Resurrection of *Hyla wavrini* Parker (Amphibia: Anura: Hylidae), a gladiator frog from northern South America

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Key words: Anura, Hylidae; *Hyla wavrini; Hyla boans;* resurrection; synonymy; call; Neotropics; Venezuela; Brazil.

During field work in Venezuela and Brazil a difference in call was noticed between specimens of large hylids of the *Hyla boans*-group. Based on this and on morphological differences, it was concluded that *Hyla wavrini* Parker, 1936, up till now considered a synonym of *Hyla boans* (Linnaeus, 1758), should be considered a valid species, of which *Hyla miranda-ribeiri* Melin, 1941 is a synonym.

Durante trabajo de campo en Venezuela y el Brasil se nota una diferencia en el canto de especimenes de gran Hílidos del grupo *Hyla boans*. Basandose en este observación y en diferencias morfológicas, se concluye que *Hyla wavrini*, considerado até horita como sinónimo de *Hyla boans* debe ser considerado como especie valido, y que *Hyla miranda-ribeiri* es un sinónimo de el.

Durante trabalhos de campo na Venezuela e Brasil, observou-se diferenças no canto entre espécimenes de grandes hilídeos do grupo *Hyla boans*. Baseado nisso e em diferenças morfológicas, conclui-se que *Hyla wavrini*, até o momento considerado sinónimo de *Hyla boans*, deve ser considerado uma espécie valida, da qual *Hyla miranda-ribeiri* é um sinónimo.

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Introduction

While traveling on the Upper Orinoco River Marquis de Wavrin collected two large treefrogs about which he (1951) provided some inconsequential information and which in the meantime had been described as a new species, *Hyla wavrini*, by Parker (1936: 2). This new species at the time was compared with *Hyla faber* Wied and *H. pardalis* Spix and said to differ from them in having a "longer, flatter head, shagreened dorsal surfaces and green bones". Apparently no comparison was made with *Hyla boans* (Linnaeus), another large treefrog from northern South America. Melin (1941) described *Hyla miranda-ribeiri* from Taracuá on the Rio Uaupes in northern Brazil. He points out differences between this new taxon and *H. appendiculata* Boulenger (= *H. geographica* Spix) and *H. crepitans* Wied. At the same time he states: "It seems not altogether impossible that many of the species, similar to *H. maxima* (Laur.) [= *H. boans* (Linnaeus)] and *faber* Wied, are only different forms of the same species".

Rivero (1961) accepted *H. wavrini* Parker as a valid species, but did not see any material. Gorham (1963, 1974) listed both *wavrini* Parker and *miranda-ribeiri* Melin as valid species, whereas Rivero (1967) reported the first specimen of *H. miranda-ribeiri* Melin from Venezuela stating that when more material of *wavrini* Parker and *miranda-ribeiri* Melin became available they might turn out to be identical. Cochran & Goin (1970: 199) synonymised *wavrini* Parker and *miranda-ribeiri* Melin with *Hyla maxima* (Laurenti) (= *H. boans* (Linnaeus)) on the basis of their examination of the type-material which showed reticulated palpebral membranes, dermal heel appendages and

dusky webbing on hands and feet, which, according to them, were characteristics of *H. maxima* (Laurenti). They were followed by Duellman (1970: 261; 1971: 398, 1977: 39), Harding (1983: 98, 272, 286) and Frost (1985: 128), who did not critically examine material. The effect of these actions was that generally it was accepted that in northern cis-Andean South America only two species of the *Hyla boans*-group (popularly known as gladiator frogs because of the sharp prepollical spines in males used in mating combat) were recognised: *Hyla crepitans* Wied in open, savanna-like situations, and *H. boans* (Linnaeus) in forested areas. The only exception being Gremone

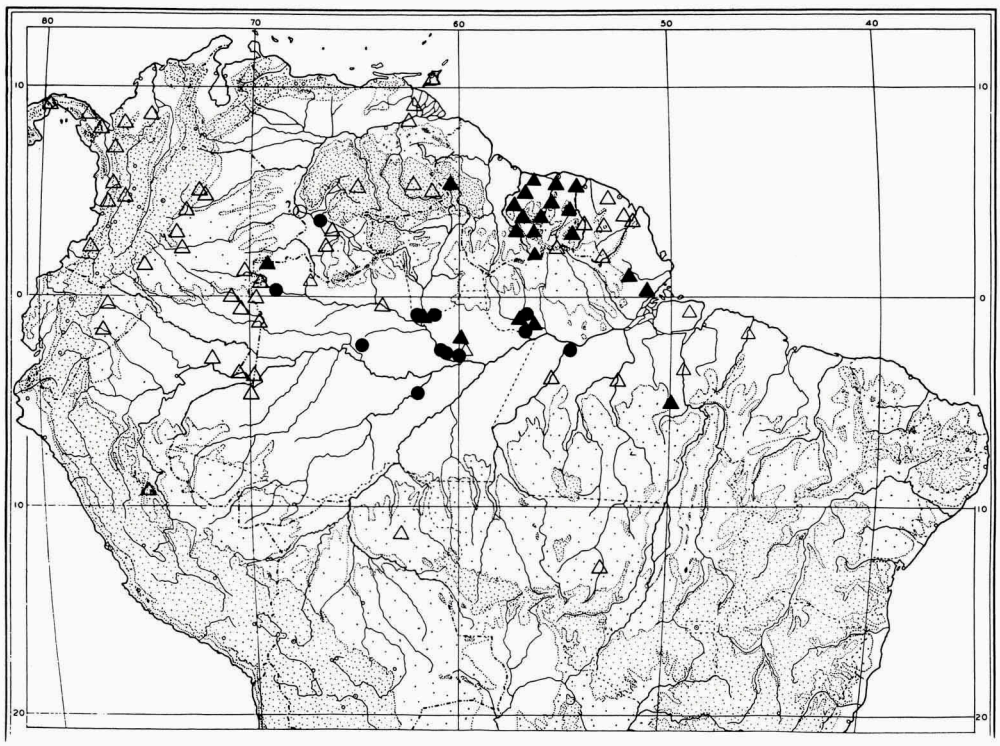

Fig. 1. Distribution of *Hyla wavrini* Parker (dots and circles) and *H. boans* (Linnaeus) (triangles). Closed symbols represent material studied by the author, open symbols are literature records based on: Cochran & Goin (1970), Kluge (1979) for Colombia and Panama, Duellman (1978) for N. Ecuador, Rivero (1961) for Venezuela, Lescure (1976) for French Guiana, Lutz (1973) for Brazil and C. Ecuador, Zimmermann & Bogart (1984) for Brazil, and Schlüter (1979) for eastern Peru.

et al. (1986) who published a picture of *Hyla wavrini* Parker from Venezuela.

During fieldwork in the upper Orinoco region (Caño Cotua at the base of Cerro Yapacana, Amazonas) in Venezuela in 1978 it was noted that the call of a "*Hyla boans*"-like treefrog sounded different from the calls of *Hyla boans* (Linnaeus) known to me from many areas in Suriname and eastern Venezuela (Bolívar). No sound recording was made at the time, but two specimens collected were in trees in a flooded caatinga forest, a habitat quite different from the rain forest environment in which *H. boans* (Linnaeus) is normally found. Again during fieldwork in the Rio Nhamundá area (Pará, Brazil) in 1988, a strange call from a large *Hyla* was noted,

reminiscent of that in Venezuela. A good series could be collected and sound recordings were made. Upon investigation in the laboratory it soon turned out that the Caño Cotua and Rio Nhamundá material was identical and agreed with the types of *H. wavrini* Parker and *H. miranda-ribeiri* Melin. Comparison with *Hyla boans* (Linnaeus) from Suriname, Serra do Navio, Carajás and Cruz Alta near the Rio Trombetas brought to light a number of differences that clearly showed that two taxa are involved: one from lowland Amazonian localities (< 200 m) in Brazil and Venezuela which should be called *H. wavrini* Parker, and one from localities in lower Central America, Chocoan trans-Andean (Atrato River valley) South America, and cis-Andean northern South America from the Andes to the mouth of the Amazon and south to 16°S, occurring from sea level to 1216 m (Cochran & Goin, 1970: 203; Duellman, 1970: 261; 1977: 40; 1978: 132; Frost, 1985: 128; Hoogmoed, 1979: 271; Kluge, 1979: 14; Lutz, 1973: 34; Schlüter, 1979: 214), and which should be called *Hyla boans* (Linnaeus). The presently known distribution of both species is plotted in fig. 1, from which some peculiarities in the distribution of *H. boans* (Linnaeus) emerge, which will be discussed later.

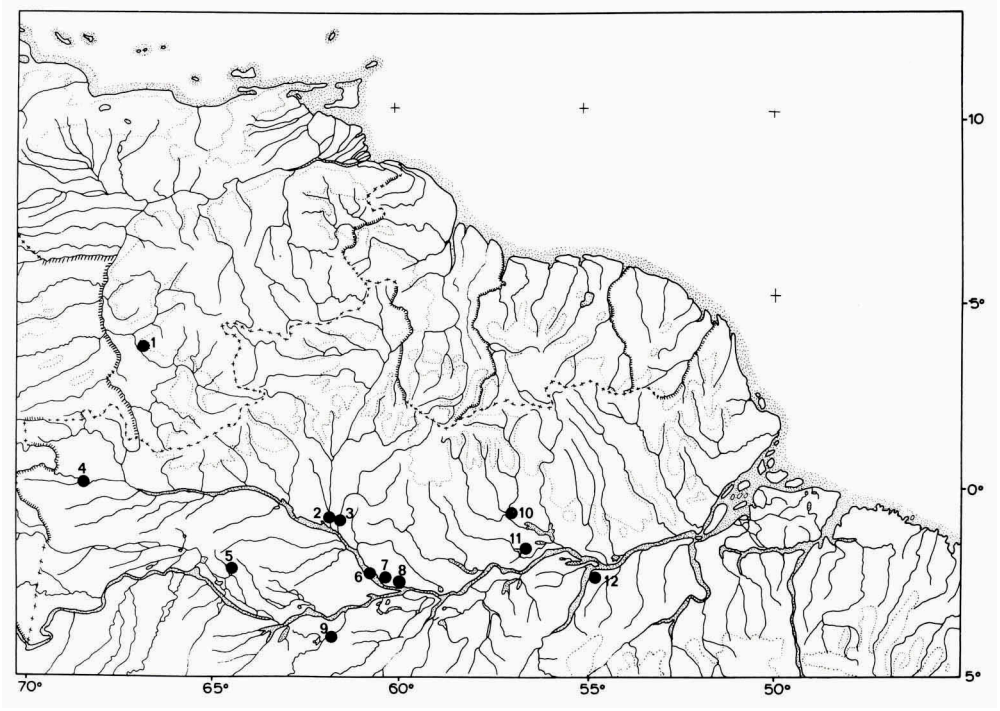

Fig. 2. Known localities from where *H. wavrini* Parker has been taken. 1. Caño Cotua, 2. Amajaú, 3. Rio Jauaperi, Lago Juda, 4. Taracuá, 5. Lago Amaña, 6. Anavilhanas, 7. Rio Cueiras, 8. Rio Negro, Lago Janauari, 9. Itapuru, 10. Rio Cuminá, 11. Rio Nhamundá, 12. Alter do Chão.

