COPEIA

# The Systematic Status and Life History of Hyla vertucigera Werner

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Hyla verrucigera Werner (Anura: Hylidae) is placed in the genus Osteocephalus. Hyla riopastazae Andersson and Hyla orcesi Funkhouser are junior synonyms of Osteocephalus verrucigerus, a species known from the Amazonian slopes of the Andes from southern Colombia, Ecuador, and central Perú. Males have tuberculate skin dorsally, whereas females are smooth. The skull of O. verrucigerus is completely roofed, smooth, and lacks a dermal sphenethmoid. The heavily pigmented tadpoles have two upper and five lower tooth rows and develop in quiet pools in streams.

### INTRODUCTION

A MONG the extensive collections of amphibians made in the summer of 1968 in eastern Ecuador by a field party from the Museum of Natural History at the University of Kansas (KU) is a series of adult frogs, juveniles, tadpoles, and eggs referable to the nominal species *Hyla verrucigera* Werner 1901. The study of these specimens and the few others extant revealed that the species has been given three names and that it is not a member of the genus *Hyla*. We are presenting herein the results of our systematic studies and a description of the breeding habits and life history of the species.

See Acknowledgments for abbreviations of names of organizations permitting examination of specimens.

### Systematics

## Osteocephalus verrucigerus (Werner)

#### New Combination

- Hyla verrucigera Werner, 1901:601 [holotype ZMB 16589 from "Ecuador"; Richard Haensch collector]. Nieden, 1923:266.
- Hyla riopastazae Andersson, 1945:72 [holotype NHRM 1960 from Baños, Río Pastaza, 1840 m. Provincia Tungurahua, Ecuador; William Clarke-MacIntyre collector].
- Hyla orcesi Funkhouser, 1956:78 [holotype CAS-SU 13150 from Río Pacayacu, a tributary of the Río Cotapino (Suno drainage), Provincia Napo, Ecuador; collector unknown].

Osteocephalus orcesi-Cochran and Goin, 1970:317.

Diagnosis.--A species of Osteocephalus characterized by having a uniformly dark brown dorsum (dull olive-green or olivebrown in life), mottled venter (in living and freshly preserved specimens), a distinct pale labial stripe and suborbital mark. The dorsum is tuberculate in males and smooth in females. Osteocephalus taurinus is like verrucigerus in having tuberculate dorsal skin in males, whereas in males of other species in the genus (buckleyi and leprieuri) the skin on the dorsum is not so tuberculate. In most males of *taurinus* the dorsum is tuberculate, but the tubercles are more scattered and less spinous than in verricigerus; in leprieuri the dorsum is covered with many minute tubercles. Both of these species differ from vertucigerus in coloration: taurinus usually lacks a pale labial stripe and ventral mottling and has dark blotches on the dorsal surface of the body, dark bars on the lips, and usually dark flecks on the chin; leprieuri is uniform creamy tan below and has an olive-tan dorsum with narrow dark olive-brown transverse bars on the body.

Description.—The following description is based on 12 fresh adults (KU 123177–84, 123187–88–33 and 123176, 123185–99). Males attain a snout-vent length of 54.3 mm and females, 65.8 mm. Snout-vent lengths in 10 breeding males 52.6–54.3 (53.1) mm; tibia length 26.8–30.0 mm, 51.1–55.2 (52.2) %



Fig. 1. Palmar view of right hand of Osteocephalus verrucigerus (KU 123177 d). × 5.

of snout-vent length; foot length (measured from proximal edge of inner metatarsal tubercle to tip of longest toe) 21.5-23.8 mm, 40.9-44.2 (42.8) % of snout-vent length; head length 16.8-18.8 mm, 32.8-34.6 (33.4) % of snout-vent length; head width 17.1-18.5 mm, 32.8-34.4 (33.7) % of snout-vent length; interorbital distance 4.6-5.4 mm, 26.6-29.6(28.0) % of head width; diameter of eye 4.6-5.3 mm; diameter of tympanum 3.8-3.7mm, 62.3-80.4 (72.6) % of diameter of eye.

