-54% of snout-vent length.
- Discs on fingers smaller than tympanum.
- 17. Subarticular tubercles 3rd and 4th finger single.
- 18. Call a double note.
- 19. Habitat: more or less open forests (in Surinam on white sand soil), near small, shallow bodies of water or near small, slow streaming creeks.

- 10. When folded and flexed at right angles to the sagittal plane the heels show a considerable overlap.
- 11. Mental gland absent in males.
- 12. Eyes large.
- 13. Snout-vent length \$ \$ 29-31 mm. Snout-vent length \$ \$ 40-42 mm.
- 14. Interorbital distance 1.1-1.8 times the width of an upper eyelid.
- 15. Tibia 54-61% of snout-vent length.
- 16. Discs on fingers larger than tym-
- 17. Subarticular tubercles 3rd and 4th finger bifid.
- 18. Call a single note.
- Habitat: dense rainforest along running creeks.

A possible explanation for the conspicuous pattern of *H. ornatissima* occurred to me in the field. All specimens collected by me were in trees or shrubs of which the leaves showed signs of insect or fungus attack, resulting in numerous brown spots (light-brown centre, dark-brown margin) or small holes with a brown margin which are surrounded by yellow to yellow-green areas. The pattern of *ornatissima* remarkably resembles these spots. When we start from the view that the animals spend the day sitting on leaves, either on the upper or on the lower surface, we could assume that the *ornatissima*-pattern serves to camouflage its owner by resembling the substrate on which the frog is sitting, and at the same time disrupting its outline. I placed specimens on such affected leaves and made some photographs with and against the light. In the last case the animals were perfectly camouflaged and therefore I think it most probable that the animals in daytime hide on the lower surface of leaves (pl. 4 fig. b).

Hyla sibleszi Rivero

Hyla albomarginata, Boulenger, 1900: 56; Crawford, 1931: 33. Hyla sibleszi Rivero, 1972: 182.

Material. — Guyana. Mazaruni-Potaro Distr. Base of Roraima, 3500 feet: 1 &, BMNH 99.3.25.20, leg. F. V. McConnell & J. J. Quelch. Roraima, northern slope, Camp VIII, 4800 feet: 3 & &, BMNH 1976.1242-44, 29-VIII-1971, 1 &, BMNH 1976.1241, 1-IX-1971, all leg. A. N. Warren. Roraima, 4600 feet: 1 Q, UGDB 12, 23-X-1973, leg. M. Tamessar (Roraima Expedition).

VENEZUELA. Estado Bolívar. Acopántepui, 5600 feet: 1 3, RMNH 17922, 4 3 3, AMNH 56241-44, February 1953, leg. E. McGuire. Auyántepui, southern slope, 1000 m: 3 3, BMNH 1975.1357-58, RMNH 18556, 15-VIII-1974, leg. A. N. Warren. Camarata:

I hgr., BMNH 1975.1355, 10-VIII-1974, leg. A. N. Warren. Road between El Dorado and Santa Elena de Uairén, La Escalera, km 112, 970 m: 2 larvae, RMNH 18736, 10-VI-1978, leg. M. S. Hoogmoed. Km 114, 1010 m: 1 &, RMNH 18721, 16-V-1978, leg. M. S. Hoogmoed & P. Gibbs. Paso del Danto, km 117-119, 1150-1300 m: 1 &, 9 & &, KU 167058-67, 16/18-VII-1974, leg. W. E. Duellman & J. R. Leon; 2 & &, UPRM 3177-78 (holo- and paratype), 22-III-1968, leg. J. A. Rivero & J. Pulido. Km 120, 1320 m: 1 &, 1 &, 9 larvae, RMNH 18733-34, 18737, 10-VI-1978, leg. M. S. Hoogmoed; 4 & &, 3 larvae, RMNH 18722-27, 18735, 16-V-1978, leg. M. S. Hoogmoed & P. Gibbs. Km 126, 1450 m: 1 &, SCNLS 6032, 16-IV-1973, 1 &, SCNLS 6045, 14-IV-1973, both leg. L. Andreani. Km 127, 1410 m: 1 &, 7 & &, RMNH 18713-20, 15-V-1978, leg. M. S. Hoogmoed & P. Gibbs. Km 129, 1410 m: 3 & &, RMNH 18710-12, 15-V-1978, leg. M. S. Hoogmoed & P. Gibbs. Km 132, 1410 m: 5 & &, RMNH 18728-32, 10-VI-1978, leg. M. S. Hoogmoed & P. Gibbs. Km 132, 1410 m: 5 & &, RMNH 18728-32, 10-VI-1978, leg. M. S. Hoogmoed.

Diagnosis. — A medium-sized *Hyla* of the *granosa* species group. Male with a distinct prepollex and large, protruding prepollical spine. Prevomerine teeth in short to long angular rows. Skin of dorsum smooth, of belly coarsely granular. Tympanum round, distinct, about half the horizontal diameter of the eye, separated from the eye by a distance about 3/4 its diameter. A distinct, supratympanic fold. Interorbital distance 1.7-2.6 times the width of an upper eyelid. Discs on fingers covering the tympanum. Subarticular tubercles 3rd and 4th finger single. When the hindlimbs are folded and flexed at right angles to the sagittal plane the heels overlap slightly. Colour in preservative pale brownish white with scattered brown spots, forming a transverse band between the eyes.

Description. — Head as long as wide, as wide as body, flat, depth 1/3 of head length. Snout round in dorsal, truncate in lateral profile, not projecting over the mouth; short, slightly longer than the horizontal diameter of the eye. Distance between eye and nostril mostly shorter than the horizontal diameter of the eye $(77.3-102.2\% (\bar{x} = 87.5, N = 4)$ in females, 72.7-111.8% ($\bar{x} = 86.8$, N = 48) in males), about 2.5 times the distance between nostril and tip of snout. Canthus rostralis distinct, rounded, straight. Loreal region slightly concave, sloping (45°) to the upper lip which does not flare. Nostrils slightly laterally and ventrally of the canthus rostralis in swollen areas, directed laterally. Distance between the nostrils distinctly more than half the interorbital distance, wider than an upper eyelid, area between nostrils concave. Interorbital space flat to slightly convex, 1.6-2.6 times ($\bar{x} = 2.0$, N = 48) as wide as an upper eyelid in males, 2.0-2.3 times $(\bar{x} = 2.1, N = 4)$ in females. No cranial crests. Temporal region sloping steeply. Tympanum large, round, about half the horizontal diameter of the eye, separated from the eye by a distance 3/4 its diameter; situated before the insertion of the forelimbs. Supratympanic fold distinct, straight to slightly curved downwards, from posterior corner of eye to insertion of forelimb, obscuring the upper edge of the tympanum.

Choanae large, oval. Prevomerine processes present, bearing two short or long angular (sometimes straight) rows of teeth, 5-14 teeth per row, situated at the level of the line connecting the posterior margins of the choanae. Tongue cordiform, large, attached to the floor of the mouth, only its lateral and posterior margins free. Males with subgular vocal sacs, opening into the mouth via long slits, one on each side of the tongue, from its midlateral base to near the corner of the mouth, 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, including top of head, flanks and limbs (except ventral surface of thighs) smooth. Skin of belly and ventral surface of thighs coarsely granular, skin of chest and posterior part of throat very coarsely

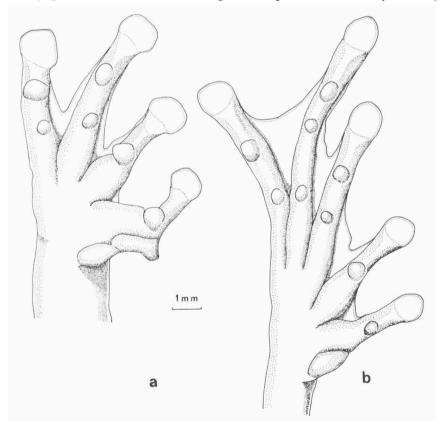


Fig. 7. Hyla sibleszi Rivero (3, RMNH 18728). a. ventral view of right hand; b. ventral view of right foot.

granular, skin of chin and anterior part of throat finely granular. Skin in groins and axils smooth. No axillary membrane.