Considering the confusion that has reigned concerning the two taxa here discussed, it is deemed useful to present a complete description of *H. wavrini* Parker, based both on type-specimens and on recently collected material.

Hyla wavrini Parker, 1936
(figs.1 - 10)

Hyla wavrini Parker, 1936: 2; Rivero, 1961: 97; Gorham, 1963: 23; Rivero, 1964: 416; 1967: 152; Gorham, 1974: 107; Gremone et al., 1986: photograph IV. 20.
Hyla miranda-ribeiri Melin, 1941: 20; Gorham, 1963: 22; Bokerman, 1966: 56; Gorham, 1974: 101.
Hyla warvini (sic!): Gines, 1959: 122.
Hyla miranda ribeiri: Rivero, 1967: 151.
Hyla maxima (partly): Cochran & Goin, 1970: 199.
Hyla boans: Rivero, 1961: 97 (partly); Duellman, 1971: 398 (partly); Lutz, 1973: 32 (partly); Duellman, 1977: 39 (partly); Hödl, 1977: 352-362; Hoogmoed, 1979: 271 (partly); Lynch, 1979: 191-214) (partly); Kluge, 1979: 6 (partly); Harding, 1983: 98, 272, 286 (partly); Zimmerman & Bogart, 1984: 477 (partly: call type B); Frost, 1985: 128 (partly); Hödl & Gollmann, 1986: 11-14, 16, 18, 19; Martins & Haddad, 1988: 56.

Material. — **Venezuela.** Upper Orinoco: 1 ♀, MRHN.IG 10.637. Reg. 1028 (holotype), 1 ♂, BMNH 1947.2.23.30 (paratype), 1935, leg. Marquis de Wavrin. Amazonas, Caño Cotua: 2 ♂♂, RMNH 24168-169, 25-v-1978, leg. M.S. Hoogmoed. **Brazil.** Roraima. Lago Juda, Rio Jauaperi: 2 ♂, INPA no number, 7-vi-1989, leg. G. Moreira. Amajaú: 1 ♂, 1 ♀, INPA no number, 10-vi-1989, leg. G. Moreira. Amazonas. Taracuá, Rio Uaupes: 1 ♀, NHMG 41-7893. BaEx 466, 24-ii-1924, leg. D. Melin (holotype of *H. miranda-ribeiri*). Rio Negro, near Lago Janauari near Manaus: 1 ♂, NHMW 23561: 2, 10-iii-1975, leg. W. Hödl. Anavilhanas: 1 ♂, MPEG 5205, 4-viii-1981;1 ♂, 1 ♀, INPA 01309-10, Igapo do Lago do Prato, 14-v-1989, leg. G. Moreira. Rio Cueiras: 2 ♂♂, INPA 1114, 1116, 11-viii-1986, leg. M.Martins. Lago Amanã: 1 ♂, INPA 1146, viii-1981, leg. R.O. Best. Itapuru, Rio Purus: 1 ♂, NHMW 23561: 1, 4-vi-1975, leg. W. Hödl. Pará. Rio Nhamundá: 12 ♂♂, RMNH 24164-24167, MPEG 4516-4523, Cabeceira Urucuxi, 13-xii-1988, leg. M.S. Hoogmoed, T.C.S. de Avila-Pires, R. Rocha, J. Vermeulen; 1 ♀, MPEG 4579, 14-xii-1988, Cabeceira Arijo, leg. local inhabitants. Rio Cuminá: 1 ex., MNRJ 5123. Alter do Chão, near Santarem: 1 ♂, 1 ♀, MPEG 3617-18, 1 ♀, RMNH 24357, 15-ix-1986, leg. J.M. Hero.
Comparative material of *Hyla boans* (Linnaeus) used for morphometrics and direct comparison. Additional material from Suriname of which only geographical distribution data were used is not listed here.
Suriname. Distr. Nickerie. Linker Kabalebo: 2 ♂♂, RMNH 17793-4, 13/15-iii-1976, leg. S.B. Kroonenberg. Kabalebo, Grote België val: 1 ♂ RMNH 24177, 22-v-1975, leg. S.B. Kroonenberg. Lucie River, 10 km NE airstrip Coeroeni: 1 ♀, 1 ♂, RMNH 24178-9, 5-ii-1975, leg. M.S. Hoogmoed. Vreedzaamkreek: 1 ♂, RMNH 24182, 6-ii-1975, leg. M.S. Hoogmoed. Sipaliwini, 4km E. airstrip: 1 ♀, RMNH 24175, 16-i-1970, leg. M.S. Hoogmoed & J.J.P. Paats. 5 km E. airstrip: 1 ♂, RMNH 16604, 30-viii-1968, leg. M.S. Hoogmoed. Distr. Saramacca. Raleighfalls: 4 ♂♂, RMNH 24358-61, 6-xi-1968, leg. M.S. Hoogmoed. Distr. Para. Zanderij: 2 ♂♂, RMNH 16605, 24176, 20-xii-1966, leg. W.N. Polder. Distr. Marowijne. 10 km W. Albina: 1 ♀, RMNH 24180, 14-i-1975, leg. M.S. Hoogmoed. Loëkreek, Camp Hofwijks VII: 1 ♀, RMNH 24181, 1-viii-1975, leg. M.S. Hoogmoed & C.W. Myers. **Brazil.** Roraima. Near mouth Rio Branco: 2 ♂♂, INPA no number, 8-vi-1989, leg. G. Moreira. Amazonas. Rio Uaupes, Jauareté: 1 ♂, MPEG 01, viii-1960, leg. J. Hidasi. Balbina, Rio Uatumã: 2 ♂♂, INPA 1121-1122, 5 km SW foz Rio Pitinga, ix-1985, leg. A. Langguth & N. Silva. Pará. Rio Trombetas, Cachoeira Porteira: 1 ♀, INPA 611, Ilha Grande da Mina, 17-viii-1985, leg. A. Langguth; 1 ♂, INPA 644, Igarapé Tramalhetinho, 28-x-1985, leg. R. Gribel. Cruz Alta, 6 km S. Rio Trombetas: 1 ♀, MPEG 4435, 7-xii-1988, leg. M.S. Hoogmoed & T.C.S. de Avila-Pires. Serra Norte, Carajás: 1 ♂, MPEG 3076, 11-xi-1984, leg. T.C.S. de Avila-Pires, R. Moraes & J.C.S. Pinto. Amapá, Serra do Navio: 2 ♂, RMNH 24170, MPEG 4116, 13-xi-1988, 1 ♀, 1 ♂, MPEG 4168-4169, 17-xi-1988, all leg. M.S. Hoogmoed & T.C.S. de Avila-Pires, Rio/Igarapé Vila Nova, 23 km SW Cupixi: 2 ♂♂, RMNH 24171, MPEG 4137, 14-xi-1988, leg. M.S. Hoogmoed & T.C.S. de Avila-Pires. Igarapé Agua Branca, Estrada BR 156, MPEG 931, 26-x-1969, leg. F. P. Nascimento.

Diagnosis. — A large treefrog with a prepollex, reticulated lower eyelids, a rather pointed, dorsally concave head, webs between fingers deeply emarginate, not connecting the discs in a straight line, ultimate two phalanges of finger IV free. Discs of fingers smaller than tympanum. Toes completely webbed, but distinctly emarginate. Dorsum olive green with darker marks. Throat in males with dark stripes or rings.

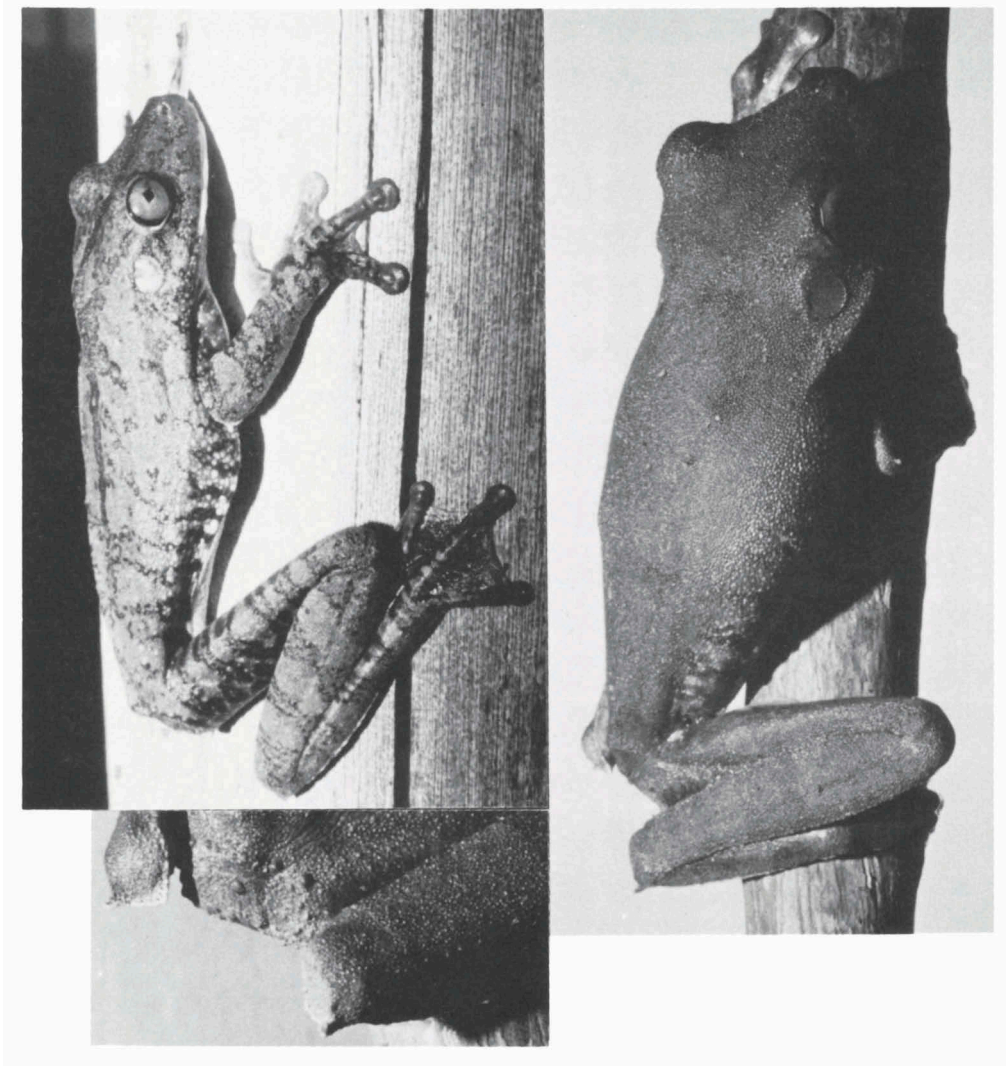

Fig. 3. Live specimens of *H. wavrini* Parker (upper left; RMNH 24164, s-vl 89.4 mm) and *H. boans* (Linnaeus) (upper right: RMNH 24180, s-vl 85.6 mm). Lower left: detail of heels of *H. boans* (Linnaeus), RMNH 24180.

