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A NEW GENUS OF TOADS (AMPHIBIA: ANURA: BUFONIDAE) FROM THE PACIFIC SLOPES OF THE ANDES IN NORTHERN ECUADOR AND SOUTHERN COLOMBIA, WITH THE DESCRIPTION OF TWO NEW SPECIES

by

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The genus *Andinophryne*, characterized by the presence of an omosternum, an externally visible tympanum, elongate parotoids and extensively webbed hands and feet is described from the Pacific versant of the Andes in northwestern Ecuador and southwestern Colombia. Two new species, *Andinophryne colomai* and *A. olallai* are described from Ecuador. The recently described *Bufo atelopoides* Lynch & Ruiz-Carranza is transferred to the new genus. Some comparisons with other atelopodid Bufonidae (*Atelopus*, *Dendrophryniscus*, *Melanophryniscus*, *Oreophrynella*, *Osornophryne*, *Rhamphophryne*) are made and some very tentative remarks on their relationships are ventilated.

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RESUMEN

Se describe el genero *Andinophryne*, caracterizado por la presencia de un omosternum, de un timpano externo visible, parotoides elongados y los manos y piernas bien palmeados, de las pendientes pacificos de los Andes en el noroeste del Ecuador y en el suroeste del Colombia. Tambien se describe dos especies nuevos, *Andinophryne colomai* y *A. olallai* del Ecuador. La especie que estuvo descrito hace poco como *Bufo atelopoides* Lynch & Ruiz-Carranza esta trasladado al genero nuevo. Se hace algunos comparaciones con otros Bufonidae atelopodidos (*Atelopus*, *Dendrophryniscus*, *Melanophryniscus*, *Oreophrynella*, *Osornophryne*, *Rhamphophryne*) y algunos observaciones prudentes sobre sus relaciones estan ponidos.

INTRODUCTION

Systematics of South American bufonid frogs have been rather hectic in the past two decades. Many species of the genera *Atelopus*, *Dendrophryniscus*, *Melanophryniscus* and *Oreophrynella*, now placed in the Bufonidae, formerly were placed in the family Atelopodidae, until McDiarmaid (1971, based on his earlier (1969), unpublished thesis) clearly showed them to be nothing but rather atypical members of the Bufonidae. Trueb (1971) removed some species from the genera *Bufo* and *Atelopus* and placed them in a newly described genus *Rhamphophryne*, composed of five species, two formerly in *Bufo*, one in *Atelopus* and two newly described ones. Members of the genus have heavily ossified, triangular heads and protruding snouts, and lack a tympanic annulus and columella. She placed the new genus in the Bufonidae, at the same time corroborating McDiarmaid's (1971) opinion about the contents of the family.

Ruiz-Carranza & Hernández-Camacho (1976) described another genus (*Osornophryne*), based on a newly described species and on a species formerly considered to belong to *Atelopus*. This genus is characterized by the reduction of the number of phalanges in the fourth finger to two, the presence of only six presacral vertebrae, a firmisternal pectoral girdle, and by the lack of parotoids and a tympanum. In their discussion of relationships, they confirmed the opinion of other authors that the so-called "Atelopodidae" (in this context including the genera *Atelopus*, *Dendrophryniscus*, *Melanophryniscus*, *Oreophrynella*, *Osornophryne* and *Rhamphophryne*) should be included in the Bufonidae.

Relationships among these six last-mentioned genera are unclear. McDiarmaid (1971: 49, fig. 11) provided a diagrammatic representation of the evolutionary relationships among the four genera studied by him. Trueb (1971) concluded that "*Rhamphophryne* seems to be most similar to *Atelopus* and *Oreophrynella* in the New World and the small group of highly specialized African genera consisting of *Laurentophryne*, *Mertensophryne*, and *Nectophryne*". Summarizing her data, Trueb (1971) postulated two hypotheses: "(1) *Rhamphophryne* is geographically isolated, but phylogenetically close to *Mertensophryne* and its African allies; or (2) *Rhamphophryne*, *Oreophrynella*, and *Atelopus* constitute a phylogenetic New World group which has evolved in a fashion closely paralleling that of an Old World line composed of *Laurentophryne*, *Nectophryne*, *Pelophryne*, and *Mertensophryne*".

In their discussion of the relationships of *Osornophryne*, Ruiz-Carranza & Hernández-Camacho (1976) concluded that similarities between this genus and *Oreophrynella* are convergent, and that *Osornophryne* + *Atelopus* were

derived from a common ancestor. They based this opinion on the firmisternal pectoral girdle shared by the two genera.

During recent studies in the systematics of the *Bufo typhonius* group, I encountered two toads which are distinctly different from anything known before, and, upon closer investigation, proved to be sufficiently differentiated from other Bufonidae to be considered as a new genus.

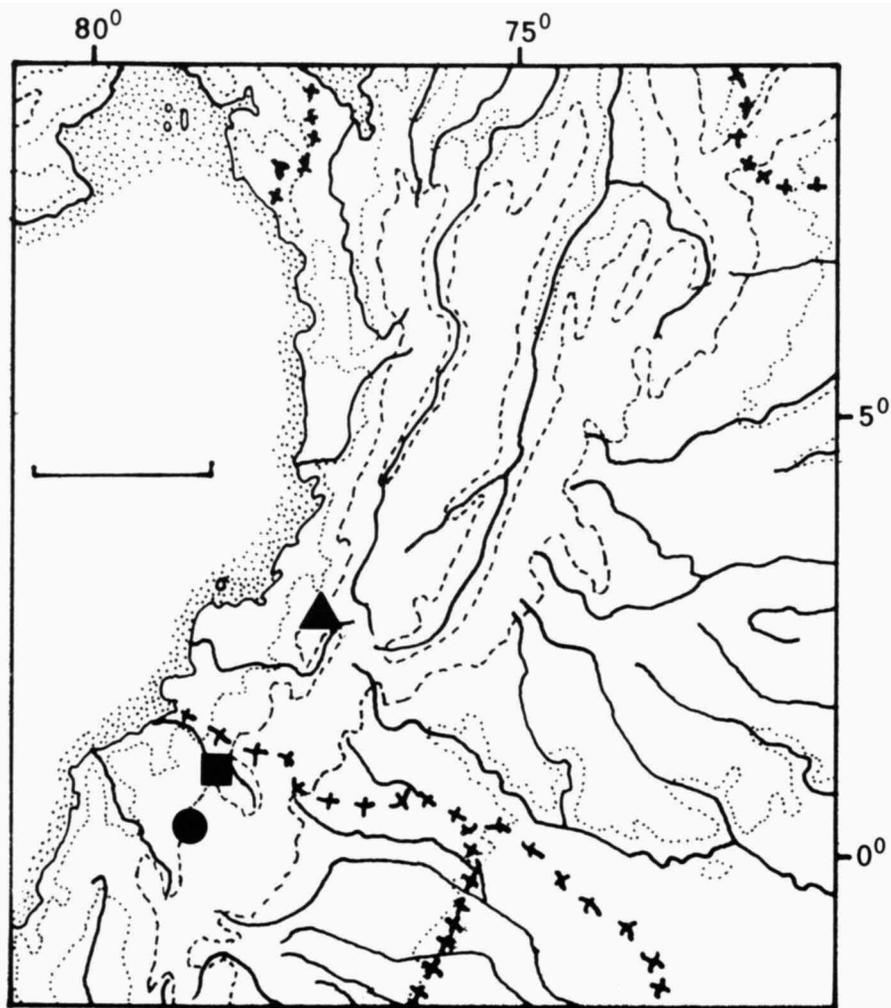


Fig. 1. Map of western South America, showing localities where species of *Andinophryne* gen. nov. were found. Dot: *A. colomai* spec. nov.; square: *A. olallai* spec. nov.; triangle: *A. atelopoides* (Lynch & Ruiz-Carranza). The lines of heavy crosses represent international boundaries, that of dots the contourline of 200 m, that of dashes the countourline of 1000 m, uninterupted lines are rivers. The horizontal line equals 250 km.