Males with a large, recurved prepollex and a protruding prepollical spine. Inner metacarpal tubercle oval, large. Outer metacarpal tubercle oval, small. Subarticular tubercles present, single, round. Skin covering palm and basal parts of fingers coarsely granular. First finger shorter than second, second shorter than fourth, third longest. Web between fingers present, virtually absent between first and second finger, webbing formula: I (3), 2i (3), 2e (2), 3i (3), 3e $(2\frac{1}{2}-2^2/3)$, 4 $(2-2\frac{1}{2})$. Fingers distinctly depressed. Discs on fingers round, with a groove around the edge, those of 2nd and 4th finger subequal, largest, that of 3rd finger slightly smaller and that of first distinctly smaller. Largest discs on fingers covering the tympanum.

A distinct, large, oval inner metatarsal tubercle. An indistinct, small, round outer metatarsal tubercle. Subarticular tubercles present, round, flat, single. Toes distinctly webbed, webbing formula: I(2), $2i(2\frac{1}{2})$, $2e(1\frac{1}{4})$, $3i(2\frac{1}{3}-2\frac{1}{2})$, $3e(1\frac{1}{3})$, $4i(2\frac{1}{4}-2\frac{1}{2})$, 4e(2), $5(1\frac{1}{2})$. Web continued to the discs as a ridge along the toes. Toes distinctly depressed. Toes with well developed round discs, subequal, smaller than those on fingers, with a groove around the edge. Basal part of toes with large supernumerary tubercles. When the hindlimbs are folded and flexed at right angles to the sagittal plane the heels overlap slightly.

The collector of the recent Auyántepui (BMNH 1975.1357-58, RMNH 18556) and Roraima specimens (BMNH 1976.1241-44) referred to them as "Green Hylid", thus indicating their colour in life as being green. The female UGDB 12 in life was described as being "olive green, with white spots; toes: orange". An extensive colour description of living specimens was provided by Rivero (1972). In translation it reads as follows: "Above greenish yellow, spotted with greenish brown, upper part of flanks yellowish green, upper eyelids yellow, with small mustard-coloured spots, axil and groin blue, upper part of eye reddish; anterior and posterior part of thigh white (or, much better, flesh-coloured); fingers and fingerdiscs orange, toediscs orange; throat green, chest and anterior part of abdomen blue; lateral parts of abdomen bluish; remainder of abdomen white; bones of the limbs bluish".

W. E. Duellman provided me with slides of living specimens and extensive colour descriptions made in the field. During a recent trip to the La Escalera region I collected this species myself and combining my field data with those of Duellman I come to the following colour description of the living animals. There is a distinct sexual dimorphism in colour. Females have a dark bluish green back with reddish brown and white spots, discs of fingers and

toes orange, throat and other ventral parts transparent, blue; peritoneum white; iris yellow with orange rim around the pupil. Males have a light green back with minute reddish brown, brownish black or black flecks and small white or yellow spots. A pale yellow or yellow interorbital bar and dorsolateral stripes may be present. Interorbital bar bordered by red posteriorly. Throat pale green, other ventral surfaces pale blue, transparent, discs of fingers and toes orange, axilla and groin bluish green; peritoneum white; iris yellow with or without an orange rim around the pupil. Both sexes have green bones.

In preservative back pale brownish white to light brown with scattered brown spots, forming a transverse band between the eyes. Other concentrations of brown spots at the posterior margins of the nostrils, extending onto the canthus rostralis, and on the loreal region. Some males with a white, transverse interorbital stripe in front of the band of brown spots, and with white dorsolateral stripes from the eyes to the groins. Spots on the back in some males (RMNH 18718, 18725) arranged in rather indistinct transverse rows. Female UGDB 12 with larger spots on the back, arranged in transverse rows, three larger spots on the shanks and also a spot on knee and heel respectively. Some specimens with a few scattered white spots on the back. Dorsal surfaces of limbs like the back, on the thigh only a narrow pigmented band. Ventral surfaces of limbs, belly and throat white to brown, transparent. The longer preserved specimens (Acopántepui, Roraima 3500 feet) are brownish rather than whitish like the more recently collected material.

Measurements. — Snout-vent length in males 30-39 mm ($\bar{x}=33.9$, N = 26), in females 35-38 mm ($\bar{x}=36.5$, N = 2). Tibiae in males 44.9-55.0% ($\bar{x}=50.7$, N = 52) of the snout-vent length, in females 49.4-54.7% ($\bar{x}=52.1$, N = 4). Head length in males 31.4-37.9% ($\bar{x}=36.0$, N = 26) of the snout-vent length, in females 36.9-37.9% ($\bar{x}=37.4$, N = 2). Diameter of eye in males 1.5-2.2 times ($\bar{x}=1.9$, N = 50) the diameter of the tympanum, in females 1.7-2.0 times ($\bar{x}=1.9$, N = 4). For a comparison with the other species see fig. 11.

Description of tadpoles. — Lot RMNH 18737 contains specimens in stages 26 to 41 (Gosner, 1960). Stage 26 specimens have snout-vent lengths of 10.5-12 mm, total lengths of 33-36 mm. Stage 36 to 41 specimens have snout-vent lengths of 15-16 mm, total lengths of 46-51 mm. The following description is based on stage 36 specimens. The body is ovoid in dorsal, wedge-shaped in lateral view, about 12/3 times as long as wide, about as

wide as its greatest height. The tail is 2-2.5 times as long as the body, 3.2-3.5 times as long as deep. The dorsal and ventral fin are high; dorsal fin proximally slightly lower than the height of the muscular part of the tail, distinctly higher than the ventral fin. Tip of tail pointed, no filament. Dorsal fin starting at the base of the muscular part of the tail. Anus dextral,

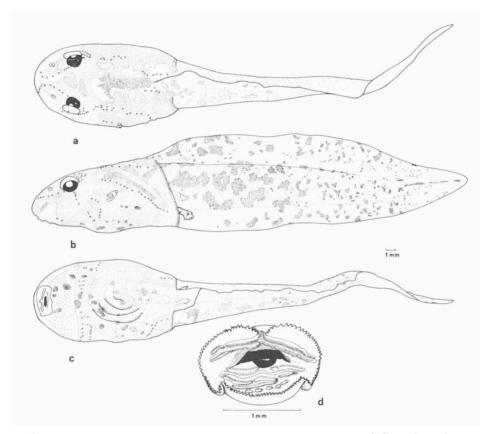


Fig. 8. Hyla sibleszi Rivero (RMNH 18737), tadpole (stage 36 of Gosner). a, b, c, dorsal, lateral and ventral view, d. detail of oral disc.

in a skin-fold connecting the body with the ventral fin, and obliterating a lateral view of the right hind limb bud. Spiraculum on the left side of the body, about halfway down its length. The eyes are situated high on the lateral surface, directed dorso-laterally, not visible from below. Nostrils in front of the eyes, with a small, pointed triangular flap, closer to the eyes than to the tip of the snout. Tip of snout rounded, both in lateral and dorsal profile. Oral disc with two ventral indentations. A row of pointed papillae

around the mouth. Denticle formula $\frac{1+1}{1+1}$. The upper outer denticle row

shows a median spur, directed dorsally, the upper inner denticle row has a wide interruption. Interruption in the lower inner denticle row narrow. There may be connections between the third and fourth lower denticle rows. The lower outer denticle row is not well developed, consisting of several isolated patches of small denticles. Lateral line system present.

Body grey, with rounded dark grey spots on the back and on the belly. Intestines clearly visible. Muscular part of tail creamish, fins opaque grey. Proximal part of tail with many, irregularly shaped dark gray spots, both on the muscular part and on the fins. Distally the spots decrease in number and diminish in size.

Specimens in stages 42 and 43 (RMNH 18726-27) already show the adult pattern, including the white interorbital and lateral lines.