Head slightly broader than body; top of head flat; snout in dorsal profile rounded, in lateral profile barely rounded, nearly truncate; canthus rostralis rounded, slightly elevated, curved anteriorly; nostrils protuberant laterally; internarial area depressed; loreal region moderately concave; lips thick, rounded, and barely flared; supratympanic fold moderately heavy, obscuring upper edge of tympanum; tympanum distinct, separated from eye by distance slightly less than diameter of tympanum.

Patagium absent; upper arm slender; forearm moderately robust; ulnar fold and tubercles lacking; weak transverse dermal fold on wrist; fingers moderately long with discs equal to about two-thirds diameter of tympanum; subarticular tubercles large, subconical; distal tubercle on fourth finger bifid in some specimens; supernumerary tubercles small, in single row on proximal segments of digits; palmar tubercle low, indistinct, bifid; pollical tubercle elongate; prepollex enlarged, in males bearing horny nuptial excrescence; fingers webbed basally (Fig. 1). Hind limbs moderately long and slender; heels of adpressed limbs overlap by about one-third length of shank; thin transverse dermal fold on heel; inner tarsal fold distinct, extending entire length of tarsus; inner metatarsal tubercle small, elliptical, not visible from above; outer metatarsal tubercle absent; toes moderately long, slender, bearing discs slightly smaller than those of fingers; subarticular tubercles large, subconical; supernumerary tubercles indistinct or absent; toes about three-fourths webbed (Fig. 2).

In females skin on dorsum smooth; in males skin on dorsal surfaces of head, body, shanks and tarsi tuberculate; in both sexes skin on throat, belly, and proximal posteroventral surfaces of thighs granular; other ventral surfaces and flanks smooth. Thoracic fold absent. Anal opening directed posteroventrally near upper level of thighs; anal flap short. Dentigerous processes of prevomers angular (/\_\_\_\_), between small elliptical choanae; total number of prevomerine teeth 16-22 (18.8) in males, 22-23 (22.5) in females. Tongue broadly cordiform, shallowly notched anteriorly and posteriorly, not free behind. Vocal slits short, along inner posterior margins of jaws; vocal sacs paired, beginning as tube posterolaterally on throat and expanding laterally behind angles of jaws.

Coloration (in life): In males, dorsum dull olive-green; groin, anterior and posterior surfaces of thighs, inner surfaces of shanks and tarsi, and upper arms dark brown; ventral surfaces of limbs pinkish tan; other ventral surfaces pale creamy tan with reddish brown flecks; suborbital spot pale greenish tan; iris deep reddish brown; palpebrum clear (Fig. 3). In females, dorsum dull olive-brown; anterior part of head tan; suborbital spot yellowish tan; groin, anterior



Fig. 2. Plantar view of right foot of Osteocephalus verrucigerus (KU 123177 d). × 5.

and posterior surfaces of thighs, inner surfaces of shanks and tarsi, and upper arms dark reddish brown; ventral surfaces of limbs brown; throat and chest creamy white, belly reddish tan, both with dark brown flecks or mottling; iris deep reddish brown; palpebrum clear (Fig. 3).

Coloration (in preservative): Dorsal surfaces nearly uniform dark brown in both sexes; anterior part of head pale brown in females; faint transverse bands evident on forearms and shanks of some specimens. Flanks in one female mottled dark brown and creamy white; in other specimens flanks, anterior and posterior surfaces of thighs, inner surfaces of shanks and tarsi, and upper arms dull reddish brown. Ventral surfaces of limbs, dorsal surfaces of feet, and webbing pale brown. Throat and belly tan to white, with or without noticeable large dark brown flecks. Suborbital bar creamy tan. Cranial osteology.--(Based on KU 123189, 3, Fig. 4): Skull slightly broader than long; snout in dorsal view rounded; dorsal surfaces of skull smooth, unornamented; overlying skin freely movable on surface of head. Prenasal, internasal, and dermal sphenethmoid absent; labial flanges and occipital crests absent. Anterior supraorbital margins of frontoparietals barely upturned in the form of an indistinct crest; frontoparietals not extending over crista parotica posterolaterally; anterior arm of squamosal extending slightly more than one-half distance to maxillary.