Lynch & Ruiz-Carranza (1981) described a rather peculiar species of *Bufo*, which they tentatively considered a member of the *typhonius* group. From the data they provide, it is clear that this species (*B. atelopoides* Lynch & Ruiz-Carranza) also belongs to the genus here described.

SYSTEMATIC PART

Andinophryne gen. nov.

Type-species: *Andinophryne colomai* spec. nov.

Diagnosis. — A genus of small bufonids having a well-developed ear and an externally visible tympanum. Pectoral girdle anteriorly firmisternal (precoracoid bridge), posteriorly arciferal (definition of McDiarmid, 1971: 45); a small omosternum present. Parotoid glands well-developed, elongate. Hands and feet extensively webbed. Limbs, fingers and toes long and slender. Eight presacral vertebrae, sacrum with bicondylar articulation with coccyx. This combination of characters distinguishes it from other small to medium-sized South American bufonids (*Atelopus*, *Bufo*, *Dendrophryniscus*, *Melanophryniscus*, *Oreophrynella*, *Osornophryne*, *Rhamphophryne*). *Andinophryne* differs from *Atelopus* (with which it occurs sympatrically) in having eight presacral vertebrae and a pectoral girdle that is partially firmisternal, and from most species (except *A. flavescens* Duméril & Bibron and *A. spumarius* Cope) in having a well-developed ear. From *Dendrophryniscus*, *Melanophryniscus*, *Oreophrynella*, *Osornophryne* and *Rhamphophryne*, it can be distinguished by the presence of a middle ear, from most species of *Bufo* (except *B. haematiticus* Cope) by the presence of an omosternum, and from *B. haematiticus* by its extensively webbed hands and feet, the arrangement of the muscles in the temporal area and the absence of the musculus adductor longus.

Description. — Medium-sized (maximum snout-vent length recorded 42.7 mm) atelopodid frogs of the family Bufonidae, with horizontally oval pupil, a distinct external tympanum and associated middle ear, a sharp, fleshy canthus rostralis, a concave loreal region, a fleshy, vertical rostral ridge, a fleshy supratympanic ridge, indistinct subarticular pads, extensively webbed (edges smooth) fingers and toes, digits long. Choanae small, round, in a lateral position. No vomerine processes. Head wide (about as wide as long) and flat, without bony crests. Snout protruding beyond the upper jaw and in dorsal aspect obtusely pointed. The elongate parotoids are up to three times as long as wide. One or more oblique lateral rows of glands or tubercles from parotoids to groin. The tongue is longer than wide, lingulate, narrow anteriorly, gradually widening posteriorly, posterior margin rounded, attached for

most of its length. Males with vocal slits.

Pectoral girdle anteriorly firmisternal (precoracoid bridge), posteriorly arciferal (cf. McDiarmid, 1971: 45), a small omosternum present, sternum elongate and cartilaginous. Limbs rather long and slender. Number of phalanges: hand, 2-2-3-3; foot, 2-2-3-4-3; phalanges ending in a knob.

Eight presacral vertebrae, sacrum with bicondylar articulation with coccyx; transverse processes present, moderately long.

The frontoparietals are of normal size, separated in the midline by an elongate slit arising anteriorly. The musculus depressor mandibulae arises for its greater part on the squamosal arm and the lateral portion of the prootic, but a considerable number of fibers arise on the postero-dorsal edge of the annulus tympanicus. This condition (or a slightly modified one) also occurs in a few species of *Atelopus* and was indicated as SQat by McDiarmid (1971: 9), who considered this a primitive condition. Apparently only the musculus adductor mandibulae posterior subexternus is present, the mandibular branch of the nervus trigeminus lies across the lateral surface of this muscle, a condition designated S by McDiarmid (1971: 9).

The musculus tensor fasciae latae is rather short and thin. It has its origin on the posterior third of the ilium and inserts on the surface of the musculus cruralis rather close to the body. The musculus adductor longus is absent.

Etymology. — Named for the Andes, the mountain range that has such a profound influence on the distribution of animals and plants in western South America, and from the Greek *phryne*, toad, in reference to the fact that these toads only are known from the western slopes of the Andes. The genus is feminine in gender.

Contents. — Three species, viz., *Andinophryne atelopoides* (Lynch & Ruiz-Carranza), *A. colomai* spec. nov. and *A. olallai* spec. nov.

Distribution. — Only known from the western slopes of the Andes in NW Ecuador and S Colombia, from low to moderate altitudes (500-2190 m) (fig. 1).

Relationships. — Because of the scarcity of material no dissections other than to establish sex, the nature of the pectoral girdle, the arrangement of temporal and thigh muscles could be made. Most data on skeletal features were obtained from X-ray photographs.

Intuitively speaking the relations of this atelopodid bufonid genus seem to lie with *Atelopus*, *Osornophryne* and *Rhampophryne*, which all occur in western South America, as opposed to *Dendrophryniscus*, *Melanophryniscus* and *Oreophrynella*, that have a cis-Andean distribution only. *Atelopus* is known to be sympatric with each of the other three western South American genera, which among themselves are allopatric. *Atelopus* ranges from the