Description. — A large treefrog (s-vl males 89-113 mm, females 75-81 mm), with robust, depressed body (fig. 3), head slightly, but distinctly longer than wide (1.0-1.2 times, $\bar{x}$ = 1.1, n = 42) (fig.4); head 33-41% ($\bar{x}$ = 35.3, n = 42) of the snout-vent length; snout long, rounded in dorsal and lateral profiles, 1.3-2.1 times ($\bar{x}$ = 1.6, n = 42) the eye diameter, nostril much closer to tip of snout than to eye; nostrils round, directed laterally, in a slightly protuberant area, internarial area convex, slightly more than half as wide as interorbital area; canthus rostralis distinct, rounded, concave; loreal region concave, falling steeply to the lips; top of head concave, canthus rostralis and elevated ridges of fronto parietals forming a concave rhomboidal figure, which may

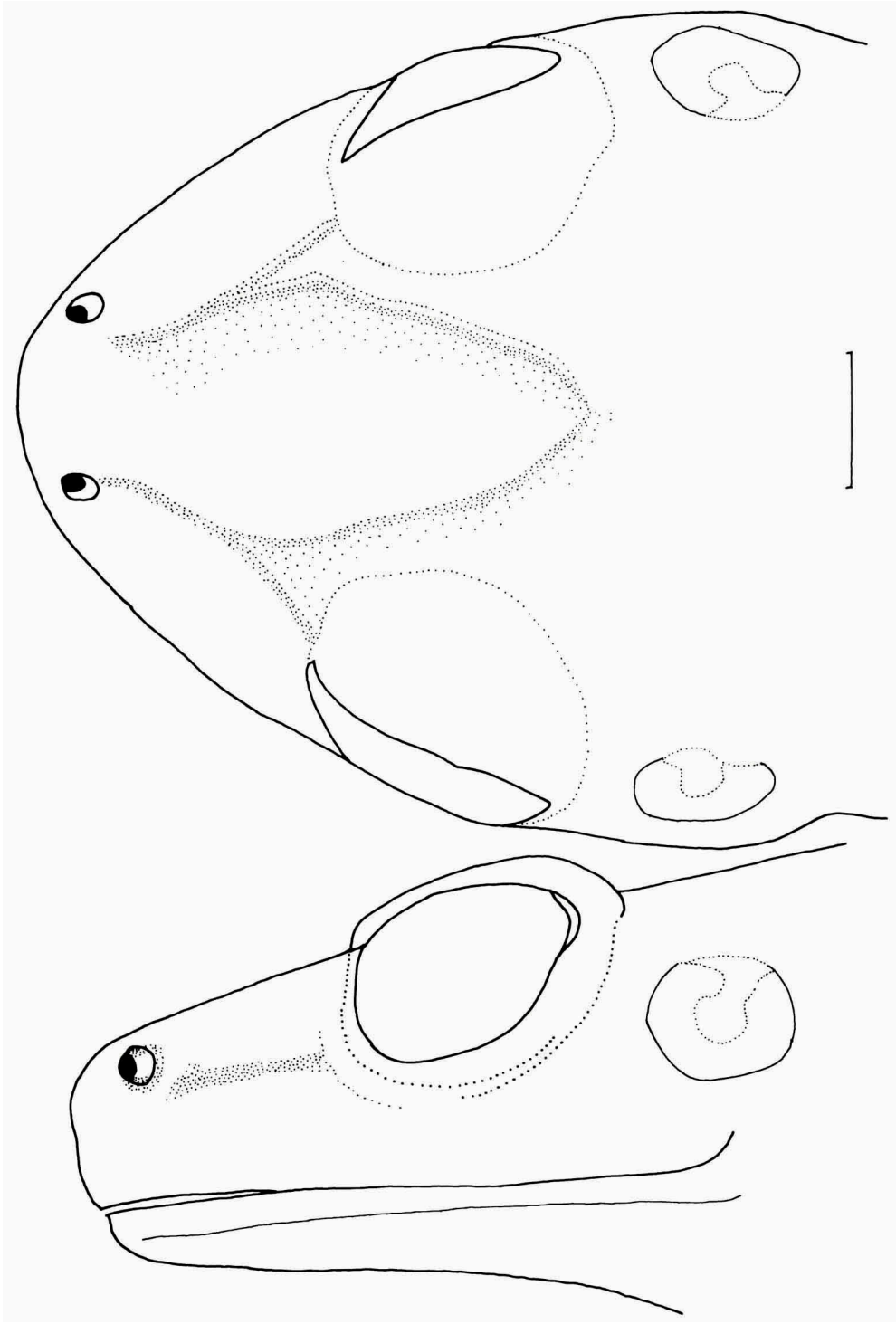

Fig.4. Dorsal and lateral profile of head of *H. wavrini* Parker (holotype of *H. miranda-ribeiri* Melin, NHMG 41-7893). The scale bar represents 5 mm.

be well pronounced (RMNH 24169, NHMG 41-7893 Ba Ex 466) or less distinct (RMNH 24164); interorbital distance 1.2-1.9 times ($\bar{x}$ = 1.5, n = 37) as wide as an upper eyelid, eyes not or only slightly protruding beyond the circumference of the head; tympanum distinct, horizontally oval, not elevated, dorsal border covered by weak supratympanic fold curving down to angle of jaw, separated from the eye by a distance of 47-84% ($\bar{x}$ = 63.5, n = 42) of its diameter, its diameter 48-70% ($\bar{x}$ = 57.3, n = 42) of the eye diameter, larger than discs of 3rd finger. Temporal region rather steep. Palpebral membrane reticulate.

No axillary membrane. Forearm more robust than upper arm, with a low notched dermal fringe, ending in a low ridge on the elbow. Males with a distinct prepollical spine (fig. 5), which in females only is indicated (fig. 5). Hand with a distinct oval inner metacarpal tubercle, no outer one. Subarticular tubercles single, large, prominent under all penultimate articulations. Base of fingers with coarsely granular skin. No supernumerary tubercles. Discs large, rounded, subequal on fingers II-IV, smaller on I, distinctly smaller than the tympanum. Fingers distinctly webbed: I(2$^1/_2$)-(2$^1/_3$)II(1)-(2)III(1$^3/_4$-2)-(2)IV, the web continued to the discs of fingers II-IV as a fringe, and rather deeply emarginated, an indistinct lateral fringe on 4th finger. Length of fingers: I<II<IV<III, fingers very depressed.

Foot with a distinct, large, protuberant, oval inner metatarsal tubercle, no outer one. Subarticular tubercles under penultimate articulations single, large, prominent (less so than on hand). Base of toes with smooth skin. Discs of toes much smaller than those of fingers. Toes completely webbed though deeply emarginate: I(1)-(1 $^1/_2$)II(1)-(1$^1/_2$)III(1)-(1$^1/_2$)IV(1)-(1)V (fig. 5), the web continued to the discs of all toes as a fringe. A low, lateral ridge on 5th toe, continued as a low notched, tarsal ridge to the heel. Length of toes I<II<III<V<IV or I<II<V<III<IV, toes very depressed. Heel with a low, transverse dermal flap, of equal height throughout, or laterally culminating in a small triangular tubercle (fig. 6). When the hindlimbs are flexed at right angles to the sagittal plane, the heels overlap distinctly, when carried forward along the body the heel reaches to between the eye and the snout (Brazilian material) or just beyond the tip of the snout (Venezuelan material). Tibia 45-58 % ($\bar{x}$ = 49.8, n = 42) of the snout-vent length. Cloaca at upper level of thighs, directed posteriorly.

Tongue large, cordiform, slightly notched posteriorly, attached to the floor of the mouth. Vocal slits large, at base of the tongue, parallel to the jaws. Prevomerine odontoids between the large, very elongate, rectangular choanae, forming a / \, with 16-22 ($\bar{x}$ = 19.2, n = 42) teeth.

Skin of back and flanks finely granular, of belly and posterior aspect of thighs coarsely granular, of chest and chin intermediate, of rest of thighs, hindlimbs and arms smooth.

Back with an intricate black pattern on a grey background, flanks, thighs and arms with black vertical, respectively transverse bands in pairs, which extend slightly on the ventral surface. Half of the specimens examined (MRHN IG 10.637 Reg. 1028, 2, INPA no number, RMNH 24164, 24165, 24357, MPEG 4516, 4519, 4520, 4522, 4523, 5205) show a wide reddish brown vertebral band from snout to the middle of the back, respectively to the sacral region. In the Rio Nhamundá area seven out of 15 specimens had a vertebral band. Brown spots or band with lighter margin may be present on limbs (figs. 7-9).

Belly and underside of thighs creamish, chest white, gular region greyish with

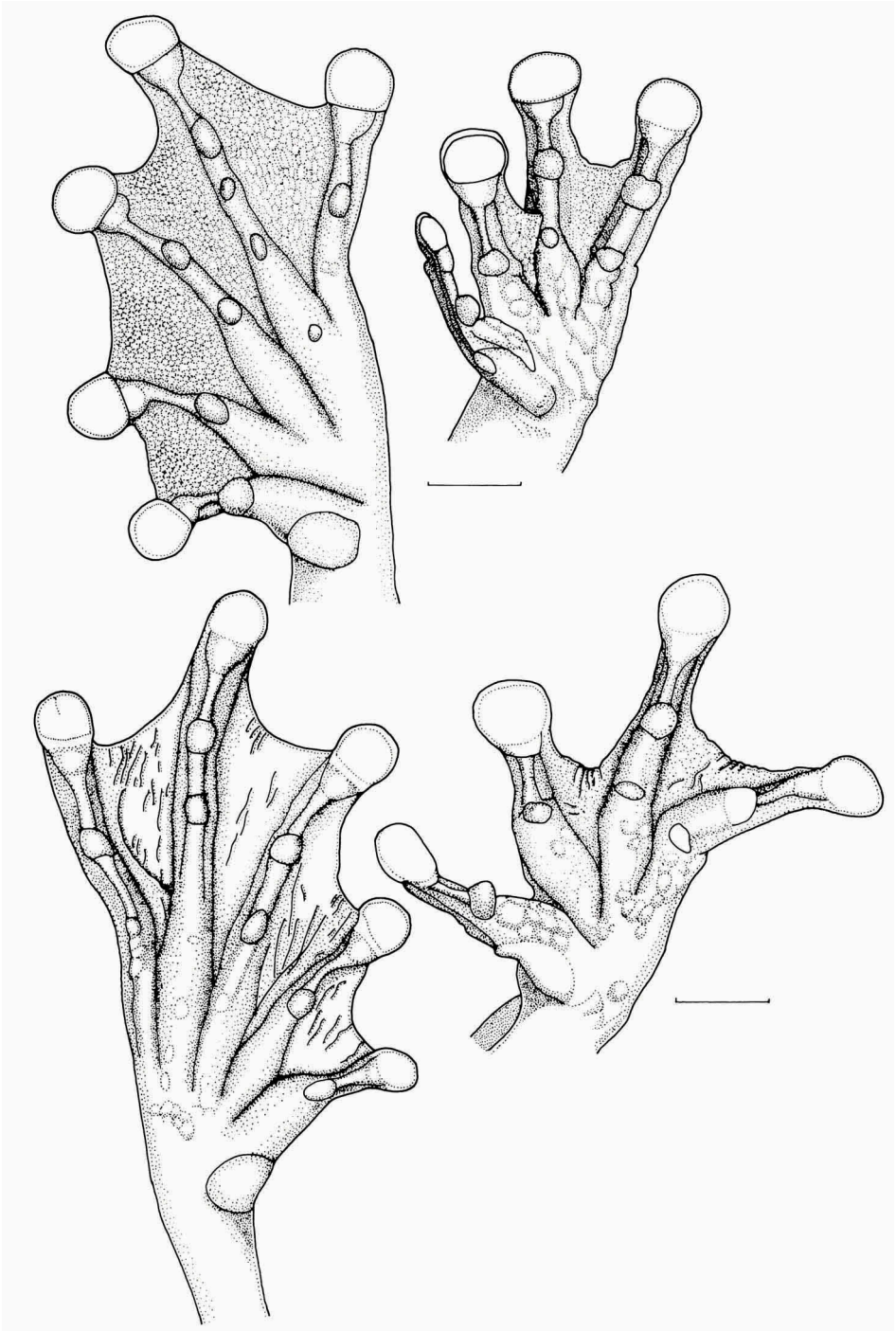

Fig. 5. Ventral views of feet and hands of *H. wavrini* Parker (upper left: combination of RMNH 24165 and 24166, upper right: holotype MRHN IG 10.637 Reg. 1028, two lower figures: holotype *H. miranda-ribeiri* Melin NHMG 41-7893). The scale bar represents 5 mm.