Natural history. — The information provided in this and the next paragraph was obtained during field work and further was taken from the field data accompanying the recently collected Roraima, Auyántepui and Paso del Danto (KU) material. The four Roraima males (BMNH 1976.1241-44) were collected during a very short period (August 29-September 1, 1971) in one locality. They were all caught at 20.30 hours, while calling. BMNH 1976.1242-43 were "caught in water in slow flowing clear water creek in weeds. Semi-submerged + croaking, when disturbed swam to bottom" (collector's note on label). The remaining two males were collected on palm fronds overhanging the water of the same creek, one of them 12 inches over the water. The KU Paso del Danto specimens also were collected during a short period (July 16-18, 1974). The males were calling at night from palm fronds and stems 1-2 m above a low gradient stream, but also from leaves of low herbs and bushes over the water. Rivero (1972) found calling males in the La Escalera region on March 22, 1968. On May 15-16 and June 10, 1978 I collected several calling males between 19.00 and 23.15 hours in the La Escalera region. Some of them, at the edge of a deep pond along the road, were calling partly submerged in the water with only the head protruding out of the water, supporting their body on submerged vegetation. The majority, however, was calling from leafs and twigs above the water of slow flowing creeks, from 10-200 cm above it. Males were calling both during dry weather (May, June) and during downpours (July). The call is a single, short, low-pitched "wraah". Duellman (pers. comm.) recorded 11 notes per minute at 17°C, I recorded 10-11 notes per minute at 19.5°C (pl. 5 fig. c). On the southern slopes of Auyántepui, on August 15, 1974 at 18.30 hours, Warren collected males "calling from water's edge, and from twigs and leaves overhanging water" in a hollow where rain had formed a temporary pool, in a belt of rain forest.

All four available females have well-developed oviducal eggs, with a black and a grey pole. UGDB 12 was collected towards the end of the dry October period at the border of a small stream. KU 167065 was sitting on a branch of a bush about 3 m from a sluggish stream, in mid-July. RMNH 18713 was sitting on a leaf over a small, overgrown, slow flowing creek in high forest in mid-May. RMNH 18733 was perched upon a branch, 10 cm over a sluggish creek at the edge of high forest in early June.

Tadpoles (stages 26-43) were collected in a low gradient creek with brown water, at the edge of high forest at an altitude of 1320 m. The larvae were hiding in a large heap of dead leaves that had been assembled between some submerged, broken branches in a quiet corner of the creek. The water was about 1 m deep, the bottom of the creek consisted of coarse Roraima sand covered with a a layer of leafs. Two other tadpoles were collected in a small, shallow, clear water trickle along the road, also in high forest surroundings. Metamorphosing larvae were found on May 16 and on June 10, 1978.

Although the area from where this species is now known basically has two dry and two wet periods a year, rainfall throughout the year apparently is high enough to enable this species to breed all the year round, as the few available data seem to indicate. From the field data on the BMNH and KU specimens it is clear that they were taken during very rainy weather, although partly in 'dry season' periods. The material I collected myself was taken during dry weather in May and during variable weather in June.

Habitat. — All available data indicate that this is a forestdwelling species, which reproduces in slow flowing creeks which are permanent and never dry up. The forest in the area where the BMNH Roraima specimens were collected was described as "montane forest" (collector's note accompanying BMNH 1976.1241). Philcox in Warren (1973) reports the trees in this forest to belong to smaller species than the ones occurring in the lower regions. Warren (1973) says about this area: "Northern slopes of Roraima, Camps 4-8. The forest here is typically montane. Everything is wet; thick moss covers the branches and trunks of trees, ferns and moss cover the ground, which is rocky and uneven with a thin layer of leaf litter. Streams and rivers are torrential; rain is frequent, even in the dry season. Altitude 2500-5000 feet". Chapman in Warren (1973) reports that August and September are supposed to constitute a transitional period between the rainy season and the dry period of October, but in 1971 "there was still heavy

rainfall in the 'transition' period, during which the British Roraima Expedition took place". And "In other words, 1971 may be rated a heavy rain year in an area noted for its consistently high rainfall". At Pipilipai, situated 28 miles east of Mount Roraima and the nearest weatherstation with regularly kept records sice 1969, the following amounts of total annual rainfall were recorded: 1969: 110.30 inches, 1970: 115.20 inches. Temperatures recorded for Camp VIII varied between 63 and 71° Fahrenheit in daytime, humidity between 95 and 100%. No evening temperatures are available (Chapman in Warren (1973)).

The region in Venezuelan Guiana along the El Dorado-Santa Elena de Uairén road, from where this species is known, apparently has an identical climate and vegetation (Rivero, 1972; personal observations 1978). Ewel et al. (1976) describe the La Escalera region as having forests of the "bosque muy humedo premontano" type which agree largely with Philcox's (1973) description cited above. There are, however, differences mainly in the size of the trees, which seem to be higher in the La Escalera region. Apparently there are no differences in the amount of epiphytic vegetation. The specimen from Camarata was collected "on wall surrounding courtyard". This apparently is in a savanna area, but close to forest.

During recent fieldwork of the author in Venezuela, the impression that $Hyla\ granosa$ and $H.\ sibleszi$ are vicariants, already strongly suggested by the material available from museum collections, was strengthened by the results obtained in the area around Las Claritas and in the La Escalera region. Apparently $H.\ granosa$ is the lowland form, not reaching altitudes of over 300 m, whereas $H.\ sibleszi$ is the form living at higher altitudes where the climate is colder and wetter and the vegetation lusher than at lower altitudes. Thus far the two species have not been found sympatrically and seem to exclude each other (fig. 2, 3).

Range and distribution. — The species is now known from the area between km 112 and 132 south of El Dorado on the road to Santa Elena de Uairén, which includes the type locality Paso del Danto (= km 117-119), from Auyántepui, from Acopántepui, from the base of Roraima and from its northern slopes. *H. sibleszi* is known to occur between 900 m and 5600 feet, all localities being in the vicinity of Mount Roraima, where the ground consists of Roraima sandstone (figs. 2, 3).

Discussion. — Rivero (1972), correctly I think, thought this species to be related with *H. granosa*. The differences reported by Rivero (1972) between the specimens from the road between El Dorado and Santa Elena de Uairén

and those from Guayaraca certainly do not serve for the recognition of subspecies as suggested by this author. He mentioned the presence of white margins on the upper eyelids in three specimens and of a white transverse line between the eyes, continued via the tympanum towards the back in two of these specimens (from Guayaraca). This pattern apparently is within the normal range of variation of the species, as SCNLS 6045 and RMNH 18710-11, 18715-16, 18719, 18728 and 18732 from the La Escalera region, close to the type-locality, also show a fine chalky-white line between the eyes and several of them have white dorsolateral lines as well.

There is some variation in the size of the prepollex, which in the Roraima specimens is slightly larger, but this could be related to the fact that the snout-vent length of the Roraima specimens is also larger than that of the Venezuelan material I examined. Moreover, the tibiae in the Roraima specimens (both sexes) relatively are slightly longer (51.8-55.0% of snout-vent length, $\bar{x} = 53.4$, N = 12) than in the Venezuelan material (47.4-54.3% of snout-vent length, $\bar{x} = 50.1$, N = 44, both sexes also). These data seem to support Rivero's suggestion that several subspecies may be involved, but my conclusion is based on other characters than the ones suggested by him. However, until more material becomes available, I prefer to consider all Venezuelan and Guyanese specimens as belonging to one monotypic species. This species most likely will turn out to be endemic to a small portion of the Guiana region, namely sandstone areas of relatively high elevations. The same may be true for Hyla kanaima Goin & Woodley of which two specimens were collected by the British Roraima Expedition 1971 (AW 74, 75, now in collection of BMNH) on the North slope of Mount Roraima, Camp VIII, 4800 feet, together with Hyla sibleszi (BMNH 1976.1241-44), and another specimen by the University of Guyana Roraima Expedition 1973 (4600 feet, 26-X-1973, UGDB 13). Among Warren's 1971 Roraima material there are three other species of Hylids which are new to science and will be described in a forthcoming paper by Hoogmoed & Duellman. They all seem restricted to higher elevations. It would be most interesting to ascertain whether these Roraima-species also do occur on Tafelberg in central Suriname, a relatively low, isolated remnant of the Roraima-sandstone formation. However, this area thusfar has mostly received botanical and geological, but hardly any zoological attention. 1)

Initially it was thought that *Hyla lemai* Rivero was a synonym of *H. sibleszi*, but after examination of the holotypes of both species, of additional material of *H. lemai* from Roraima, Auyántepui and Paso del Danto (a total

¹⁾ During a recent herpetological expedition (June-July 1979) to Tafelberg, no Roraima-species were found.

of 18 specimens) and after field work in the La Escalera region, it was clear that they are two distinct species, occurring sympatrically, and probably not even closely related. *H. lemai* will be discussed more extensively in the forthcoming paper on Guiana Hylid Frogs by Hoogmoed & Duellman.