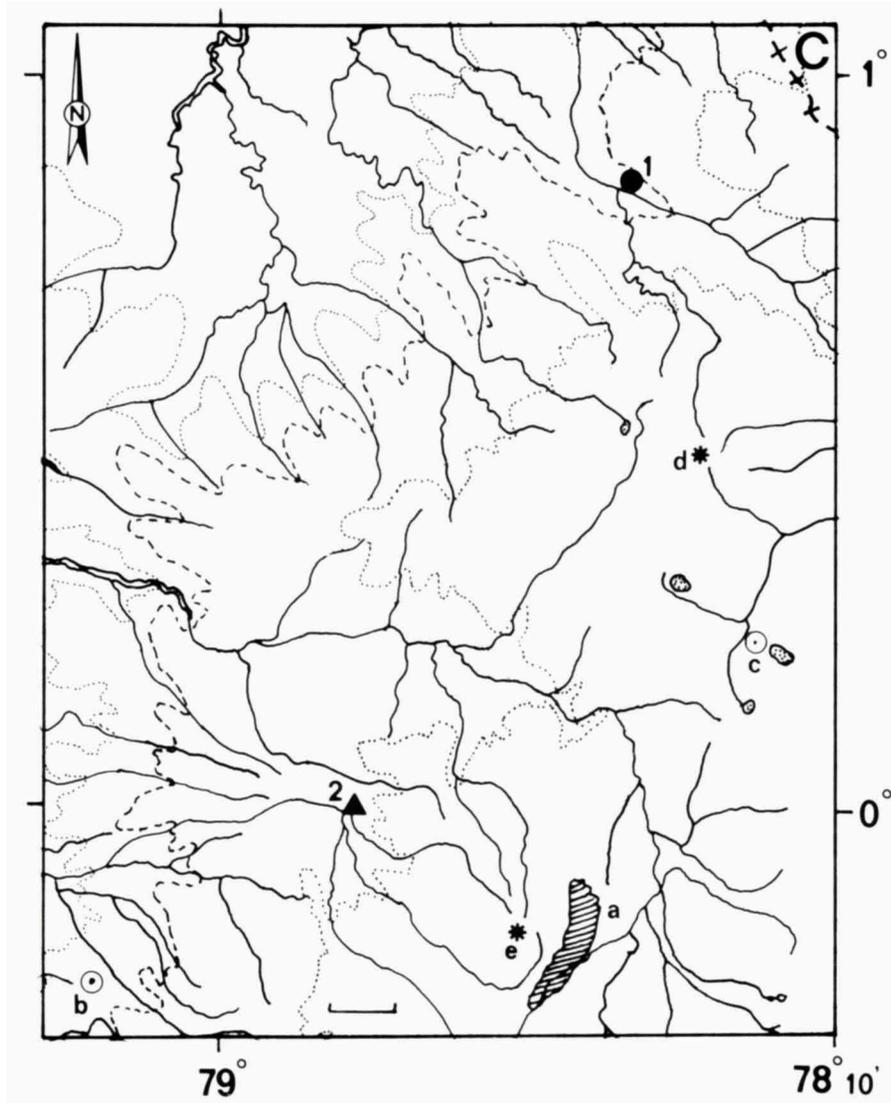


Fig. 2. Map of NW Ecuador and part of adjacent Colombia (large C), showing the type-localities of *Andinophryne colomai* spec. nov. (1 = Rio Baboso, near Lita) and of *A. olallai* spec. nov. (2 = Tandayapa, $0^{\circ}01' S$ $78^{\circ}46' W$), some larger cities for reference (a = Quito, b = Santo Domingo de los Colorados, c = Otavalo) and some larger volcanos (asterisks: d = Cotacachi (4937 m), e = Pichincha (4794 m)). The horizontal line represents 10 km, the line of heavy dots crosses the border with Colombia, the line of small dots the contourline of 300 m, that of dashes the contourline of 600 m and that of heavy dots the contourline of 1500 m (from left to right in map). Uninterrupted lines are rivers.

western foothills of the Andes, via the high Andean páramo's to the eastern foothills of the Andes, the adjacent Amazonian lowlands and even reaches the coastal range of Venezuela and the Guianas. *Andinophryne* is known only from the western (Pacific) Andean slopes from low to moderate elevations, *Osornophryne* is known only from the páramo-region at high altitude, and *Rhamphophryne* only is known from the eastern (Atlantic) Andean slopes and adjacent lowlands. Thus, it may be that *Andinophryne*, *Rhamphophryne* and *Osornophryne* occupy similar niches, which are not occupied by *Atelopus*.

In the following considerations I have strictly adhered to McDiarmid (1971: 43-46) interpretation of whether character states are primitive or advanced, based on an outgroup comparison with *Bufo*. In a few cases (squamosal, presacral vertebrae, phalangeal formula, egg colour and number) character states not mentioned by McDiarmid (1971) are found in the genera described since 1971 (*Rhamphophryne*, *Osornophryne* and *Andinophryne*) and the data have accordingly been adapted in table 1. Also a few more character states (omosternum, amplexus, parotoids) which seem to be of importance have been considered here.

Comparing the genera for a number of characters (presacral vertebrae, atlas, sacrum, coccyx, skull, pectoral girdle, phalangeal formula of the hand, middle ear, thigh and head musculature, presence of parotoids, eggs, amplexus) *Andinophryne* seems to have mostly primitive character states and the lowest number of advanced character states (table 1). Only in three characters (no.'s 3, 5 and 28 of McDiarmid (1971: 46)) it shows an advanced condition. The absence of the musculus adductor longus (no. 3) is an advanced character it shares with all other genera considered here, and which serves to distinguish the group as such from *Bufo*. Thus, this character does not give us any information on the relations within the group and it is not included in any of the computations presented here. The condition of the musculus adductor mandibulae (no. 5), of which only the adductor mandibulae posterior subexternus is present, is an advanced character state which distinguishes *Andinophryne* from *Bufo*, in which two parts of the adductor mandibulae are present, but which *Andinophryne* shares with a.o. *Atelopus*. The pectoral girdle (no. 28) shows a strange mixture of advanced and primitive character states. It is relatively advanced in having the posterior part arciferal, the anterior part firmisternal (precoracoid bridge) and in this it agrees with *Rhamphophryne*, *Dendrophryniscus*, *Melanophryniscus* and *Oreophrynella*, both *Atelopus* and *Osornophryne* having completely firmisternal pectoral girdles, *Bufo* having an arciferal one (the more primitive condition). The pectoral girdle is primitive in having a small cartilaginous omosternum, which is absent in all other Bufonidae, except *Bufo haematiticus* Cope, and the African genus

Characters	1	2	3	4	5	6	7	10	13	14	16	17	20	21	23	24	25
<i>Atelopus</i>	A	1	A	P, A ₂	A ₁	P	3	P	1	P ₁ , P ₂	A	P	A	1	A ₂	A	P
<i>Dendrophryniscus</i>	P	2	A	A ₂ , A ₃	:A ₁	P	1	P, A	1	P ₂	A	P	P	1	P	P	P
<i>Melanophryniscus</i>	P	1	A	A ₂	A ₁	P	2	P, A	2	P ₂ , A	A	A	P	2	P	P	P
<i>Oreophrynella</i>	P	1	A	A ₂	A ₂	A	1	P	3	A	P	P	P	1	A ₃	A	A
<i>Rhamphophryne</i>	A ₁ , P	-	A	-	-	P	3	P	3	-	A	-	-	-	P ₁ , A ₂	P	P
<i>Andinophryne</i>	P	-	A	P	A ₁	P	-	-	-	-	-	-	-	-	P	P	P
<i>Osornophryne</i>	A	-	A	A ₂	A ₁	P	-	A	4	P ₂	P, A	P	P	-	A ₄	A ₁ , P	A
<i>Bufo</i>	P	-	P	P	P	P	-	P	-	P ₁	P	P	P	1	P	P	P
C (ctd)	26	28	31	33	35	36	37	38	39	40	41	42	parotoids	amplexus	omosternum	hypobr. 2	
<i>At</i>	P, A	A ₂	A	P, A ₁	P, A	P, A ₃	P, A	1	1, 2	A	1, 2	P ₁	A	A	A	A	A
<i>Den</i>	A	A ₁	A	P, A ₁	A	A ₃	A	1	3	A	2	P ₂	A	A	A	A	A
<i>Mel</i>	P	A ₁	P	P	A	P	P	2	4	A	1, 2	P ₂	A	A	A	A	A
<i>Or</i>	A	A ₁	P	P	A	A ₂	A	2	4	A	1	A ₁	A	-	A	A	A
<i>Rham</i>	P, A	A ₁	-	P	A	-	P, A	1	4	-	-	A ₂	P	-	A	-	-
<i>And</i>	P	A ₁	?	P	P	-	P	1	2	-	-	P ₁	P	-	P	-	-
<i>Oso</i>	A	A ₂	A	A ₂	A	A ₃	A	2	4	A	2	A ₂	A	P	A	A	-
<i>Bufo</i>	P	P	P	P	P, A	P, A	P, A	2	1, 4	A	1, 2	P ₃	P	A	A, P	P	P

Table 1. Distribution of character states among the atelopodid genera of the Bufonidae and the outgroup *Bufo*. Numbers and letters agree with those used by McDiarmid (1971: 43-46). Character states that could not be checked or on which no data could be traced in the literature, are indicated with a dash, a question-mark indicates that the character was checked, but that no decision on its condition could be made. In a number of instances more character states than found by McDiarmid are present and new symbols had to be used. 13:4 = no anterior process, posterior arm over prootic; 23: A₄ = six - advanced; 33: A₂ = 2-2-3-2 - advanced (A of McDiarmid (1971) becomes A₁); 42: P₃ = several thousand eggs, black animal pole, light vegetal pole - primitive, A₂ = unpigmented, 53-145 - advanced (A of McDiarmid (1971) becomes A₁). Some additional characters were added: parotoids - two character states, P = present - primitive, A = absent - advanced; amplessus - two character states, P = inguinal - primitive, A = axillar - advanced; omosternum - two character states, P = present - primitive, A = absent - advanced; hypobranchial 2 - two character states, P = present - primitive, A = absent - advanced.