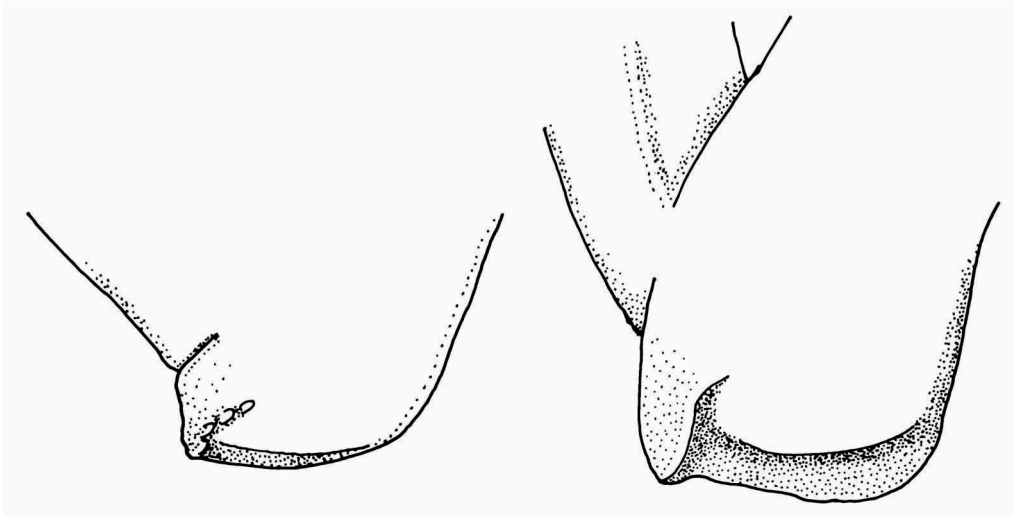

Fig. 6. Heels of *H. wavrini* Parker (left, RMNH 24165) and *H. boans* (Linnaeus) (right, RMNH 24179).

more or less radiating dark grey lines, or dark lines enclosing lighter, round, spots near rim of mouth. Throat never immaculate dark grey as in *H. boans* (Linnaeus). Palms and soles greyish to brownish, webs darker grey. Bones green (figs. 7-9).

In life the back is olive green with blackish or dark green marks, and sometimes (RMNH 24164, 24165) a reddish brown vertebral band. Creamish bands (tibia) and spots (thighs, fore arm) may be present (RMNH 24167) Tympanum brown, webs dark grey. Iris greyish (Rio Nhamundá) to reddish (Caño Cotua) brown. The type of *Hyla miranda-ribeiri* Melin according to field notes of Melin in life had a grey brown dorsum with violet sheen and a yellowish white belly.

Distribution. — So far the species is only known for certain from twelve localities, six in the Rio Negro basin, one in the Upper Orinoco River, one on the Rio Solimoes, one on the Rio Purus, one on the Rio Nhamundá, one on the Rio Trombetas and one at the confluence of Rio Madeira and Rio Amazonas. The distribution of *Hyla boans* (Linnaeus) as it emerges from the literature presents some problems, not only in the trans-Andean area, but also in cis-Andean South America. Several authors dealing with Amazonian *Hyla boans* (Linnaeus) admit there are differences within the area. Rivero's (1961: 97) remark that USNM 80652 from San Fernando de Atabopo is a large animal with variegated coloration, which might represent some other form [than *Hyla boans* (Linnaeus)] leads me to speculate that it might be *H. wavrini* Parker and I plotted it accordingly in fig. 1 with a questionmark. Rivero's (1971: 97) comment that specimens of *Hyla boans* (Linnaeus) "with less web than usual are found in Amazonia and in the eastern base of the Andes of Colombia" also is rather suggestive of *H. wavrini* Parker. The same holds true for Lutz's (1973: 33) remarks about a specimen with a very wide vertebral stripe, and about vertebral stripes ending somewhere between the axilla and the sacrum. Kluge (1979: 6-7) also noted some differences between the Amazonas-Orinoco sample and the rest but it is not clear how his samples were composed, so I cannot interpret his remarks. Cochran

& Goin (1970: 201) also noted differences, especially in two frogs (USNM 152630-31) from Serrania de La Macarena, which were smaller than the general sample and which had reduced much darker webbing on the fingers, and in USNM 80652 (mentioned by Rivero (1961) as well). However, they conclude that all this material is *Hyla boans* (Linnaeus), but considering the fact they also include the types of *H. wavrini* Parker and *H. miranda-ribeiri* Melin this was to be expected: their perception of *H. boans* (Linnaeus) was not correct. Thus, I think that quite a few of the localities indicated for *H. boans* (Linnaeus) in fig. 1 and based on literature records eventually will turn out to represent records of *H. wavrini* Parker. Because I did not examine the material on which the aforementioned authors based themselves, I will not discuss this matter further here.

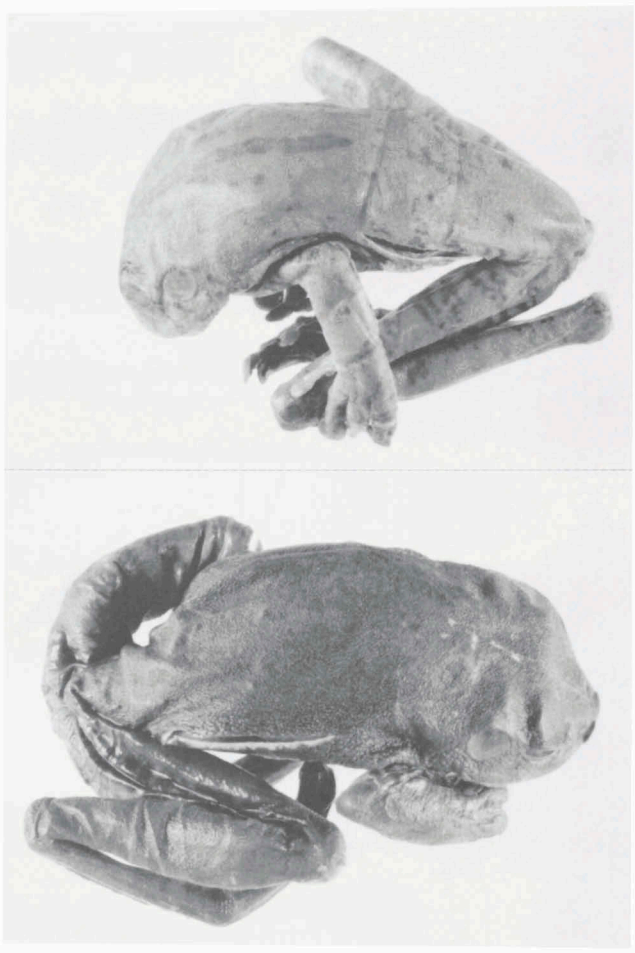

Fig. 7. Holo- (upper, MRHN IG 10.637 Reg. 1028, s-vl 75 mm) and paratype (lower, BMNH 1947.2.23.30, s-vl 75 mm) of *H. wavrini* Parker.

Records from eastern Ecuador and eastern Peru actually seem to represent *H. boans* (Linnaeus), as do records from Guiana, central- and southern Amazonia, thus suggesting that *H. boans* (Linnaeus) occurs around or throughout the Amazonian basin, but in its core area it is either replaced by or sympatric with *H. wavrini* Parker. A revision of the large hylids of the *Hyla boans* group seems to be called for, but it would spring the framework of this paper to do that here.

Ecology. — All specimens recently collected were calling from leafless (dead) trees in inundated areas (igapó, varzea). In Caño Cotua, Venezuela they were found in inundated caatinga forest along the creek at the foot of Cerro Yapacana. In the Rio Nhamundá, Cabeceira Urucuxi they were in trees, standing isolated in the water, some 5-10 meters from the sandy shore, which either was covered with terra firme forest (southern shore) or with grassland (cut and burnt terra firme forest). Most specimens were sitting in the lower part of the tree-crown, 5-100 cm above the water,

some, apparently after disturbance, were found swimming in the water. The holotype of *Hyla miranda-ribeiri* Melin was sitting on a shelf of rock along the river, whereas no ecological data are known for holo- and paratype of *H. wavrini* Parker. However, De Wavrin (1951: 183-184) does provide some scanty data, which are not very reliable though. From his text it is clear that the specimens he donated to MRHN were captured in his boat while he was travelling on the Orinoco River. According to him one specimen lived on his boat for two weeks, at night going ashore to forage and returning in the morning. This story certainly should be regarded with much reserve.

Several members of the *Hyla boans* group (*H. boans* (Linnaeus), *H. rosenbergi* Boulenger, *H. faber* Wied) are known to construct basins of sand or mud at the edge of pools, creeks and rivers to deposit their eggs, or alternatively deposit them in suitably small rock pools or other natural depressions at the water's edge (Duellman, 1973: 72; Kluge, 1981; Martins & Haddad, 1988; pers. observ.). In the Cruz Alta region just south of the Rio Trombetas, in rainforest, *Hyla boans* (Linnaeus) and its typical basins were found. In the Rio Nhamundá area, where, as far as could be ascertained, only *H. wavrini* Parker occurs, no such basins were found, and considering the calling stations of the males this would not be very likely. It seems most likely that eggs are directly deposited on or in the water of the Rio Nhamundá, where hardly any current is noticeable.

Ethology. — Kluge (1981) discussed the behaviour connected with mating in *Hyla rosenbergi* Boulenger and reported that males were extremely aggressive and might severely wound or even kill others in courtship battles, which involved wrestling in which the prepollipical spine was set to work (e.g. Kluge, 1981: 101, fig. 62). Martins & Haddad (1988) report similar behaviour for *H. faber* Wied, but do not elaborate beyond saying that fighting occurred. Though no direct observations are available on mating behaviour in *H. wavrini* Parker, there is some indirect evidence that suggests males wrestle and use their relatively small prepollical spines in wounding opponents. E.g. male MPEG 4521 shows numerous scratches on the skin of the head, on the back and on the left upper arm. There is a small wound on the left dorsolateral area that passes into a scratch and further back there is an open cut. Apparently these injuries did not bother the specimen, as during collecting no aberrant behaviour was noticed.