Hyla punctata (Schneider)

Calamita punctata Schneider, 1799: 170.

Hyla rhodoporus Günther, 1868: 488, Lutz, 1951: 329.

Hyla punctata, Gravenhorst, 1829: 30; Günther, 1872: 663; Boulenger, 1882: 357; Baumann, 1912: pl. 6 map 6; Beebe, 1919: 207; Nieden, 1923: 307; Jones & Jones, 1969: 617; Kenny, 1969: 40; Stettler, 1970: 173; Meeuwen, 1971: 103; Anon., 1971: 118; Goin, 1971: 16; Hoogmoed, 1972: 127; Duellman, 1974: 10; Lescure, 1975: 72; Lescure, 1976: 499; Duellman, 1977: 89; Lescure, 1977: 90.

?Hyla helenae, Barbour, 1920: 287.

Hyla granosa, Crawford & Jones, 1933: 90 (partly).

Material. — Surinam. 3 ex., RMNH 1905, 17892, 17898; 2 ex., ZMA 5843a, 13026. 15; I ex., ZMB 8033; I ex., BMNH 70.3.10.71; I ex., MZUSP 74. Paramaribo: I ex., RMNH 17894, 25-IV-1940, leg. D. C. Geijskes; 1 ex., RMNH 17896, Combé, 21-III-1939, leg. H. W. C. Cossée; 3 ex., RMNH 17895, 1911, leg. W. C. van Heurn; 1 9, 4 hgr., RMNH 17897, Botanical Garden, 17/18-VII-1968, 1 hgr., RMNH 18227, 15-XI-1968, 1 9, 1 hgr., RMNH 17910, 17-XII-1974, all leg. M. S. Hoogmoed; 1 9, RMNH 17905, 12-I-1975, leg. D. Ammersingh; 1 hgr., RMNH 17938, 5-XII-1968, leg. P. H. v. Doesburg; 1 hgr., ZMB 25967, leg. Heller; 1 ex., CM 49445, 29-VI-1968, leg. D. A. Jones; 4 ex., CM 49450, 49452-54, Charlesberg, 5-VII-1968, leg. D. A. Jones. Distr. Nickerie. Nieuw Nickerie: 1 9, 3 hgr., RMNH 17912, 10 km SW, 22-X-1975, 2 9 9, 1 &, 2 hgr., 1 juv., RMNH 17913, SE, 23-X-1975, both leg. M. S. Hoogmoed. Wageningen: 2 & &, 1 hgr., RMNH 17907, 10-XI-1974, leg. M. S. Hoogmoed. Distr. Coronie. East-West Road, 93 km W. Paramaribo: 1 &, RMNH 17909, 20-XI-1974, leg. M. S. Hoogmoed. Distr. Saramacca. East-West Road, 27 km W. Paramaribo: 1 ex., CM 49443, 24-VI-1968, leg. D. A. Jones; Uitkijk Road: 1 ex., CM 49451, 8-VII-1968, 4 ex., CM 49455-56, 49460-61, 10 km S. Kwatta Road, 29-VII-1968, 3 ex., CM 49457-59, 8 km S. Kwatta Road, 29-VII-1968, all leg. D. A. Jones. Distr. Para. Corner Meursweg/ Kennedy Highway: 1 &, 1 &, 3 juvs., RMNH 15027, 18-V-1968, leg. M. S. Hoogmoed. Onverwacht: 3 ex., CM 49444, 49448-49, 26-VI-1968, leg. D. A. Jones. Overtoom: 2 9 9, 2 & &, RMNH 15018, 16-V-1968, leg. M. S. Hoogmoed. Kennedy Highway, 36 km S. Paramaribo: 3 & &, RMNH 17906, 7-XI-1974, leg. M. S. Hoogmoed. Republiek: 1 &, RMNH 17911, 26-IV-1975, leg. M. S. Hoogmoed; 1 Q, RMNH 18228, 13-V-1967, leg. W. N. Polder; 6 & &, RMNH 15015, 3 km E., 18-V-1968, leg. M. S. Hoogmoed. Zanderij: 2 ex., RMNH 17899, leg. W. N. Polder; 1 9, 1 juv., RMNH 17901, 21-III-1975, leg. M. S. Hoogmoed; 1 &, RMNH 17908, 20/21-XII-1974, leg. M. S. Hoogmoed; 2 ex., CM 49446-47, 27-VI-1968, leg. D. A. Jones. Berlijn: 1 &, RMNH 15056, 4-VI-1968, leg. M. S. Hoogmoed. Distr. Suriname. 5 km E. Meerzorg: 1 &, 1 juv., RMNH 17936, 6-XII-1976, leg. M. S. Hoogmoed; 10 tadpoles, 1 juv. (raised in captivity) RMNH 17937, 28-IV-1975, leg. M. S. Hoogmoed. Distr. Marowijne. Moengo: 1 3, RMNH 17935, early July 1969, leg. H. M. van Meeuwen. East-West Road, 2 km W. of Ricanau Creek: 2 & &, RMNH 17900, 15-I-1975, leg. M. S. Hoogmoed. Third swamp, km 19: 1 ex., RMNH 17893, 23-X-1948, leg. Surinam Expedition 1948-49. Djai Creek: 1 ex., RMNH 17891, 5-X-1948, leg. Surinam Expedition 1948-49. Mooi Wane Creek: 1 &, RMNH 15088, 8-VI-1968, leg. M. S. Hoogmoed. Moengo Tapoe: 1 &, RMNH 15093, 9-VI-1968, leg. M. S. Hoogmoed. East-West Road, 10 km W. Albina: 1 3, RMNH 17904, 14-I-1975, leg. M. S. Hoogmoed. Between Albina and Papatam: 1 &, RMNH 17902, 17-I-1975, leg. M. S. Hoogmoed.

French Guiana. Cayenne. Crique Cabassou: 1 3, RMNH 17903, 1-IV-1975, leg. M.S. Hoogmoed.

GUYANA. North-West Distr. Yarakita River: 2 ex., UMMZ 83552, 28-XII-1937, leg. A. S. Pinkus; 4 ex., UMMZ 83553, mouth of dito, 29-XII-1937, leg. A. S. Pinkus.

Brazil. Upper Amazon. 1 ex., BMNH 1947.2.23.5 (66.9.26.4) leg. Bartlett (lectotype of H. rhodoporus Günther). Estado Amazonas. Benjamin Constant, Rio Javari: 11 ex., MNRJ 3151, leg. A. Parko. Municipio Borba, Rio Madeira: 1 9, MNRJ 2963, leg. A. Parko. Igarapé Belém, Rio Solimões: 2 ex., MZUSP 26533, 26538, 8/28-IV-1966, leg. B. Malkin. Estado Mato Grosso. S. Luiz Cáceres: 7 & \$\frac{1}{2}\$, MNRJ 3027, leg. Passarelli. Estado Acre. Tarauacá: 1 9, WCAB 2509. Estado Goiáz. Jaraguá: 1 ex., MZUSP 1420, leg. O. Pinto. Estado Alagõas. Fazenda Canõas, Rio Largo: 1 ex., MZUSP 9278, October 1951, leg. E. Dente. Territorio Rondonia. Cachoeira Samuel, Rio Jamari, Guaporé: 1 \$\frac{1}{2}\$, MNRJ 2376, leg. A. Parko.

PERU. Estiron. Rio Ampyiacu: 8 ex., MZUSP unnumbered, 15/22-V-1966, leg. B. Malkin

PARAGUAY. Asuncion: 3 hgr., BMNH 04.3.14.165-167, leg. J. Bohls.

Venezuela. 2 ex., AMNH 13056-57. Territorio Delta Amacuro. Guayo: 4 ex., SCNLS 4640-4643, April 1969, leg. J. Bilbao & A. Alvaredo. Araguaimojo: 28 ex., SCNLS 4601-4628, leg. J. Bilbao & A. Alvaredo.