Nectophrynoidea (Lynch, 1971: 210, McDiarmid, 1971: 56; Trueb, 1971: 16; Lynch & Ruiz-Carranza, 1981: 2). As the omosternum is present in many primitive families and also in the Leptodactylidae (from which the Bufonidae are derived (Lynch, 1971: 209; Ruiz-Carranza & Hernández-Camacho, 1976: 94), the presence of an omosternum can be considered primitive, as it does not seem likely that it arose secondarily in the taxa mentioned before. For all other character states considered (no.'s 1, 4, 6, 23, 24, 25, 26, 33, 35, 37, 42 of McDiarmid (1971: 46) + parotoids and omosternum) *Andinophryne* shows the primitive condition (as defined by McDiarmid, 1971).

When comparing the different genera (tables 2, 3) it turns out that *Andinophryne* shares "all" its advanced character states (table 2) with both *Dendrophryniscus* and *Melanophryniscus*, with any of the other genera it only shares one. The condition of the musculus adductor mandibulae complex is a result of reduction and the process could take either of two ways only (see McDiarmid, 1971: 9). The most common situation is that found in *Andinophryne*; *Oreophrynella* is unique in this character by having a different muscle remaining (McDiarmid, 1971: 9). The other advanced character, the condition of the pectoral girdle, is a transitional stage between a completely arciferous and a completely firmisternal situation. However, as these advanced character states either occur throughout all atelopodid genera, or are distinctly related to adaptive changes in the mode of locomotion, they do not

	Advanced characterstates	of which partly	unique
<u>Atelopus</u>	17 (53%)	6 (35%)	1 (6%)
<u>Dendrophryniscus</u>	14 (44%)	3 (21%)	0 -
<u>Melanophryniscus</u>	11 (34%)	2 (18%)	1 (9%)
<u>Oreophrynella</u>	15 (48%)	0 -	5 (33%)
<u>Rhamphophryne</u>	8 (42%)	4 (44%)	0 -
<u>Andinophryne</u>	2 (11%)	0 -	0 -
<u>Osornophryne</u>	18 (64%)	1 (5%)	2 (11%)

Table 2. Numbers and percentages of advanced character states among the atelopodid Bufonidae. Percentages in the first column were calculated based on the total number of characters for which data were available (excluding character 3). Characters showing different states among species of the same genus are listed in the column "partly" and also are included in the first column. Percentages in the second and third column refer to the numbers in the first column. Also see legend of table 4.

provide much information on relationships (see below). When considering the primitive character states (tables 4, 5), the picture slightly changes, *Andinophryne* sharing eight of these with *Atelopus*, *Melanophryniscus* and *Rhamphophryne*, six with *Dendrophryniscus*, two with *Oreophrynella* and only one with *Osornophryne*. These latter two genera have been considered by different authors (McDiarmid, 1971; Ruiz-Carranza & Hernández-Camacho, 1976) as being the most specialised in their respective lines of des-

	At	Den	Mel	Or	Rham	And	Oso
<u>Atelopus</u>	--	12	7	7	6	1	13
<u>Dendrophryniscus</u>	12	--	9	7	5	2	11
<u>Melanophryniscus</u>	7	9	--	6	3	2	7
<u>Oreophrynella</u>	7	7	6	--	4	1	8
<u>Rhamphophryne</u>	6	5	3	4	--	1	6
<u>Andinophryne</u>	1	2	2	1	1	--	1
<u>Osornophryne</u>	13	11	7	8	6	1	--

Table 3. Matrix showing numbers of shared advanced character states within the genera of atelopodid Bufonidae.

	Primitive characterstates	of which	
		partly	unique
<u>Atelopus</u>	12 (38%)	7 (58%)	(1) (8%)
<u>Dendrophryniscus</u>	11 (34%)	2 (18%)	0 -
<u>Melanophryniscus</u>	14 (44%)	2 (14%)	0 -
<u>Oreophrynella</u>	7 (22%)	0 -	0 -
<u>Rhamphophryne</u>	9 (47%)	4 (44%)	0 -
<u>Andinophryne</u>	12 (66%)	0 -	0 -
<u>Osornophryne</u>	6 (21%)	1 (17%)	1 (17%)

Table 4. Numbers and percentages of primitive character states among the atelopodid Bufonidae. For further explanation see legend of table 2. The number between brackets indicates that for the character involved (no. 14) there are several character states, only one of which is unique within the group. Numbers in the second column may differ from those in the same column in table 2, because sometimes there are two primitive (no. 14), or two advanced (no. 4) character states within one genus.

cent; this serves to strengthen the impression that *Andinophryne* is a primitive member of the group of atelopodid genera.

As pointed out by Trueb (1971) our state of knowledge of several of the smaller genera of Bufonidae is still too incomplete to make well founded guesses about their relationships. The situation has hardly changed since, though now two additional genera have been described, but the material available does not yet permit an extensive osteological, myological study, not to mention a study of blood serum proteins, which could yield very important data. Comparison of genera is still hampered by insufficient data on internal morphology, life histories and behaviour (cf. table 1). The picture is further complicated by the occurrence of a number of derived (advanced) character states which apparently arose independently, and along different pathways, several times (Ruiz-Carranza & Hernández-Camacho, 1976: 106, 108). E.g., the fusion of presacral vertebrae in *Atelopus* is due to the fusion of the atlas and the first trunk vertebra into an atlas complex; in *Oreophrynella* it is due to the fusion of two trunk vertebrae with the sacral vertebra (synsacrum), and also to the fusion of the atlas and the first trunk vertebra; in *Osornophryne* the situation is different in the two known species, one (*O. bufoniformis* (Peracca)) having an atlas complex, the other (*O. percrassa* Ruiz-Carranza & Hernández-Camacho) having a free atlas; *O. bufoniformis* has a synsacrum composed of the sacrum and two presacral vertebrae, one of which is still discernable individually, in *O. percrassa* the synsacrum is one unity, containing the sacrum and two trunk vertebrae (Ruiz-Carranza & Hernández-Camacho, 1976: 107, 137, 138). Because of the variation observed within the genera *Atelopus* and *Osornophryne*, Ruiz-Carranza & Hernández-Camacho (1976: 107) come to the conclusion that there cannot be a correlation between

	At	Den	Me1	Or	Rham	And	Oso
<u>Atelopus</u>	--	6	8	3	5	8	3
<u>Dendrophryniscus</u>	6	--	10	5	6	6	4
<u>Melanophryniscus</u>	8	10	--	5	8	8	3
<u>Oreophrynella</u>	3	5	5	--	3	2	3
<u>Rhamphophryne</u>	5	6	8	3	--	8	1
<u>Andinophryne</u>	8	6	8	2	8	--	1
<u>Osornophryne</u>	3	4	3	3	1	1	--

Table 5. Matrix showing numbers of shared primitive character states within the atelopodid Bufonidae.

the decrease in number of presacral vertebrae and the type of locomotion, as several species exhibiting different presacral conditions move in the same way. The loss of phalanges in the hand in *Atelopus*, *Dendrophryniscus* and *Osornophryne*, which followed two different pathways, resulting in non-homologous character states, is another example. These character states therefore do not express relationships, but are cases of convergence. The simple fact that within several genera species showing advanced and primitive character states occur, is indicative of the problems encountered. Further research might show that part of this heterogeneity is due to insufficient knowledge of the genera concerned, and especially the genus *Atelopus* might prove to harbour some more species that do not really belong there. Indications that the genus is rather heterogeneous can be found in past changes of opinion on species formerly belonging to it, e.g. *bufoniformis*, *festae*, and *minutus*, now considered species of *Osornophryne*, *Rhamphophryne* and *Dendrophryniscus*, respectively, until recently were considered members of *Atelopus*. Another complicating factor is that both among primitive and advanced character states several conditions, that are mutually equivalent, but do not form clear-cut transitional series, prevail (e.g. advanced character states: different ways of reduction in the number of phalanges in the hand, reduction of the number of presacral vertebrae, condition of the musculus depressor mandibulae; primitive character states: eggs). We still need to gather much more data in order to make educated guesses as to the mutual relationships within this group. However, judging from the few advanced character states (none of them unique and one intermediate between a primitive and a more advanced character state) occurring in *Andinophryne*, it seems possible that this genus is the most primitive of the group and closely resembles the ancestral stock (most probably *Bufo haematiticus*-like) that gave rise to this group of genera characterized by the loss of the musculus adductor longus, a pectoral girdle that is at least anteriorly firmisternal, and an adductor mandibulae muscle that either shows a S or an E condition (for definition see McDiarmid, 1971: 9).