As mentioned above, males call from leafless trees in inundated areas. The call differs from that of *Hyla boans* (Linnaeus) by being less continuous, with the separate notes further apart. No complete call sequence was registered, but the animals seemed to call for extended periods without a break. Two partial sequences yielded 35 and 38 notes per minute. The notes have a duration of 0.46-0.71 ($\bar{x}$ = 0.55) sec, and are 0.43-1.40 ($\bar{x}$ = 1.07) sec apart. The notes are long, well-pulsed trills, which start with two or three solitary pulses, followed by two or three pairs of pulses, one or two triplets of pulses and the remainder in a group close together. There are 30-34 ($\bar{x}$ = 31.9) pulses per note, 45-81 ($\bar{x}$ = 59.8) pulses/sec. The fundamental frequency varies from 233-281 ($\bar{x}$ = 249) Hz with a 300 Hz filter to 332-395 ($\bar{x}$ = 369) Hz with a 45 Hz filter. The upper level of the dominant frequency is 673-730 ($\bar{x}$ = 697) Hz with a 300 Hz filter, 460-534 ($\bar{x}$ = 491) Hz with a 45 Hz filter. Maximum frequency 1150-1545 ($\bar{x}$ = 1282) Hz but in several sonagrams with 300 Hz filter the frequency in the middle of a note may reach 2000-2948 Hz ($\bar{x}$ = 2719) (mostly 2924-2948 Hz). The frequency of a note slowly increases, reaches a maximum in the middle and then drops fast (fig. 10).

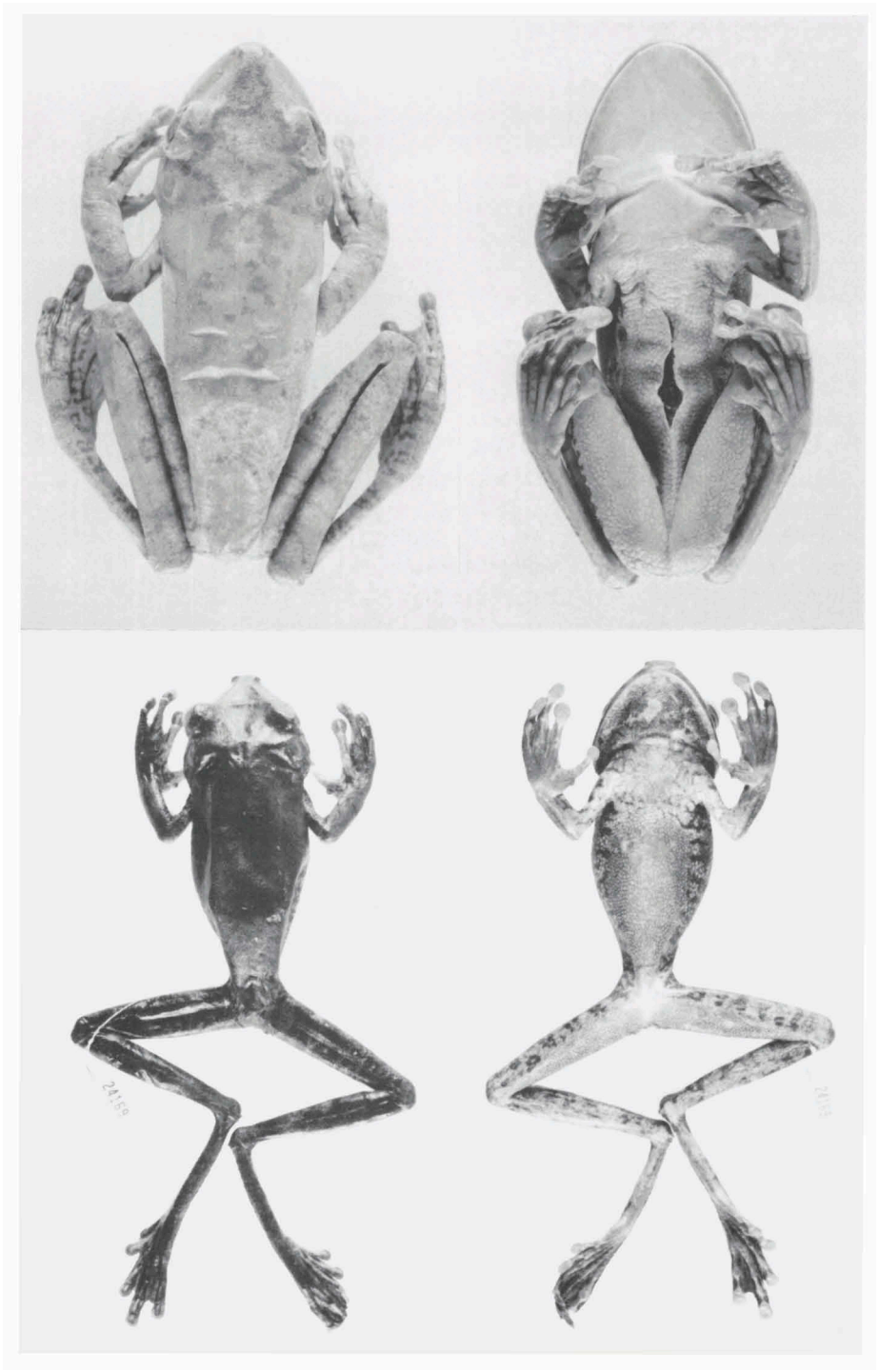

Fig. 8. Habitus of *H. wavrini* Parker (upper: holotype of *H. miranda-ribeiri* Melin, NHMG 41-7893, s-vl 81 mm; lower: RMNH 24169, s-vl113 mm).

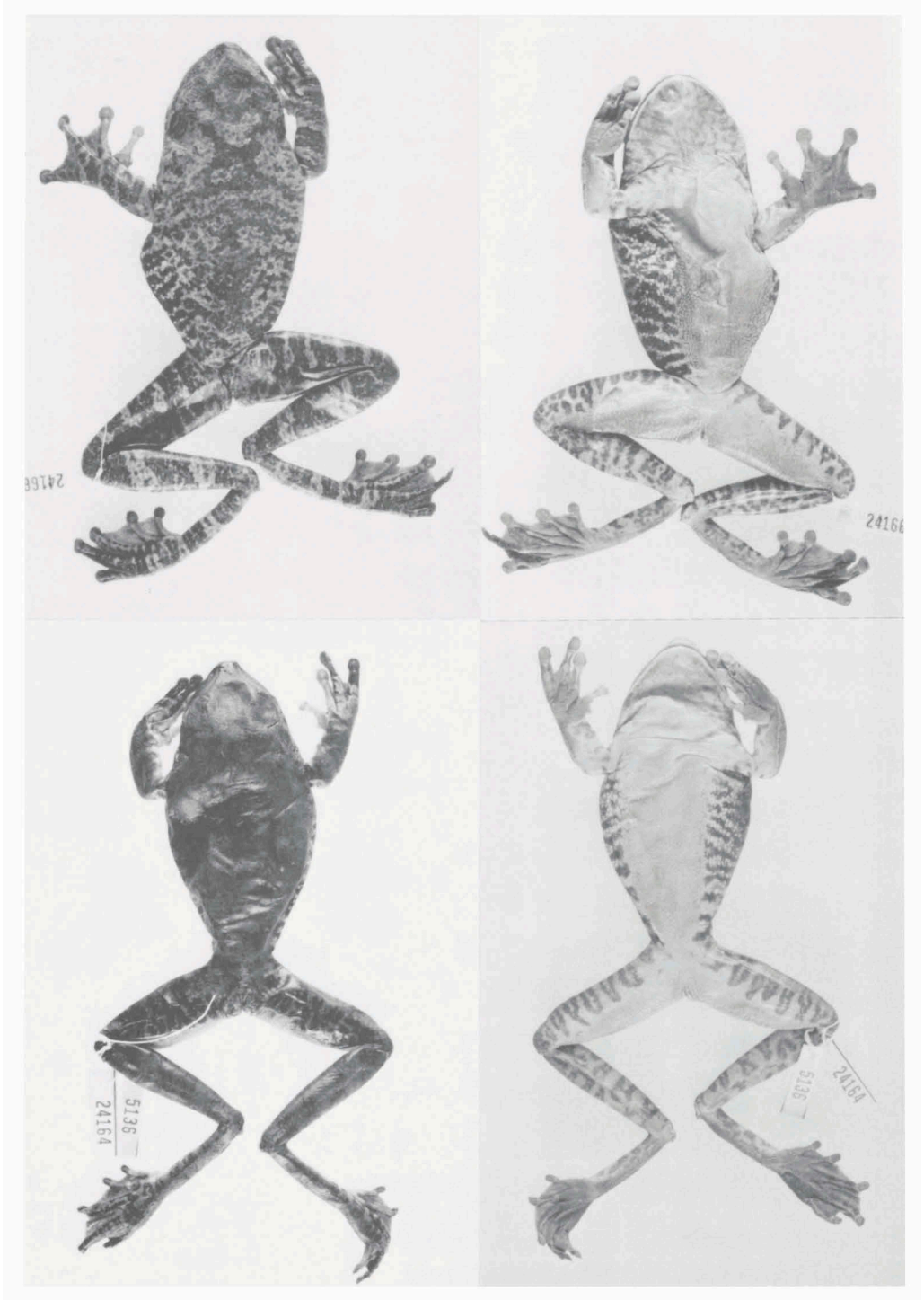

Fig. 9. Habitus of *H. wavrini* Parker (upper: RMNH 24166, s-vl 98 mm; lower: RMNH 24164, s-vl 89.4 mm).

In general the call agrees with that published by Hödl (1977), though the duration of notes as given by him seems to be longer than in the Rio Nhamundá specimen (RMNH 24164) analysed here.

Table 1. Call parameters of *Hyla boans* (Linnaeus) and *Hyla wavrini* Parker.

parameters	Hödl, 1977	Duelmann, 1970	Duelmann, 1978	Schlüter, 1979	Zimmerman Bogart, 1984	present *H.wavrini*
notes/call group	1	3-10 (41)	3-10	—	—	—
note repetion rate (notes/minute)	—	44-82 (69)	21.4-66.7 (38.2)	—	—	35-38
duration notes (sec)	—	0.25-0.28 (0.26)	0.18-0.27 (0.23)	0.6	—	0.46-0.71 (0.55)
pulse rate (pulses/sec)	54-66 (60.9)	100-120 (107)	100-140 (117)	—	—	45-81 (59.8)
pulses/note	—	—	—	—	—	30-34 (31.9)
fund. freq(Hz)	—	104-130 (114)	435-565 (512)	—	—	233-281* (249) 332-395+ (369)
dom. freq(Hz)	200-700 (380)	832-910 (869)	435-565	600-1100	—	673-730* (697) 460-534+ (491)
number harmonics	—	—	2	—	—	—
freq. range	—	104-910	—	300-1700	300-1750	—
emphasized freq.	—	—	—	—	440-980 (710)	—
low freq. range	—	—	—	—	300-350 (330)	—
high freq. range	—	—	—	—	1460-1730 (1600)	2000-2948 (2719)
calls/minute	14	—	—	—	88.18-106.07 (97.13)	—
call duration	0.65-1.19 (0.8)	—	—	—	0.19-0.24 (0.22)	—
intercall interval	2.28-4.7 (3.48)	—	—	—	0.57-0.68 (0.63)	—

The values with * were measured on a sonagram made with a 300 Hz filter, those with + on one made with a 45 Hz filter. Values between brackets are means. It will be clear that Zimmermann & Bogart used different names for several parameters than other authors.