Trinidad. Port of Spain: 7 & &, MNRJ 3348, 3350, 3352, 3353, 3356-3358, leg. Quesnel & B. Lutz.

Diagnosis. — A medium-sized Hyla of the punctata species group. Male with a small prepollex, prepollical spine small, not protruding. Prevomerine teeth in two short, arched rows. Skin of dorsum shagreened to smooth, of belly coarsely granular. Tympanum round, distinct, large, 1/2-2/3 the horizontal diameter of the eye, separated from the eye by a distance 1/2-3/4 its diameter. A distinct, straight supratympanic fold, continued posteriorly as a feeble dorsolateral fold. Interorbital distance 1.1-2.2 times the width of an upper eyelid. Discs on fingers at the most covering half the tympanum. Subarticular tubercles 3rd and 4th fingers single. When the hindlimbs are folded and flexed at right angles to the sagittal plane the heels are narrowly separated. Colour in preservative ivory-white to yellowish, with more or less distinct white spots on the back and a white dorsolateral line.

Description. — Head slightly wider than long, as wide as the body, depth 35-45% of the head length. Snout pointed in dorsal, rounded in lateral profile, not projecting over the mouth; short, slightly longer than the horizontal diameter of the eye. Distance between eye and nostril shorter than the horizontal diameter of the eye (64.4-87.2% ($\bar{x}=76.4$, N = 22) in females, 65.2-92.5% ($\bar{x}=78.3$, N = 49) in males), about 2.5 times the distance between nostril and tip of snout. Canthus rostralis indistinct, rounded, concave. Loreal region slightly concave, steeply (60°) sloping to the upper lips which do not flare. Nostrils slightly laterally and ventrally of the canthus rostralis, in slightly swollen areas, directed laterally. Distance between the

nostrils 2/3 to once the interorbital distance; slightly wider to slightly narrower than upper eyelid; area between the nostrils flat to slightly concave. Interorbital space flat, in males 1.1-1.9 times ($\bar{x} = 1.4$, N = 49) as wide as an upper eyelid, 1.1-2.2 times ($\bar{x} = 1.5$, N = 19) in females. No cranial crests. Temporal region sloping steeply. Tympanum large, round, 1/2-2/3 the horizontal diameter of the eye, separated from the eye by a distance 1/2-3/4 its diameter; situated well in front of the insertion of the forelimbs. Supratympanic fold distinct, straight, continued posteriorly as a dorsolateral fold, obscuring the extreme upper margin of the tympanum. Dorsolateral fold recognisable along the anterior part of the back, gradually disappearing posteriorly.

Choanae medium-sized, oval; prevomerine processes present, bearing two short arched rows or small groups of 3-10 teeth, situated between the posterior part of the choanae or on the line connecting their posterior margins. Tongue cordiform, attached to the floor of the mouth, only its lateral and posterior margins free. Males with paired vocal slits, one on each side of the tongue, extending from the midlateral base of the tongue to near the angle of the mouth, close to the median edge of the mandible.

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

Skin of dorsum, including top of head, flanks and dorsal surfaces of the limbs shagreened to smooth. Skin of belly and ventral surface of thighs coarsely granular, skin of throat coarsely wrinkled, skin of ventral surface of forelimbs and rest of ventral surfaces of the hindlimbs smooth. Skin in groins and axils smooth. Males with a small mental gland.

Males with a small prepollex, prepollical spine small, not protruding. Inner metacarpal tubercle large, oval, indistinct, merging with the prepollex. Outer metacarpal tubercle absent. Subarticular tubercles round, flat, single. Skin covering palm coarsely wrinkled. First finger shorter than second, second shorter than fourth, third longest. Web between fingers present, basal, absent between first and second finger, webbing formula: I (3), 2i (3), 2e (2), 3i (3-3½), 3e (3), 4 (2²/3). Discs on fingers round, with a groove around the edge, disc of first finger smaller than the others. Disc of third finger at the most covering half the tympanum. Fingers distinctly depressed.

A small oval inner metatarsal tubercle, a small, round, indistinct outer metatarsal tubercle. Subarticular tubercles round, flat, single. Toes distinctly webbed, webbing formula: I $(1\frac{3}{4}-2)$, 2i $(2-2\frac{1}{3})$, 2e $(1\frac{1}{2})$, 3i $(2\frac{1}{2}-3)$, 3e $(1\frac{1}{2}-1\frac{3}{4})$, 4i (3), 4e $(2\frac{1}{2}-2\frac{3}{4})$, 5 $(1\frac{1}{2})$. Web continued to the discs as a fleshy ridge along the toes. Toes with well developed round discs, subequal, smaller than those on fingers, a groove around the edge.

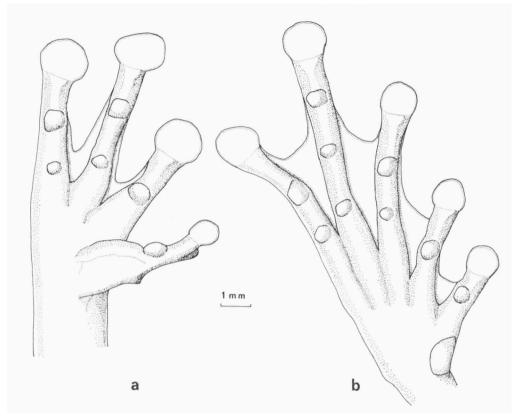


Fig. 9. Hyla punctata (Schneider) (3, RMNH 17911). a. ventral view of right hand; b. ventral view of right foot.

When the hindlimbs are folded and flexed at right angles to the sagittal plane the heels are narrowly separated.

In living specimens the back in daytime is green with yellow spots; yellow to yellowish-green upper eyelids and a yellow dorsolateral line which is bordered ventrally by a red line. Ventral parts transparent, green with a large chalky white spot on the belly. Bones green. Iris grey to light-blue with a brown area directly around the pupil. At night the back is orange with orange yellow spots, dorsolateral line and upper eyelids. Dorsolateral line bordered ventrally by a red line. Upper surface of limbs orange with red dots. Flanks green. Throat and lower surface of limbs glassy green. Belly white. Iris brown. Apparently at night the brown zone around the iris (daytime) expands at the cost of the grey to light blue area.

In preservative the back is white to creamish to pale yellowish-brown, with more or less distinct, irregularly dispersed, small round white spots,

small red to purple dots and a white dorsolateral line from the nostril via the eye to the groin. Dorsolateral line bordered ventrally by a narrow red line. Upper eyelids lighter than the remainder of the dorsum. Ventral surfaces immaculate, white to creamish to pale yellowish-brown. A large chalky-white spot in the centre of the anterior part of the belly, caused by a white area in the abdominal muscle layer. Bladder and heart enclosed by white integuments.

Measurements. — Snout-vent length in males 31-40 mm ($\bar{x}=36.2$, N = 25), in females 31-39 mm ($\bar{x}=35.2$, N = 11). Tibiae in males 42.4-50.6% ($\bar{x}=47.9$, N = 50) of the snout-vent length, in females 46.9-52.5% ($\bar{x}=49.5$, N = 22). Head length in males 28.1-34.9% ($\bar{x}=33.0$, N = 25) of the snout-vent length, in females 31.1-35.0% ($\bar{x}=32.7$, N = 11). Diameter of eye in males 1.5-2.0 times ($\bar{x}=1.7$, N = 50) the diameter of the tympanum, in females 1.5-1.9 times ($\bar{x}=1.7$, N = 22). For a comparison with the other species see fig. 11.

Description of tadpoles. — Lot RMNH 17937 when collected only contained specimens in stages 25 to 36 (Gosner, 1960). A stage 25 specimen has a total length of 13.5 mm, 5.2 mm of which is snout-vent length. A stage 36 specimen has a snout-vent length of 10.4 mm, a total length of 31.5 mm. The body is ovoid, flattened dorso-ventrally, about 1.5 times as long as wide, 1.2 times as wide as deep. The tail is 1.5-2 times as long as the body and more than three times as long as deep. The dorsal and ventral fins are low, proximally lower than the height of the muscular part of the tail, dorsal fin higher than the ventral one. Tip of tail pointed, no filament. Dorsal fin starting at the base of the muscular part of the tail. Anus dextral. Spiraculum on the left side of the body, 2/3 down its length. The eyes are situated high on the lateral surface, directed dorso-laterally, not visible from below. Nostrils in front of the eyes, with a large, rounded flap, closer to the eyes than to the tip of the snout. Tip of snout rounded, both in lateral and dorsal profile. Oral disc with two ventral indentations. A row of papillae

around the mouth. Denticle formula $\frac{2+2}{1+1}$. The two upper outer denticle

rows overlap, the interruption in the inner row is wide. The lower inner denticle row has a narrow median interruption. Lateral line system present.