Remarks. — Andersson's (1945) remark in the description of *Atelopus palmatus* Andersson, that "Behind the orbit there is a swollen short vertical ridge forming a right angle with the protruding edge of the frontoparietal bone, which is broadly swollen, forming a kind of a low and narrow but rather distinct parotoid gland and continuing as a more os (!) less distinct ridge along the dorsolateral line", prompted me to investigate the type series of that species (NRM NNN 1937418.4908), because from that sentence I got the impression that this might be another species of *Andinophryne*. Upon investigation, the type specimens proved to be real *Atelopus*, without a trace of

a parotoid gland. The edge of the frontoparietal indeed forms a swollen (not necessarily glandular) supratympanic ridge, but that ridge does not continue beyond the head. Thus, in the neck there is no parotoid gland, nor is there a ridge along the dorsolateral line. The initial doubt I had about the proper allocation of this species consequently was due to an inadequate formulation by Andersson (1945: 13).

KEY OF THE SPECIES OF *ANDINOPHRYNE*

1. Dorsum with many, irregularly dispersed conical warts; three rows of conical warts on the flanks; heels not touching; parotoids 2.2-2.3 times as long as wide; bold pattern on back *atelopoides*
 – Dorsum without or with only a few small conical warts; only one or two rows of warts or glands on the flanks; heels touching or overlapping; parotoids 2.7-3.0 times as long as wide; no bold pattern on back 2
2. Parotoids very distinct, elongate; an oblique, interrupted row of conical glands and one of smaller conical warts on the flanks; back without tubercles; margin of upper eyelid distinctly protracted; heels overlapping; outer metatarsal tubercle round, low *otallai*
 – Parotoids present, elongate; only one oblique, continuous row of low tubercles on the flanks; back with few dispersed tubercles; margin of upper eyelid not protracted; heels touching; outer metatarsal tubercle oval, protruding *colomai*

***Andinophryne atelopoides* (Lynch & Ruiz-Carranza)**
(fig. 1)

Bufo atelopoides Lynch & Ruiz-Carranza, 1981: 4; 1983: 110; Hoogmoed, 1985: 36.

Diagnosis. — A relatively large (up to 43 mm) atelopodid toad with a wide, flat head, a projecting snout, a protruding rim along the margin of the upper eyelid, well developed oval parotoid glands, three rows of conical tubercles on the flanks, dorsum with conical tubercles. Limbs long and slender. Brown with creamish blotches on head and along upper edge of flanks.

Description. — See Lynch & Ruiz-Carranza (1981).

Ecology. — The habitat at Quebrado Sopladero (type-locality) was described as “very humid and the forests are primary” by Lynch & Ruiz-Carranza (1981: 7), and as “upper cloud forest” by Lynch & Ruiz-Carranza (1983: 110).

Remarks. — Lynch & Ruiz-Carranza (1981) hesitantly considered this species a member of the *Bufo typhonius* group, but they noted a number of important differences (webbed fingers, short first finger, presence of three rows of conical tubercles on the flanks, oval parotoids, presence of an omosternum and absence of bony supraorbital and parietal cranial crests), which led them to be very careful in venturing any comments on the relationships of this species.

Judging from the description and the illustrations provided by Lynch & Ruiz-Carranza (1981), I come to the conclusion that this species, without any doubt, belongs to the genus *Andinophryne*, which is characterized by the condition of the pectoral girdle, the presence of a well developed ear and externally visible tympanum, elongate parotoid glands, extensively webbed hands and feet.

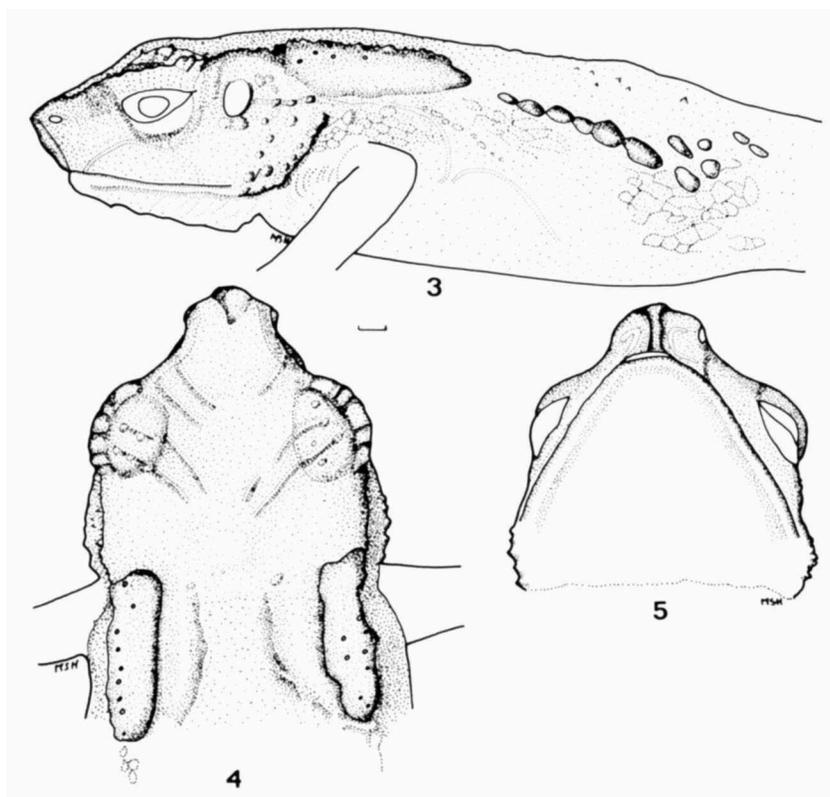
Andinophryne atelopoides can be distinguished easily from the other two species in the genus by its bold pattern, its shorter legs, the presence of three rows of conical tubercles on the flanks and of irregularly dispersed conical tubercles on the back.

***Andinophryne colomai* spec. nov.**
(figs. 1-7, 10-12)

Holotype. — ♀, RMNH 21905, "Cabeceras del Rio Baboso, cerca a Lita", Carchi Province, Ecuador, 10-ix-1984, leg. L. Coloma & A. Yépez.

Diagnosis. — A medium-sized atelopodid toad with a wide, flat head, a projecting snout, margin of upper eyelid with a sharp rim and elongate, indistinct parotoids. Flanks with an oblique, continuous row of small, flat warts, broken up in the inguinal region, no isolated tubercles further down the flanks. Limbs long and slender, with long fingers and toes, which are extensively webbed. Dorsum with few scattered, small warts. Ear present, tympanum externally hardly visible. Entire temporal region with small conical warts, no isolated ones near the corner of the mouth. Subarticular tubercles present.