Discussion. — Hödl (1977: 356) reported *Hyla boans* (Linnaeus) from the SW end of Lago Janauari near Manaus, calling "from the edge of or within the inundation forest, perched on nearly or completely leafless branches at a height of 1 to approximately 4 m above water level". This calling site exactly agrees with those of *Hyla wavrini* Parker in the Rio Nhamundá and at Caño Cotua. Hödl (1977: 358-359) also provided an analysis of the mating call of his *Hyla "boans"* from which it is clear that the dominant frequency is at 376 (variation 200-700) cycles per second, that call duration is 810 (variation 650-1190) milliseconds and that call intervals are 3.48 (variation 2.28-4.70) seconds. These data do not agree with data provided in any of the other publications (Duellman, 1970; Schlüter, 1979; Zimmerman & Bogart, 1984) discussing

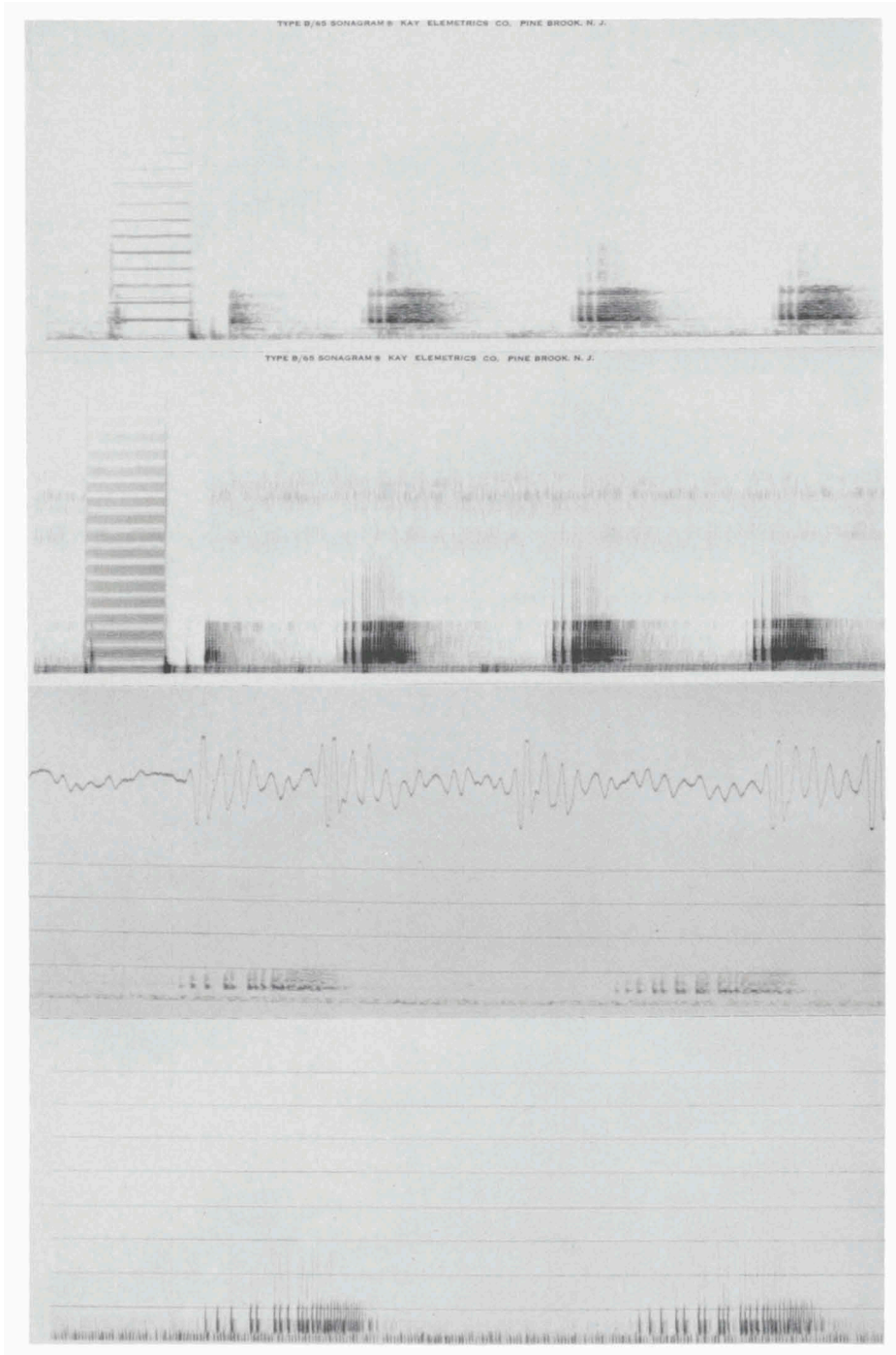

Fig. 10. Sonagrams of *H. boans* (Linnaeus) (upper one with filter 30 - 7500 Hz, second one with bandselector wide, both recorded at Sipaliwini,30-viii-1968, 19.30 h, RMNH 16604) and *H. wavrini* Parker (third with filter 45 Hz and waveform of three signals, signal length 0.053 sec, fourth with 300 Hz filter, both recorded at Rio Nhamundá, 13-xii-1988, 21.51 h, RMNH 24164). The total length of the figures equals 2.56 sec.

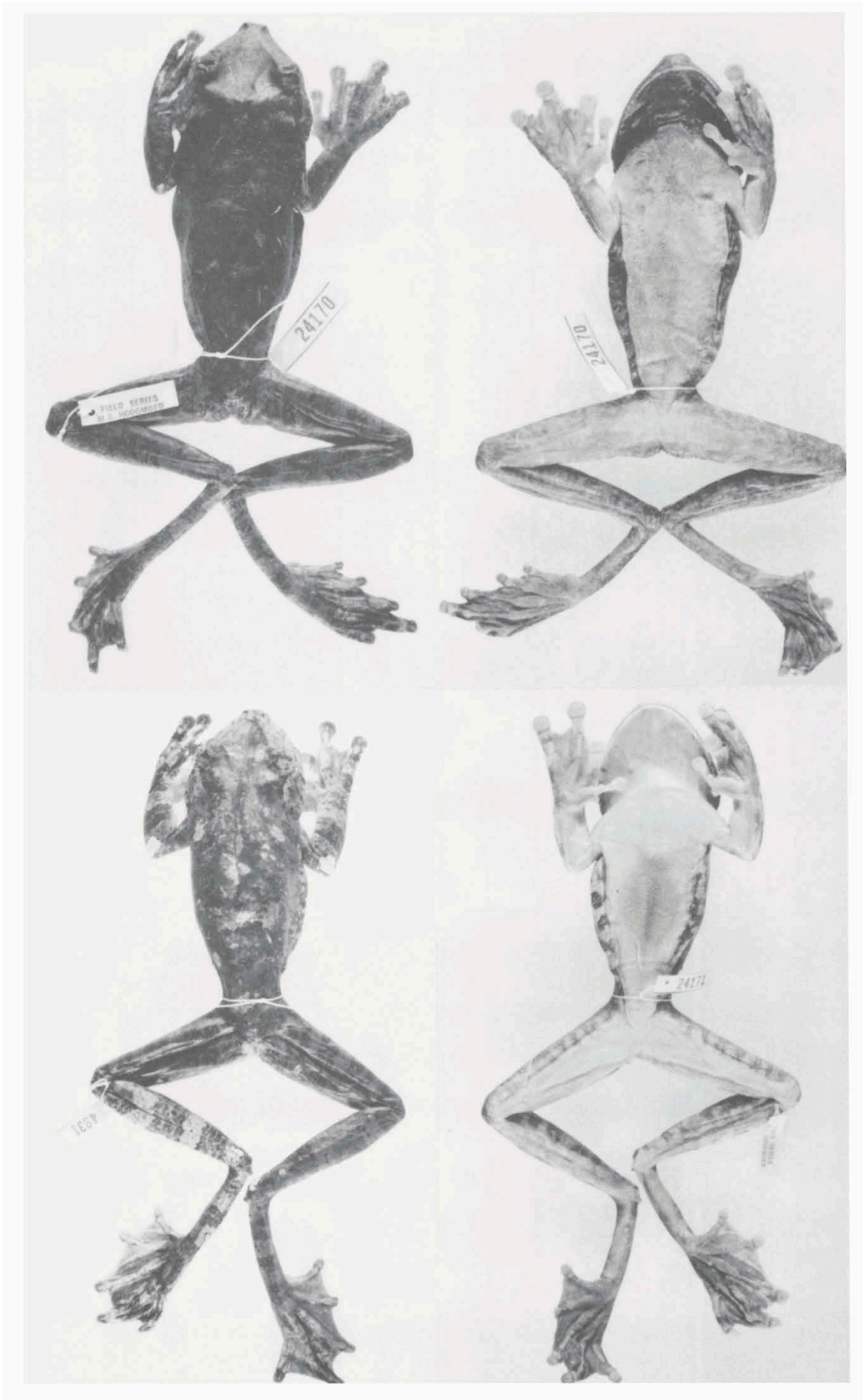

Fig. 11. Habitus of *H. boans* (Linnaeus) (upper: RMNH 24170, s-vl 91.3 mm; lower: RMNH 24171, s-vl 111 mm).

the call of *Hyla boans* (Linnaeus). On the basis of the data on ecology and mating call I was inclined to consider Hödl's *H. "boans"* as *H. wavrini* Parker, an assumption that was proved right by the examination of one of Hödl's specimens (NHMW 23561: 2). Duellman (1970, 1978), Schlüter (1979) and Zimmerman & Bogart (1984) provided sonagrams and/or an analysis of the call of *Hyla boans* (Linnaeus), from respectively Panama, eastern Ecuador, eastern Peru and north of Manaus in Brazil. The sonagrams published by Duellman (1970) (copied in Kluge, 1979), Schlüter (1979), Zimmerman & Bogart (1984) and sonagrams of calls recorded by me in Suriname agree in showing two or three introductory pulses, which are about 0.05 seconds apart and which are followed by the complex part of the call which lasts about 0.20-0.30 seconds (table 1). These data are very different indeed from those given by Hödl (1977, fig. 50). The use of different terminology by authors complicates comparisons of the analyses, though direct comparison of the sonagrams does not present a problem.