Body brown, with a few dark-brown spots on the back, base of tail dorsally with several pairs of dark-brown spots. Muscular part of tail creamish, fins opaque. In life the back is dark grey-green with irregularly dispersed small black spots. Throat dark grey, belly light grey, intestines

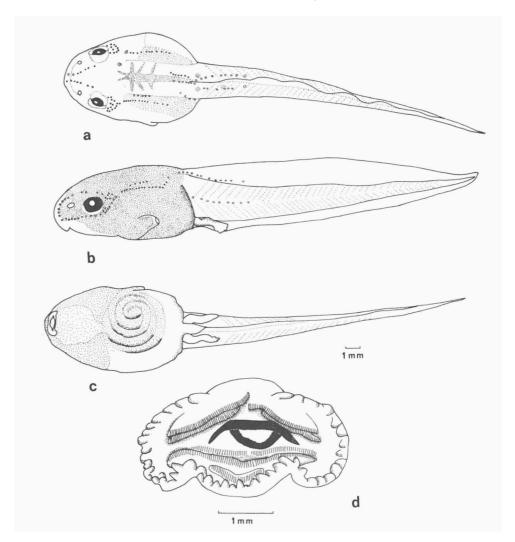


Fig. 10. Hyla punctata (Schneider) (RMNH 17937), tadpole (stage 36 of Gosner).

a, b, c, dorsal, lateral and ventral view, d. detail of oral disc.

clearly visible. Base of tail yellow-brown, more posteriorly glassy grey. Dorsally along muscular part of tail a bloodvessel, which sends branches down along it to the bloodvessel under the muscular part of the tail. Iris golden with narrow reddish-golden rim around pupil. A recently metamorphosed specimen (10-VI-1975) had a green back with many small silver-white spots, upper eyelids whitish-green. Pale yellow canthal and dorsolateral stripes. Ventral parts transparent bluish-green, entrails visible, white inte-

gument around heart and intestines. Liverlobes visible, dark red. Iris grey with a brown rim around the pupil.

Natural history. — A nocturnal species. In Surinam specimens were caught in the months January, March-July, October-December. Calling males were collected or heard in all these months, which cover the short rainy season, the long rainy season and the end of the long dry season. Females with large oviducal eggs (with a black and a light grey pole) were collected in January, March, June and July; in December females did not contain eggs. Larvae were collected on April 28, 1975. They were reared in captivity and the first specimen metamorphosed on June 10, 1975. On June 19 the specimen had a snout-vent length of 15 mm. These data indicate that the breeding season of the species covers both the short and the long rainy season. There seems to be no activity during the beginning of the short dry season in February and during the early long dry season in August and September. However, males start calling at the end of the dry seasons, probably activated by the rain-showers which during that period gradually increase, both in number and in intensity. Females may lag a little behind the males, since during the start of the short dry season in December females did not contain eggs. Calling males were collected between 18,00 and 02,00 hours, they start calling just before sunset and continue through most of the night. Females were collected during the same period. Males call sitting on leaves of grass or herbs or on twigs of low bushes, as a rule directly over water or very close to it, from 5-100 cm above the surface of the water or the ground. One specimen (RMNH 15056) was found in a somewhat aberrant situation in a village where it was calling from a tree in a back-yard, 200 cm above the ground, at least 100 m from the nearest body of water. When calling, the males assume a more or less horizontal position, dividing their weight over several blades of grass, or, when on herbaceous vegetation, sit on one leaf which is not necessarily large. Specimens calling from bushes may straddle small branches and grasp them with the hands close to each other, the feet grasping the branch on each side of the hands. The call emitted is very characteristic and consists of a loud, high pitched, short purring sound, which cannot be heard very far off (pl. 6 figs. a, b).

The larvae were found in a road-side ditch in a cultivated, originally swampy area. The ditch was choked with vegetation, both in the water and above it. An important component of the vegetation was *Montrichardia arborescens* ('mokko-mokko'), emerging from the water. The tadpoles were collected with a dipnet in the upper 30 cm of water between the aquatic vegetation. In captivity the larvae fed well on a mixture of fishfood con-

taining both animal and vegetable ingredients. The food was only taken from the bottom. The greater part of the time the tadpoles were lying on the bottom, but sometimes they swam very fast along the bottom, or to the surface and immediately back. My observations in the laboratory agree with Kenny's (1969). The same author observed these tadpoles in the field "lying in shallow water in the typical habitat of the adult".

This species probably serves as prey for a number of snakes (Liophis cobella (L.), Leptodeira annulata (L.), Leptophis ahaetulla (L.), Helicops angulatus (L.), Thamnodynastes spec.) which are found in the same habitat. RMNH 17891 was noted on the label as being the prey of a lizard (Uranoscodon superciliosa (L.), RMNH 16068).

Habitat. — The species occurs in extensive swamps, in roadside ditches, along the edges of pools in cultivated areas and in inundated grasslands (Hoogmoed, 1972). All these localities have two factors in common: they are wet and very open, with in daytime a high amount of light. In French Guiana (Lescure, 1976) and Trinidad (Kenny, 1969) the species is found in similar situations. The species is not found in savannas, which also are open, but lack sufficient water. There are few localities I know of where Hyla punctata and H. granosa were taken together (figs. 1, 2). Only between Albina and Papatam, in a cultured field on sandy, swampy bottom surrounded by forest, the two species were actually found in the same habitat.

Range and distribution. — The species ranges over the greater part of the Amazon region and the Guianas, from Colombia to Venezuela, Trinidad, the Guianas and Brazil, south to Paraguay and Argentina (Duellman, 1977). In Surinam the species is only known from the coastal area, from the coast south to the southern border of the coastal savanna belt. It is absent from the interior which is mainly covered by dense primary forest. It is only known from low altitudes, from sea level to 20 m above it.

Discussion. — Crawford & Jones (1933), reported Hyla granosa from near Kartabo on the basis of three specimens they collected in a swamp and of which the call was described as a medium-pitched "pink". I did see one of their specimens, which indeed was H. granosa, but on the basis of the colour description, the habitat and the call, I suppose that they also had H. punctata at hand. In his description of H. rhodoporus, Günther mentions two specimens, one from the Upper Amazon and one from Surinam. Thus, the species was described on the basis of two syntypes, and not only after the specimen (BMNH 1947.2.23.5(66.9.26.4)) which has been considered

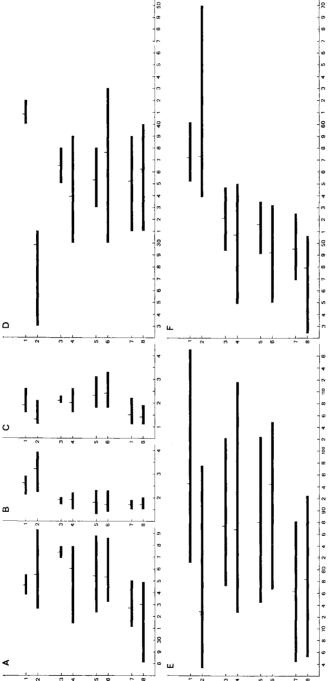


Fig. 11. Graphical illustration of the range of variation of several characters in Hyla ornatissima Noble (1 = 9, 2 = 3), H. sibleszi = 3) and H. punctata (Schneider) (7 = 9, 8 = 3). Vertical bars indicate for computations of averages and ranges are for H. ornatissima: RMNH 17879-83; AMNH 13491, 90790; BMNH 1905.11.141-42; WCAB 5692-95; MNHNP 1977. 635-636, 1977.638-643, 1977.666; for H. siblessi BMNH 99.3.25.20, 1975.1357-58, 1976.1241-44; RMNH 15099, 17884-90, 17921; BMNH 1947-2.12-93-95, 1947-2.12-97-99, 1934-11.141, 1936-42-37-38, 1939.1.1.60; WCAB 2244; MNRJ 3336, 1640, 3143; MZUSP 10861, 21828-30; MNHNP 1977-637, 1977-644-665; UPRM 119-125; and for *H. punctata* RMNH 15015, 15018, = interorbital distance/upper eyelid; D = length X 100; F = length tibia/snout-vent length X 100. Specimens used 6045; UPRM 3177-78; UGDB 12; KU 167058-67 mean. A = head length/snout-vent length \times 100; B = eye length/tympanum length; C 15027, 15056, 15088, 15093, 17897, 17900-13. Rivero (3 = 9, 4 = 3), H. granosa Boulenger (5 = 9, 6)snout-vent length in mm; E = distance eye-nostril/eye 17922, 18556; AMNH 56241-44; SCNLS 6032,