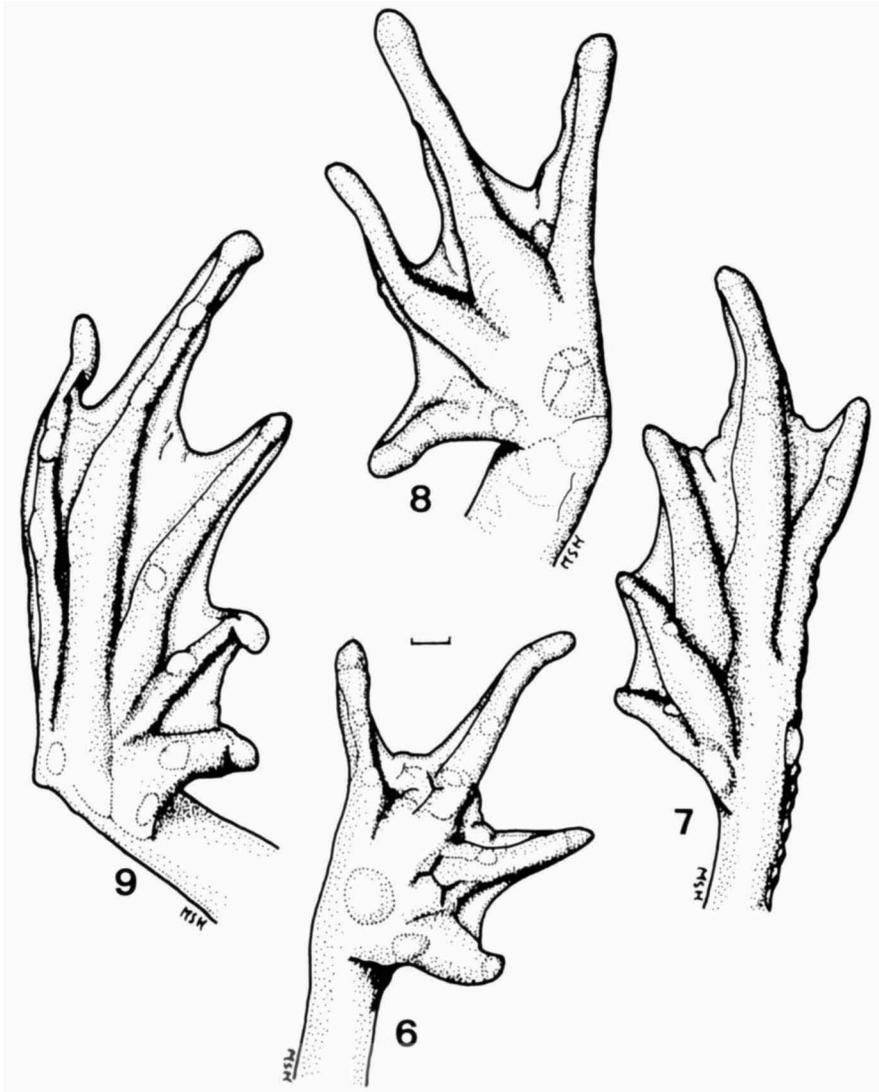
Description of holotype. — Female, snout-vent length 31.0 mm. Head slightly longer than wide, as wide as adjacent part of body. About half as deep as wide. Width of head at corners of jaws slightly wider than width at tympanum level, or at the supratympanic level (10.3 mm versus 9.8 mm, respectively 9.4 mm). Eyelids projecting from the head, width of head measured



Figs. 3-5. *Andinophryne colomai* spec. nov., holotype, RMNH 21905. 3, lateral view of head and flank; 4, dorsal view of head; 5, ventral view of head. The line equals 1 mm.

across the eyelids 10.0 mm. Snout obtusely pointed in dorsal and obliquely truncate in lateral profile, distinctly projecting beyond the upper jaw. Tip of snout with a fleshy vertical ridge. Distance between nostril and tip of snout 50% of the distance between nostril and eye. Nostrils situated just above the commissure of the mouth, below the canthus rostralis in a slightly bulbous area. Nostrils round, directed laterally. Distance between nostrils equal to that between nostril and eye, 69% of the interorbital distance. Internarial area slightly concave. Top of head flat with a slight central convexity in the occipital region. Interorbital area 1.5 times as wide as an upper eyelid. Upper eyelid with several pointed tubercles in the central area, arranged in two more or less parallel, radial rows. Outer rim of upper eyelid shallowly indented, not projecting beyond the eye, but sloping vertically to it. Canthus rostralis distinct, angular, not projecting over the loreal region, which is concave and

slopes almost vertically to the upper lips. Lips not flaring. Eyes with horizontally oval pupil. Lower eyelid translucent. Temporal region sloping steeply. Tympanum very small, indistinct, vertically oval; surrounded by a complete, cartilaginous annulus; upper margin obscured; its vertical diameter 28-29% of the horizontal diameter of the eyesocket, 31-34% of the eyeopening. Tem-



Figs. 6-9. Palmar (6, 8) and plantar (7, 9) surfaces of hands and feet. 6 and 7, *Andinophryne colomai* spec. nov. (RMNH 21905); 8 and 9, *A. olallai* spec. nov. (BM 1970.98). The line equals 1 mm.

poral region and area near the corner of the mouth covered with medium-sized rounded warts with a sharp conical tip. Musculus adductor mandibulae posterior subexternus hardly visible externally. Supratympanic fleshy ridge distinct, angular, not projecting over the temporal area, running in a nearly straight line, slightly sloping upward posteriorly in lateral view, converging posteriorly in dorsal view, from posterior corner of eye to the parotoid; margin with small, sharp-tipped warts. Parotoids only slightly swollen, distinct, elongate, 2.8-3.0 times as long as wide, of the same length throughout, extending as much on the dorsal surface as on the side of the neck, median margin smooth.

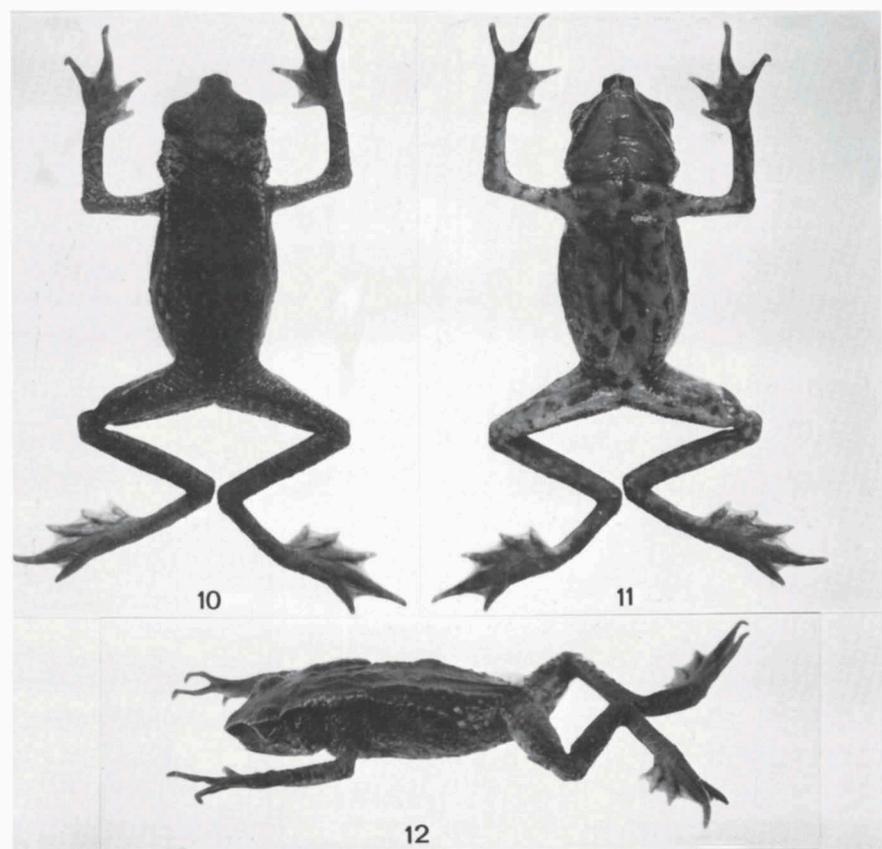
Side of the neck coarsely areolate, without larger warts. Flanks coarsely areolate, area in between shagreened, no dispersed larger tubercles. A rather indistinct, continuous, oblique row of low, conical tubercles from parotoids to groin, where it dissolves into a group of isolated low tubercles. Skin of back and top of head finely shagreened, with dispersed, low tubercles on the back, especially numerous in the area above the groins and bordering on the oblique lateral tubercles. Skin of limbs finely shagreened with numerous low, conical warts.