Though in general the sonagram of *Hyla boans* (Linnaeus) provided by Duellman (1970) agrees with those presented by Schlüter (1979) and Zimmerman & Bogart (1984), there are some notable differences in the frequency range (104-4454 Hz) and in some of the other parameters described and I hesitate to consider the Panamanian specimens described by Duellman (1970) as conspecific with the Amazonian material. This opinion is strengthened by the fact that the population in Panama and northwestern Colombia seems to be well separated geographically from the populations of the same 'species' in cis-Andean South America. The distribution-pattern as shown by *Hyla boans* in that area is typical for mesic-adapted species with a Panamanian-Chocoan distribution like *H. rosenbergi* Boulenger (Kluge, 1979: 6), several Dendrobatidae (Savage, 1968; Silverstone, 1975) and many other examples, mentioned by Dixon (1979: 221, 232-233), Duellman (1979: 17-18), Lynch (1979: 195-196), Müller (1973: 39-40) and Savage (1966, 1982). This distribution pattern contrasts with that of xeric-adapted species with a Panamanian-northern Colombian/Venezuelan distribution like *Hyla crepitans* Wied (probably *H. pugnax* Schmidt also belongs in this category) (Kluge, 1979) and the lizard *Cnemidophorus l. lemniscatus* (Linnaeus) (Burt, 1931). On the basis of these zoogeographical considerations and the differences in call, I am inclined to consider the Panama-NW.Colombia population of *Hyla 'boans'* as described by Duellman (1970) and Kluge (1979) as a taxon different from the populations known under that name in cis-Andean South-America. Study of relevant material will have to be done to test this hypotheses, but that is outside the framework of the present paper.

Zimmerman & Bogart (1984) noted the differences between the calls recorded by them and those recorded by Hödl (1977) in an area not more than 100 km air distance away. They explain this as *Hyla boans* (Linnaeus) having two call types, *viz.* "type A, the advertisement call, [which] is most commonly heard in the dry season and in aggregations at breeding sites", and "call type B, which was analysed by Hödl (1977) and involved solitary males calling in flooded forest (igapo)". As Zimmermann & Bogart (1984) correctly state "*H. boans* has only been observed to breed during the dry season and is not known to oviposit in igapo". They therefore conclude that the function of call type B is not understood presently. From the foregoing it will have become clear that Hödl's identification was wrong and that actually he was reporting

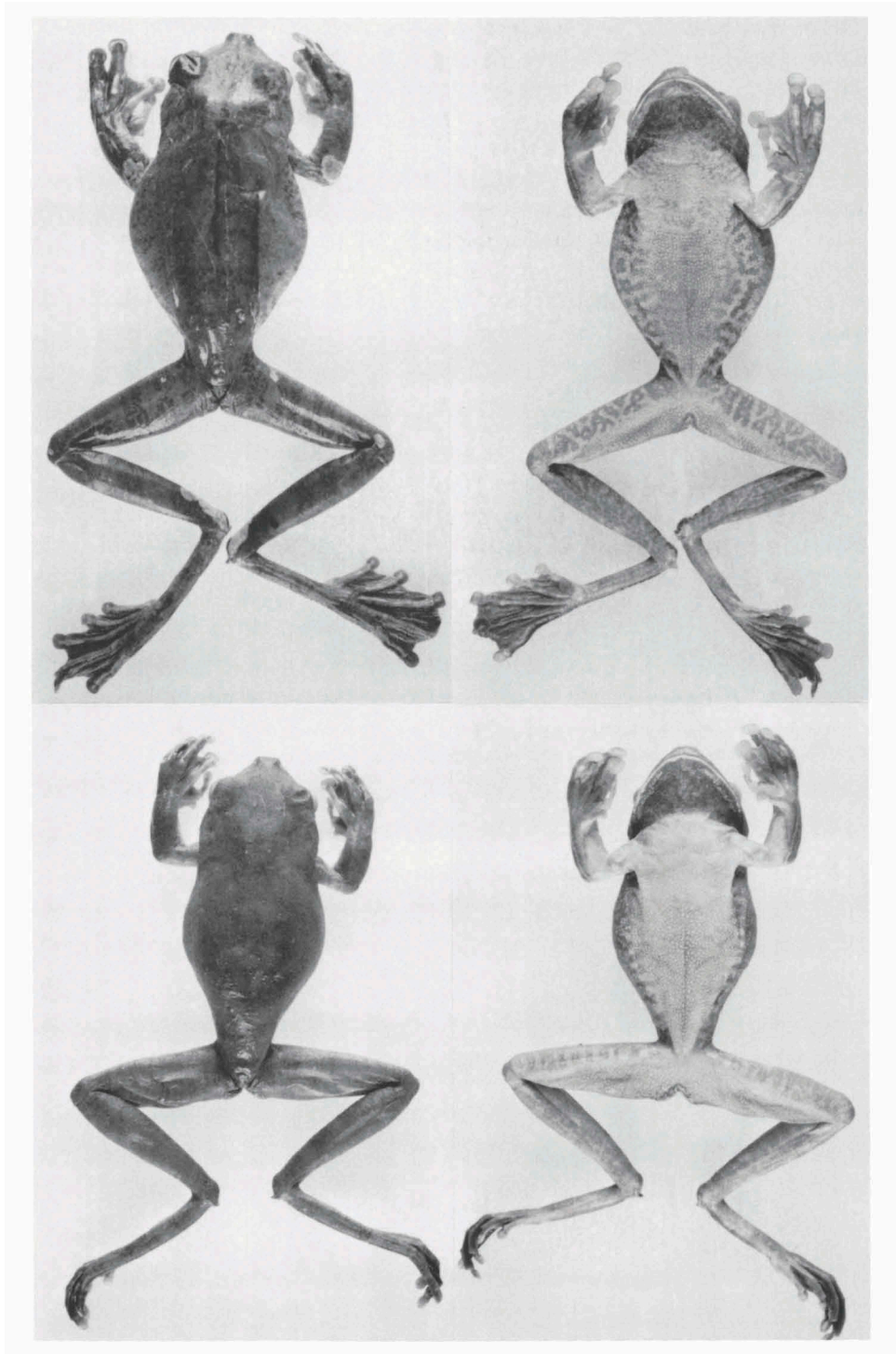

Fig. 12. Habitus of *H. boans* (Linnaeus) (upper: RMNH 24358, s-vl 115 mm; lower: RMNH24361, s-vl 92 mm).

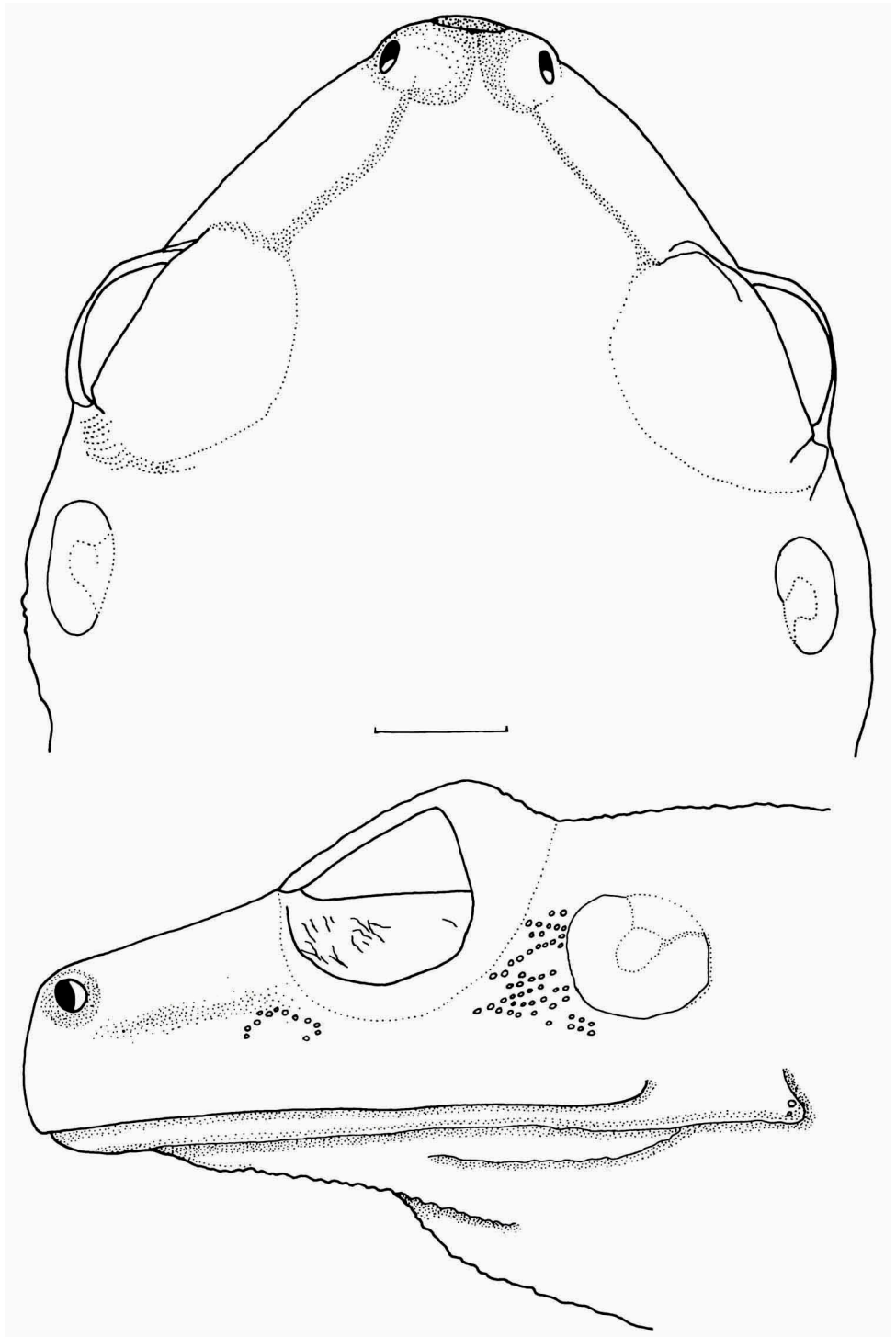

Fig. 13. Dorsal and lateral profile of head of *H. boans* (Linnaeus) (RMNH 24180). The scale bar equals 5 mm.