the holotype by Duellman (1977: 90). The second specimen included by Günther in his type-series is BMNH 70.3.10.71, from Surinam, purchased of A. Kappler. As we are dealing with two syntypes it is useful to indicate a lectotype and for this I propose to select BMNH 1947.2.23.5(66.9.26.4) from the Upper Amazon, Bartlett. BMNH 70.3.10.71 thus automatically becomes a paralectotype.

KEY TO THE SPECIES OF THE HYLA GRANOSA AND PUNCTATA SPECIES GROUPS IN THE GUIANA AREA

1. Dorsal pattern consisting of a dark transverse band between the eyes and a large intricate figure on the back; skin of back smooth; fingers and
toes extensively webbed; subarticular tubercles 3rd and 4th fingers bifid
· · · · · Hyla ornatissima
Dorsal pattern with or without a transverse band between the eyes, back
with isolated dark or white spots; skin of back smooth, granular or shag-
reened; fingers and toes not extensively webbed; subarticular tubercles 3rd
and 4th fingers single
2. Skin of back smooth, mental gland in males absent, prepollical spine in
males projecting, tympanum as large as largest disc on fingers . Hyla sibleszi
Skin of back granular or shagreened, mental gland in males present,
prepollical spine in males not projecting, tympanum larger than largest disc
on fingers
3. Skin of back granular, tympanum slightly larger than largest disc on
fingers, no dorsolateral fold, pattern of dark spots on back, no dorsolateral
lines, snout rounded in dorsal profile
Skin of back shagreened, tympanum twice as large as largest disc on
fingers, a supratympanic fold continued as a dorsolateral fold, pattern on
back of white spots and white dorsolateral lines, snout pointed in dorsal
profile

ZOOGEOGRAPHY

Two of the species dealt with here apparently are endemics of the Guiana region. Hyla sibleszi at present seems to be restricted to a small area near Mount Roraima in altitudes over 900 m, but it is my guess that it may turn up in other localities at higher elevations in Venezuelan Guyana and possibly on the Tafelberg in Surinam. H. ornatissima has a wider distribution in the Guiana area where it occurs in low-lying localities at the northern edge of the mountain-ranges forming the divide between the Guiana's and Amapa on the one hand and northern Amazonia on the other. The

distribution probably reflects that the species was restricted to a forestrefuge covering the northern versants of the divide during the last dry period in northern South America which is estimated to have ended about 2500 years ago (Haffer, 1974; Hoogmoed, 1973).

Probably because more humid conditions began near the mouth of the Amazon, and from there extended their influence westward (Hoogmoed, 1973), the forest-refuge (and the animals in it) on the northern slopes of the divide could not expand southward and consequently a number of species is (still) missing from northern Amazonia.

The remaining two species (*H. granosa* and *H. punctata*) are wideranging forms which apparently were not affected by the partitioning of their area of distribution. As far as our present knowledge goes it is not possible to discern subspecies and the species appear very homogeneous throughout their range. Possibly *Hyla granosa* succeeded in occupying its present day area from a refuge situated on the eastern slopes of the Andes (Napo refuge). *Hyla punctata* may have survived the dry period in an area near the mouth of the Amazon, in a region where at this moment extensive swampy areas are present: Marajo, coastal Amapá and coastal eastern French Guiana, an area having a yearly amount of rainfall of well over 3000 mm.

ACKNOWLEDGEMENTS

Thanks are due to the following persons, who kindly loaned me material in their care and/or provided working space during my visits to their respective institutions: W. C. A. Bokerman, Sao Paulo (WCAB); Dr. A. Leitao de Carvalho, Museu Nacional, Rio de Janeiro (MNRJ); Dr. W. E. Duellman, Museum of Natural History, The University of Kansas, Lawrence (KU); Miss A. G. C. Grandison, British Museum (Natural History), London (BMNH); Dr. J. Lescure, Muséum Nationale d'Histoire Naturelle, Paris (MNHNP); Carlos A. de Lima, Sociedad de Ciencias Naturales La Salle, Caracas (SCNLS); Dr. C. J. McCoy, Carnegie Museum, Pittsburgh (CM); Dr. C. W. Myers and Dr. R. G. Zweifel, American Museum of Natural History, New York (AMNH); Dr. J. R. Ramsammy and Mr. T. B. Singh, Department of Biology, University of Guyana, Georgetown (UGDB); Dr. J. A. Rivero, University of Puerto Rico, Mayagüez (UPRM); Dr. P. E. Vanzolini and Mrs. R. Rebouças-Spieker, Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP). Field work in Surinam was supported by grants W 956-2, W 87-78 and W 87-127, the work in Brazilian, Venezuelan and U.S. museums by travel-grants WR 87-131 and WR 956-4 from the Netherlands Foundation for the Advancement of Tropical Research

(WOTRO) and by grants from the Foundation Ian Ioost ter Pelkwijk Fund and the legacy of Miss A. M. Buitendijk. Field work in Venezuela was financed by grants from the Melchior Treub Foundation of the Royal Dutch Academy of Sciences and from the Treub Society. During several stays in Surinam much help was provided by Mr. J. Douglas of the Surinaams Museum (Paramaribo), who kindly put at my disposal working space and other facilities at the museum. For providing the means to reach areas of difficult accessibility in Surinam I am much in debt to Dr. S. B. Kroonenberg and Dr. E. W. de Roever (Geological and Mining Service), to Dr. J. P. Schulz (Forestry Service) and to Dr. J. J. Janssen (SURALCO). The Division de Fauna of the Ministerio del Ambiente y de Recursos Naturales Renovables (MARNR) enabled me to take part in an expedition of the Corporacion Desarrollo del Sur (CODESUR) to the Cerro Yapacana area. During field work in Venezuela Dr. J. Cerda, P. Gibbs, Dr. S. J. Gorzula and Dr. O. Huber, during that in Surinam Dr. S. B. Kroonenberg, Dr. C. W. Myers and W. N. Polder were agreeable, reliable and stimulating companions.

The sonagrams were made through the courtesy and with the help of Mr. A. G. Rol of the Division of Animal Taxonomy and Zoogeography of the Biological Laboratory of the Free University of Amsterdam. Fig. 5 and the graphs were made by Mr. W. C. G. Gertenaar, the photographs of preserved specimens (except that of the type of *H. ornatissima*) were made by Mr. E. L. M. van Esch, both of the Rijksmuseum van Natuurlijke Historie. The photograph of pl. 4 fig. b was made after a colour slide by the author.