Hand with a distinct, large, undivided, low, round outer and a smaller, low, oval inner metacarpal tubercle. Subarticular tubercles present, indistinct, low, rounded, single (only second, third and fourth fingers). No supernumerary tubercles. Fingers webbed, web rather thick, edges smooth, formula: $I(1\frac{1}{2})-(1\frac{2}{3})II(1)-(2)III(2)-(2)IV$. Fingers depressed, pointed. Dorsal side of articulation between ultimate and penultimate phalanges with a transverse fold of skin. Length of fingers: $I < II < IV < III$. Phalangeal formula: 2-2-3-3.

Tarsus smooth, without a tarsal ridge or tubercle. Heel with some low tubercles. An elevated medium-sized oval outer and a larger, low, oval inner metatarsal tubercle. Toes with indistinct subarticular pads rather than tubercles. No supernumerary tubercles. Toes depressed, tips of toes pointed. Toes extensively webbed, web rather thick, edges smooth, formula: $I(\frac{1}{2})-(1)II(1\frac{1}{2})-(2)III(1\frac{1}{2})-(2)IV(2)-(1)V$, web extending as lateral fringe along the toes to the tips. Dorsal side of articulation between ultimate and penultimate phalanges with a transverse fold of skin. Length of toes: $I < II < III < V < IV$. Phalangeal formula: 2-2-3-4-3.

When the hindlimbs are flexed at right angles to the sagittal plain, the heels just touch; when carried forward along the body, the heel reaches the anterior border of the eye. Tibia 45-46% of the snout-vent length.

Eight presacral vertebrae, of which seven bear moderately long transverse processes. There is a distinct difference in the shape of the processes: those of vertebra 2 are distinctly expanded, those of vertebrae 3 and 4 are stout, rod-



Figs. 10-12. *Andinophryne colomai* spec. nov., holotype, RMNH 21905, dorsal, ventral and lateral habitus (snout-vent length 31.0 mm).

shaped, of equal width throughout, those of vertebrae 5-8 are more slender and pointed; those of vertebrae 3-6 are slightly curved (convexity directed anteriorly), those of vertebrae 7 and 8 are straight. The processes of vertebrae 2 and 8 are directed anteriorly, those of 3-6 posteriorly and those of 7 are transverse. Transverse width of the processes: $2 < 3 < 8 < 7 < 6 < 4 < 5$. Sacral diapophyses dilated.

In preservative the back is greyish brown with a white line extending from the tip of the snout via the canthus rostralis, the rim of the upper eyelid, the supratympanic edge, the parotoid and the oblique row of tubercles on the flanks, to the groin. Lower arm with a trapezoid, darker spot, edged with white. Tips of fingers and toes darker than remainder of digit, transverse fold of skin over the articulation between ultimate and penultimate phalange with

a transverse black line. Flanks creamish with a brown reticulum. Side of head just below canthus rostralis and on tympanic area blackish. Upper lips light brown, mottled, with a narrow, white, semicircular line arising at the margin of the mouth, just touching the eye and returning to the mouth. Throat creamish, chest and belly creamish with large black spots. Ventral side of thighs with a wide, creamish central stripe along its length, with darker areas anteriorly and posteriorly.

Natural history. — The holotype has enlarged, elongate ovaries with numerous small, white ovules. The specimen was collected on a branch, 50 cm above the ground in the valley of a small creek, at 21.00 h. Its stomach contained many rather large ants. A species of *Atelopus* occurred sympatrically.

Distribution. — Only known from the type-locality, the headwaters of the Rio Baboso near Lita, in Carchi Province, NW Ecuador, on the western slopes of the Andes. Although the altitude at which the specimen was caught was not stated, we may assume that it was about 500-600 m, Lita being situated in the valley of the Rio Mira, just downstream from where it crosses the 600 m contourline (fig. 2).

Remarks. — This species differs from *A. atelopoides* and *A. olallai* spec. nov. in its smaller size, its less prominent parotoids, the presence of a single, continuous row of warts on the flanks, its less well developed cranial ornamentation and eyelids that hardly project.

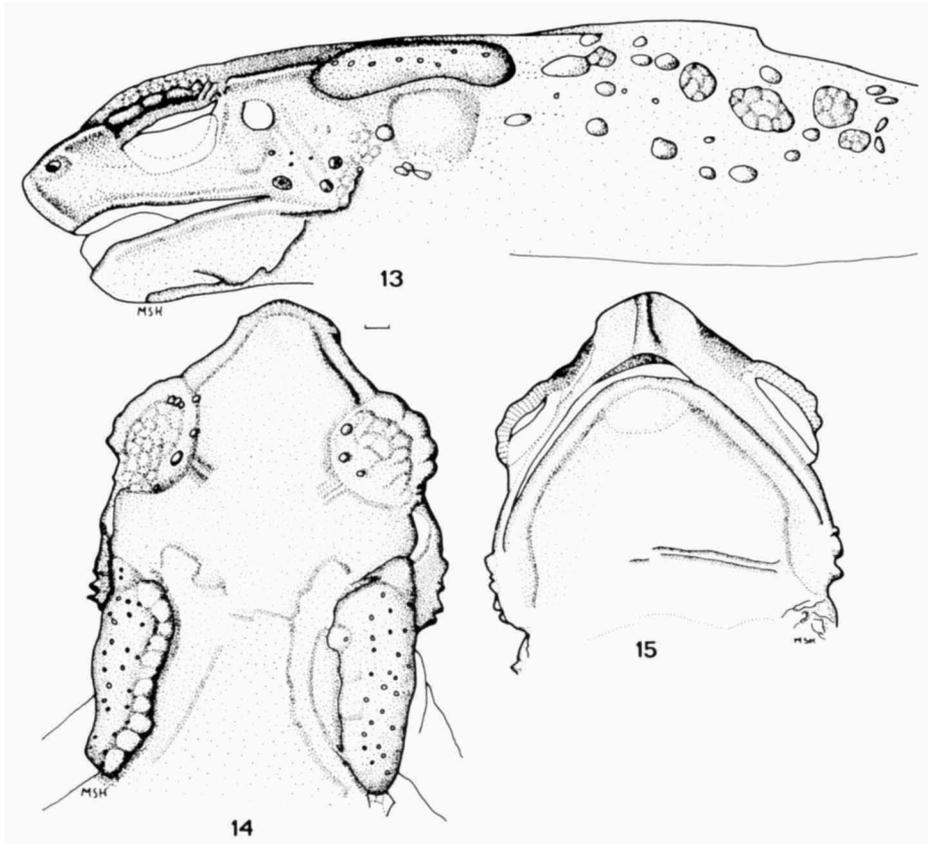
Etymology. — Named for the collector, Luis Coloma, who accompanied me during fieldwork in western and central Ecuador in April 1983. He proved to be an enthusiastic and reliable field companion, whose enthusiasm for herpetology resulted in continued collections, of which the holotype of the present species formed a part.