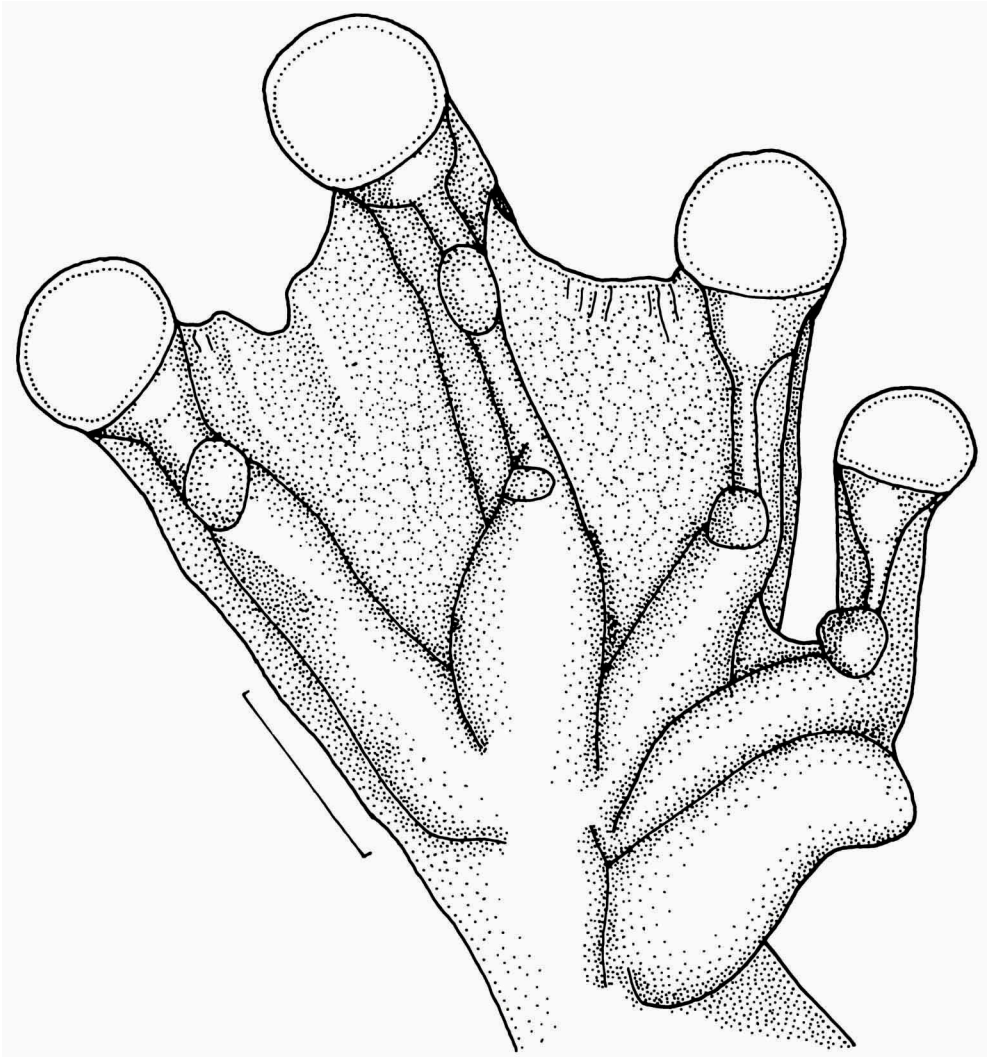

Fig. 14. Ventral view of hand of *H. boans* (Linnaeus) (RMNH 24170). The scale bar represents 5 mm.

on *H. wavrini* Parker. Consequently the so called call type B is the advertisement call of *H. wavrini* Parker, which apparently does breed in igapó, but of which no nest basins have been found yet.

Hödl & Gollmann (1986) in discussing distress calls of Amazonian frogs under *H. boans* (Linnaeus) actually describe the distress call of *H. wavrini* Parker.

Considering the confusion concerning *Hyla wavrini* Parker and *Hyla boans* (Linnaeus) it seems useful to point out in a table the differences between the two species. They do agree, among members of the *H. boans* group, in their large size and in having a golden reticulated palpebral membrane, the last character being (incorrectly) described by Kluge (1979: 6) for *H. boans* (Linnaeus) as unique within the group.

Table 2. Comparison of *Hyla boans* (Linnaeus) and *Hyla wavrini* Parker (figs. 3 - 14)

	Hyla boans (Linnaeus)	*Hyla wavrini* Parker
Webbing of fingers	I(2) - (2)II(1)-(2)III(1) - (1) IV	I(2$^1/_2$ - (2$^1/_2$)II(1) - (2)III(1$^3/_4$-2) - (2)IV
Web between fingers I and II	rudiment distinct	rudiment small
Fourth finger	webbing reaches disc	penultimate phalanx free
Subarticular tubercles fingers	not very distinct	pronounced
Supernumerary tubercles hand	hardly present	pronounced
Discs fingers	completely covering tympanum	distinctly smaller than tympanum
Webbing toes	I(1) - (1)II(1) - (1)III(1) - (1)IV(1) - (1)V	I(1) - (1)II(1) - (1)III(1) - (1$^1/_2$) IV(1$^1/_2$) - (1)IV
Discs toes	large, transversely oval	relatively small, ca.round to longitudinally oval
Fourth toe	webbing reaches disc	webbing does not reach disc
Heels overlap	slightly	distinctly
Heel appendage	transverse ridge with lateral triangular flap	transverse ridge with small triangular tubercle
Ulnar ridge	strong, ending in flap of skin on elbow	weak, no flap of skin on elbow
Ridge median side tibia	on posterior part, connected with heel appendage	absent
Tarsal ridge	very distinct	absent to very weak
Shape of head	as long as wide	longer than wide
Eyes	protruding well beyond circumference of head	not or only slightly protruding beyond circumference of head
Canthus rostralis	concave	straight
Nostrils	protuberant	not very protuberant
Snout	anteriorly concave	anteriorly truncate
Prepollical spine males	rather large	present but small
Colour of back	mainly brown or beige	greenish-grey with darker pattern
Vertebral stripe	narrow, dark; sometimes present, either throughout length or only on head and anterior part of body	wide, brownish; may be present, never beyond sacrum

Throat males	anteriorly uniform dark grey, or dark grey with indistinct darker spots	grey with dark radiating stripes, or with indistinct lighter, rounded spots separated by dark network
Flanks	without or with single (sometimes) dark stripes	with distinct double transverse stripes
Colour iris	golden	greyish to reddish brown
Call	notes close together, fewer pulses per note, two or three separate pulses at start of note	notes further apart, more pulses per note, many separate pulses, either single, in pairs or in triplets at start of note

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References

Bokerman, W.C.A., 1966. Lista anotada das localidades tipo de anfíbios brasileiros: 1-183. Sao Paulo.

Burt, C.E., 1931. A study of the teiid lizards of the genus *Cnemidophorus* wih special reference to their phylogenetic relationships. — Bull. U.S.N.M. 154: i-vi, 1-286.

Cochran, D.M., & C.J. Goin, 1970. Frogs of Colombia. — Bull. U..S.N.M. 288: i-xii. 1-655.

Dixon, J.D., 1979. Origin and distribution of reptiles in lowland tropical rainforests of South American herpetofauna. In: W.E. Duellman (ed.) The South American herpetofauna: its origin, evolution and dispersal. — Mon. Mus. Nat. Hist. Univ. Kansas 7: 217-240.

Duellman, W.E., 1970. The hylid frogs of Middle America. — Mon. Mus.Nat. Hist. Univ. Kansas 1: i-xi, 1-753.

Duellman, W.E., 1971. The nomenclatural status of the names *Hyla boans* (Linnaeus) and *Hyla maxima* (Laurenti) (Anura: Hylidae) — Herpetologica 27 (4): 397-405.

Duellman, W.E., 1973. Nest-building Hylid frogs. — HISS News-Journal 1(3): 72-75.

Duellman, W.E., 1977. Liste der rezenten Amphibien un Reptilien. Hylidae, Centrolenidae, Pseudidae. — Das Tierreich 95: i-xix, 1-225.

Duellman, W.E., 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. — Misc. Publ. Univ. Kansas Mus. Nat. Hist. 65: 1-352.

Duellman, W.E., 1979. The South American herpetofauna; a panoramic view. In: W.E. Duellman (ed): The South American herpetofauna: its origin, evolution and dispersal. — Mon. Mus. Nat. Hist. Univ. Kansas 7: 1-28.

Frost, D.R., 1985. Amphibian species of the world. A taxonomic and geographical reference: i-v, 1-732. Lawrence, Kansas.

Gines, H., 1959. Familias y generos de anfibios - Amphibia - de Venezuela. — Mem. Soc. Cienc. Nat. La Salle 19(53): 85-146.

Gorham, S.W., 1963. The comparative number of species of Amphibians in Canada and other countries. III. Summary of species of Anurans. — Can. Field Nat. 77: 13-48.

Gorham, S.W., 1974. Checklist of World Amphibians up to January 1, 1970: 1-172, 1p. New Brunswick.

Gremone, C., F. Cerrigón, S. Gorzula, G. Medina & D. Novoca, 1986. Fauna de Venezuela, Vertebrados: 1-269. Caracas.

Harding, K.A., 1983. Catalogue of New World Amphibians: i-xiv, 1-406. Oxford, etc.

Hödl, W., 1977. Call differences and calling site segregation in anuran species from Central Amazonian floating meadows. — Oecologia 28: 351-363.

Hödl, W., & G. Gollmann, 1986. Distress calls in Neotropical frogs.— Amphibia-Reptilia 7(1): 11-21.

Hoogmoed, M.S., 1979. The herpetofauna of the Guianan region. In: W.E. Duellman (ed.): The South American herpetofauna: its origin, evolution, and dispersal. —Mon. Univ. Kansas. Mus. Nat. Hist. 7: 241-279.

Kluge, A.G., 1979. The gladiator frogs of Middle America and Colombia - a re-evaluation of their systematics (Anura: Hylidae). — Occ. Pap. Mus. Zool. Univ. Mich. 688: 1-24.

Lescure, J., 1976. Contribution à l'étude des Amphibiens de Guayane française. VI. Liste préliminaire des Anoures. — Bull. Mus. nat. Hist. Nat. Paris, 3e sér. 377, Zoologie 265: 475-524.

Lutz, B., 1973. Brazilian species of Hyla: i-xviii, 2 pp., 1-260, 5 pp. Austin, London.

Lynch, J.D., 1979. The amphibians of the lowland tropical forest. In: W.E. Duellman (ed.): The South American herpetofauna: its origin, evolution, and dispersal. — Mon. Univ. Kansas Mus. Nat. Hist. 7: 189-215.

Martins, M. & C.F.B. Haddad, 1988. Vocalizations and reproductive behaviour in the smith frog, *Hyla faber* Wied (Amphibia: Hylidae). — Amphibia-Reptilia 9(1): 49-60.

Melin, D., 1941. Contributions to the knowledge of the Amphibia of South America. — Göteb. Kungl. Vet. Vitt. Samh. Handl. Sj.F. ser B(1)4: 1-71.

Müller, P., 1973. The dispersal centres of terrestrial vertebrates in the Neotropical realm. A study in the evolution of the Neotropical biota and its native landscapes. — Biogeographica 2: i-vi, 1-244.

Parker, H.W., 1936. A collection of reptiles and amphibians from the Upper Orinoco. - Bull. Mus. roy. Hist. nat. Belg. 12(26): 1-4.

Rivero, J.A., 1961. Salientia of Venezuela. — Bull. M.C.Z. 126(1): 1-207.

Rivero, J.A., 1964. The distribution of Venezuelan frogs. V, The Venezuelan Guyana. — Carib. J. Sci. 4(2-3): 411-420.

Rivero, J.A., 1967. Anfibios collecionados por la Expedicion Franco-Venezolana al Alto Orinoco 1951-1952. — Carib. J. Sci.7 (3-4): 145-154.

Savage, J.M., 1966. The origins and history of the Central American herpetofauna. — Copeia, 1966(4): 719-766.

Savage, J.M., 1968. The dendrobatid frogs of Central America - Copeia 1968(4): 745-776.

Savage, J.M., 1982. The enigma of the Central American herpetofauna: dispersal or vicariance? - Ann. Missouri Bot. Gard. 69: 464-547.

Schlüter, A., 1979. Bio-akustische Untersuchungen an Hyliden in einem begrenzten Gebiet des tropischen Regenwaldes von Peru. — Salamandra 15 (4): 211-236.

Silverstone, P.A., 1975. A revision of the poison-arrow frogs of the genus *Dendrobates* Wagler. — Sc. Bull. Nat. Hist. Mus. L.A. County 21: 2 pp., 1-55.

Wavrin, Marquis de, 1951. Les bêtes sauvages de l'Amazonie et des autres régions de l'Amérique du Sud: 1-301. Paris.

Zimmerman, B.L., & J.P. Bogart, 1984. Vocalizations of primary forest frog species in the Central Amazon. — Acta Amazonica 14(3-4): 473-519.

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