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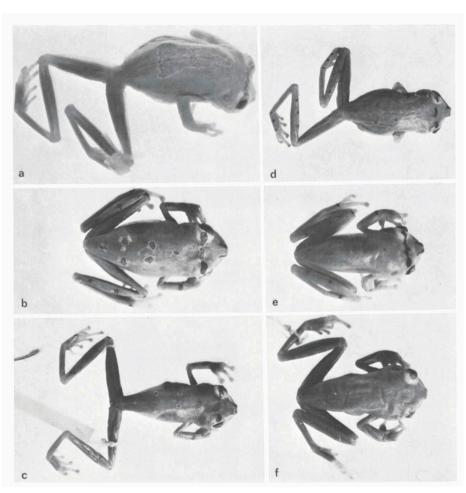
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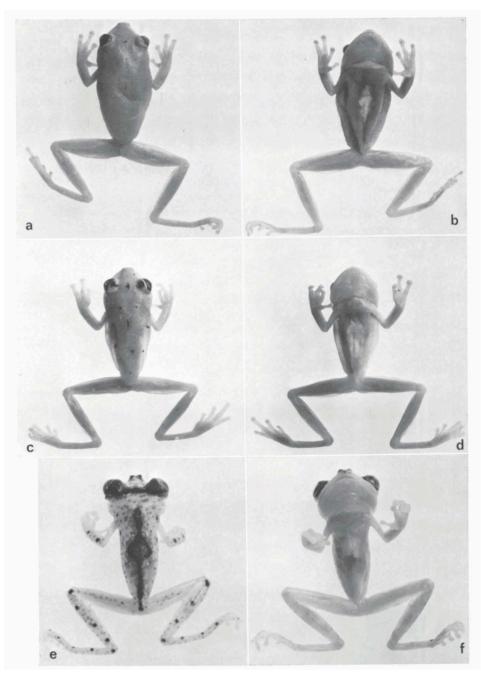
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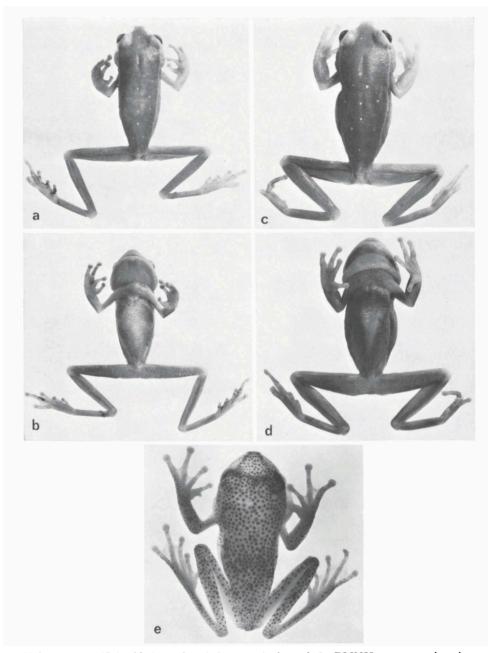
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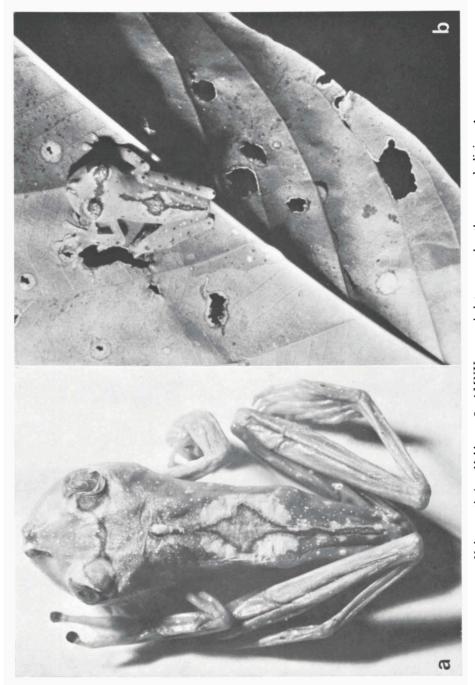
Variations in pattern in *Hyla granosa* Boulenger. a. &, UPRM 119, snout-vent length 38 mm; b. &, BMNH 1947.2.12.97, s-v length 36 mm, paralectotype, figured by Boulenger, 1882, pl. 24 fig. 3; c. &, BMNH 1947.2.12.93, s-v length 34 mm; d. &, BMNH 1934. 11.1.41, s-v length 37 mm; e. &, BMNH 1939.1.1.60, s-v length 34 mm; f. &, BMNH 1947.2.12.99, lectotype, figured by Boulenger, 1882, pl. 24 fig. 2.



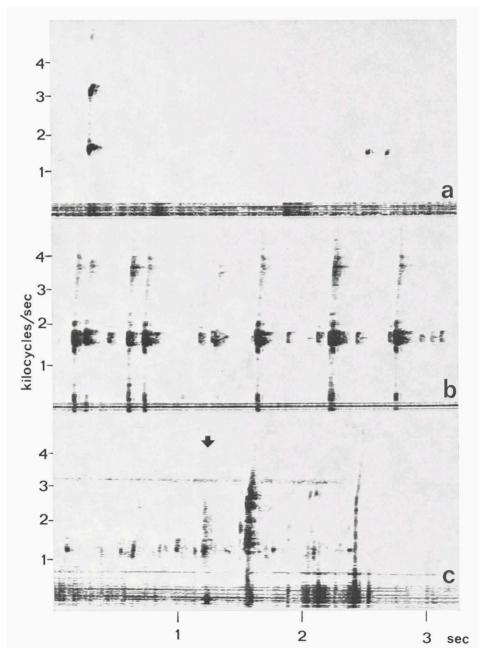
Hyla granosa Boulenger, a. dorsal, b. ventral view of &, RMNH 17886a, s-v length 37 mm; c. dorsal, d, ventral view of \$\rho\$, RMNH 17886b, s-v length 35 mm. Hyla ornatissima Noble, e dorsal, f. ventral view of \$\rho\$, RMNH 17879, s-v length 31 mm.



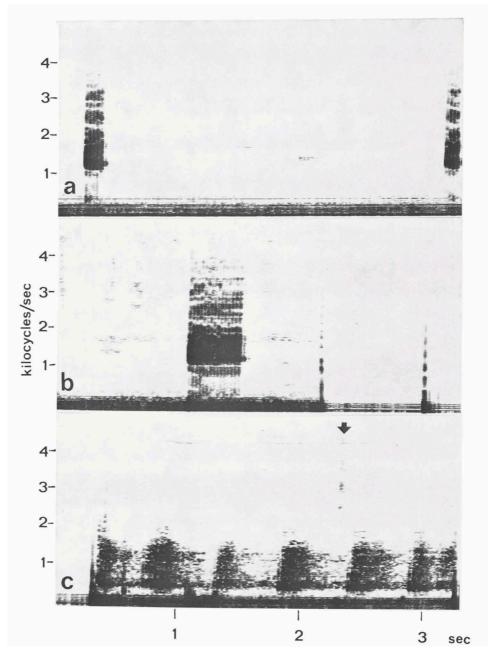
Hyla punctata (Schneider), a. dorsal, b. ventral view of \$\mathbb{Q}\$, RMNH 17905, s-v length 38 mm; c. dorsal, d. ventral view of \$\mathcal{Z}\$, RMNH 17900a, s-v length 38 mm. Hyla sibleszi Rivero, e. dorsal view of \$\mathcal{Z}\$, KU 167066, s-v length 37 mm.



Hyla ornatissima Noble, a. 9, AMNH 13491, holotype, s-v length 40 mm, b. living \$, RMNH 17881, showing the agreement between dorsal pattern and substrate.



Hyla granosa Boulenger, a. sonagram of call of & RMNH 17885, recorded 10 km W. of Albina, Surinam, at 23.30 h, 15-I-1975, 25°C, b. sonagram of call of & RMNH 18706, recorded at Canaripo, Venezuela, at 23.15 h, 28-V-1978, 25.5°C. Hyla siblessi Rivero, c. sonagram of call of & RMNH 18732, recorded at La Escalera, km 132, Venezuela, at 19.45 h, 10-VI-1978, 19.5°C, note specimen in background (arrow). In b. and c. during processing of the sonagrams mechanical failure of the sonagraph caused the upper part of the sonagrams (above 2 kilocycles per second) to shift slightly to the right. However, it does not distort the total picture too much.



Hyla punctata (Schneider), a. sonagram of call of & RMNH 17900, recorded 2 km W. of Ricanau Creek, Surinam, at 22.15 h, 15-I-1975, 24.5°C, "normal" short call, b. dito, long call. Hyla ornatissima Noble, c. sonagram of call (arrow) (specimen not collected) recorded at Loë Creek, Camp Hofwijks III, Surinam, at 20.20 h, 31-VII-1975, 24°C. The other call (not exceeding 2 kilocycles per second) is that of Hyla boans (L.).