***Andinophryne olallai* spec. nov.**

(figs. 1-2, 8, 9, 13-18)

Holotype. — ♀, BM 1970.98, Tandayapa, Pichincha Province, Ecuador, 0°01'S 78°46'W, leg. J. Olalla.

Diagnosis. — A medium-sized atelopodid toad with a wide, flat head, a projecting snout, a protruding rim at the margin of the upper eyelid, well developed, elongate parotoids. An oblique row of large, distinctly separated glands on the flanks and another row of warts below it. Limbs long and slender, with long fingers and toes, which are extensively webbed. Dorsum without warts. Ear present, tympanum well visible. A few isolated, conical



Figs. 13-15. *Andinophryne olallai* spec. nov., holotype, BM 1970.98. 13, lateral view of head and flanks; 14, dorsal view of head; 15, ventral view of head. The line equals 1 mm.

tubercles near the corner of the mouth. Hand without subarticular tubercles, feet with low subarticular pads.

Description of holotype. — Female, snout-vent length 39.6 mm. Head about as long as wide to slightly longer, as wide as adjacent part of body. About half as deep as wide. Width of head at corners of jaws distinctly wider than width at tympanum level, or at the supratympanic ridge level (13.0 mm versus 11.4 mm, respectively 11.7 mm). Eyelids distinctly projecting from the head, width of head measured across the eyelids 12.8 mm. Snout obtusely pointed in dorsal and obliquely truncate in lateral profile, distinctly projecting beyond the upper jaw. Tip of snout with a fleshy vertical ridge. Distance between nostril and tip of snout 60% of the distance between nostril and eye.

Nostrils situated just above the commissure of the mouth, below the canthus rostralis, in a slightly bulbous area. Nostrils obliquely oval, directed laterally. Distance between nostrils about equal to the distance between nostril and eye, 83% of the interorbital distance. Internarial area slightly concave. Top of head flat, with a slight convex area in the occipital region. Interorbital area slightly wider than an upper eyelid. Upper eyelid with a circle of three or four large, rounded tubercles along the medial side, a central area with warts of different sizes and a fleshy outer ridge with scalloped rim, well projecting beyond the eye. Canthus rostralis distinct, fleshy, projecting over the loreal region, which is concave and slopes almost vertically to the upper lips. Lips not flaring. Eyes with horizontally oval pupil. Lower eyelid translucent. Temporal region sloping steeply. Tympanum small but distinct, \pm round; located rather high; inclined from dorsomedially to ventrolaterally; surrounded by a complete, cartilaginous annulus; upper margin obscured; separated from the eye by a distance of 66-86% of its diameter; its diameter 28-30% of the horizontal diameter of the eyesocket, 34-35% of the eyeopening. Three or four large, conical warts near the corner of the mouth. Between tympanum and eye, extending to the upper lip, the musculus adductor mandibulae posterior subexternus is visible as a light, bulbous area through the skin. A fleshy supratympanic ridge, projecting over the temporal area, running in a straight line, horizontal in lateral view, curved and approximately parallel in dorsal view, from posterior corner of eye to the parotoid; margin smooth. Parotoids bulbous, very distinct, elongate, 2.7-3.0 times as long as wide; slightly wider anteriorly than posteriorly; most extensively developed on dorsal surface, but extending onto side of neck as well; medial margin scalloped.

Side of neck coarsely areolate, with a single, large, conical wart above the insertion of the forelimb, anteriorly of the scapula, which is visible externally because of a distinctly swollen muscular area. Flanks coarsely areolate, area in between shagreened with dispersed larger tubercles. A very distinct, interrupted, oblique row of large glands from parotoids to groin, increasing in size posteriorly; each gland being made up of several smaller entities. Below it another, less distinct, row of isolated warts. Skin of back and top of head finely shagreened, without tubercles. Skin of limbs like that of back, but forearm, thigh and shank with low, conical warts.

Hand with an indistinct, large, undivided, low, round outer and a smaller, low, oval inner metacarpal tubercle. No subarticular or supernumerary tubercles. Fingers webbed, web rather thick, edges smooth, formula: I(1)-(2)II(2)-(2 $\frac{3}{4}$)III(2 $\frac{3}{4}$)-(2 $\frac{1}{4}$)IV. Fingers depressed, bluntly pointed. Length of fingers: I < II < IV < III. Phalangeal formula: 2-2-3-3. The X-ray photographs do not show distinct centralia, but a rather undifferentiated mass of dense tissue.



Figs. 16-18. *Andinophryne olallai* spec. nov., holotype, BM 1970.98, dorsal, ventral and lateral habitus (snout-vent length 39.6 mm).

Tarsus smooth, without a tarsal ridge or tubercle. Heel with some low tubercles. A rather elevated, small, round, outer and a larger, flat, oval inner metatarsal tubercle. Toes with subarticular pads rather than tubercles. No supernumerary tubercles. Toes depressed, tips of toes bluntly pointed. Toes extensively webbed, web rather thick, edges smooth, formula: I(1)-(1)II(1)-(1 $\frac{2}{3}$)III(1 $\frac{1}{3}$)-(3)IV(2 $\frac{3}{4}$)-(1 $\frac{1}{2}$)V, web extending as lateral fringes along the toes to the tips. Length of toes: I < II < III < V < IV. Phalangeal formula: 2-2-3-4-3, terminal phalanges rounded.

When the hindlimbs are flexed at right angles to the sagittal plain, the heels distinctly overlap; when carried forward along the body, the heel reaches the posterior corner of the eye. Tibia 44% of the snout-vent length.

Eight presacral vertebrae, of which seven bear moderately long transverse processes. There is a distinct difference in the shape of the processes: those of vertebra 2 are distinctly expanded, those of vertebrae 3 and 4 are stout, rod-shaped, of equal width throughout, those of vertebrae 5-8 are more slender and pointed; those of vertebrae 3 and 4 are slightly curved (convexity directed anteriorly), those of vertebrae 5-8 are straight. The processes of vertebrae 2, 7 and 8 are directed anteriorly, those of 3, 4 and 5 posteriorly and those of 6 are transverse. Transverse width of the processes: $2 < 3 < 8 < 7 < 6 < 4 < 5$. Sacral diapophyses dilated.

In preservative the back and flanks are uniformly brown. Large glands on flanks whitish. Side of head brownish without pattern. Throat pale brown, belly and underside of thighs creamish with large brown spots. Musculus adductor mandibulae posterior subexternus visible as a pale brow area.

Natural history. — The holotype has enlarged, elongate ovaries with numerous small, white ovules. The stomach contained many large ants and the remains of two very hard-bodied beetles (rather large Curculionidae).

Distribution. — Only known from the type-locality, Tandayapa, Pichincha Province, NW Ecuador, northwest of Quito on the western versant of the Andes. The altitude from which the animal was taken probably was between 1400 and 1600 m (altitude of Tandayapa according to maps 1500 m). Tandayapa is located about 100 km SSW of Lita, whence the holotype of *A. colomai* spec. nov. hails (fig. 2).

Remarks. — This species differs from *A. colomai* spec. nov. by its greater size, its better developed parotoids, the presence of a row of large, isolated glands on the flanks, its better developed cranial ornamentation of fleshy canthal and supratympanic ridges and its projecting eyelid. From *A. atelopoides* it differs in having longer legs, a smooth back and in lacking an ornamental pattern.

Etymology. — Named for J. Olalla, one of the famous Olalla family, who, since the forties, provided several museums in Ecuador and abroad with numerous rare reptiles and amphibians. They were among the first to systematically explore Ecuador for animals.

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those of RMNH 21905 were made by Mr. S. Zijlstra, Dept. of Morphology, Zoological Laboratory, University of Leiden. The habitus photographs were made by Mr. E.L.M. van Esch (RMNH).

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