Premaxillaries narrowly separated medially by connective tissue; laterally, premaxillary separated from pars palatina and pars dentalis of maxillary by area of dense connective tissue; small palatine process present posteromedially on premaxillary; alary processes of premaxillaries straight, about twice as long as depth of pars dentalis of premaxillary, widely separated medially, inclined posteriorly at about 80° angle. Prevomers not converging medially; anterior ends of prevomers acuminate, lying posterior to premaxillaries; dentigerous prosesses of pre-vomers slightly angled; lateral wings of prevomers well developed, forming anterior, medial, and posteromedial margins of ovoid choanae. Palatines narrow, thin, forming posterior margins of choanae; distal ends slightly expanded and lying adjacent to maxillaries; proximal ends lying on anterior, ventrolateral corners of sphenethmoid; palatines bearing small posteroventral ridges with irregular surfaces.

Nasals moderately large; anterior tips obviously separated from dorsal tips of alary processes of premaxillaries; nasals separated from one another medially, overlapping and in broad sutural contact with sphenethmoid posteriorly; canthal ridge rounded and indistinct; maxillary process of nasal slim, articulating with posterior process of pars facialis of maxillary. Maxillary bearing welldeveloped pars facialis anterior to orbit; all margins of pars facialis free except for posterior process, articulating with maxillary process of nasal, forming bony anterior margin of orbit; medially, pars palatina small, extending length of maxillary ventromedial to pars dentalis; maxillary firmly articulating with short, stout quadratojugal at level of prootic foramen.

Sphenethmoid well ossified; anterior ter-



Fig. 3. Osteocephalus verrucigerus. Dorsum (KU 123177 d), Venter (KU 123176 ?). ×2.

minus lying at level of anterior tips of nasals; margins of orbitonasal foramina bony; posterior terminus of bony sphenethmoid lying at level of optic foramina; sphenethmoid overlain by nasals anterolaterally and frontoparietals posteriorly; dorsally, central part of sphenethmoid exposed between nasals and frontoparietals; posterodorsally, roof of sphenethmoid split to form frontoparietal fontanelle ventral to frontoparietals; margins of fontanelle apparently bony. Frontoparietals thin (medial and anterior margins nearly indistinguishable), convergent throughout their lengths; anteriorly, in area of overlap of frontoparietal on sphenethmoid, both bones forming narrow slightly upturned supraorbital flange, terminating at posterior margin of orbit; frontoparietal having smooth distal margins, not extending posterolaterally over crista parotica, not elevated posteriorly into occipital crest.

Parasphenoid bearing inconspicuous odontoid structure at level of optic foramen; anterior end of parasphenoid lying at level just posterior to orbitonasal foramen. Squamosal delicate; anterior arm slender, extending slightly more than half distance from dorsal union of three squamosal rami to maxillary; posterior arm about half length of anterior arm, articulating medially with, and overlapping dorsal edge of, crista parotica; ventral arm well developed, distally articulating with quadratojugal laterally and posterior ramus of pterygoid medially. Pterygoid robust; anterior ramus moderately long, anterior terminus lying at about midlevel of orbit; medial ramus long, well developed, articulating firmly with anteroventral corner of otic capsule ventrally; posterior ramus articulating with ventral half of ventral arm of squamosal.

Prootics and exoccipitals fused; entire posterior region of skull well ossified; oculomotor, prootic, and jugular foramina having bony margins; probably two acoustic foramina present, both having bony margins. Crista parotica well developed, in bony sutural contact with squamosal; pars externa plectri and pars ascendens plectri cartilaginous; pars media plectri (columella) bony.

The skull of O. verrucigerus is very similar to that of O. taurinus (see Trueb, 1970a, for detailed description and illustrations). Most of the differences between the species can be attributed to less extensive ossification in O. verrucigerus. The skull of O. taurinus is rugose, whereas that of O. verrucigerus is smooth. The former species has a dermal sphenethmoid, which is absent in the latter. The alary processes of the premaxillaries, the nasals, the frontoparietals, and the prevomers are better developed in O. taurinus than in O. verrucigerus. Two minor exceptions to the general trend toward reduced ossification



Fig. 4. Dorsal and ventral views of the skull of Osteocephalus verrucigerus (KU 123189 °). × 3.

in O. verrucigerus are evident. The pars facialis of the maxillary is much better developed, and the anterior arm of the squamosal is somewhat longer in O. verrucigerus than in O. taurinus.

#### Allocation of Specific Names

Justification for our assignment of the specific name verrucigerus to the population in the Cordillera del Dué and for the synonymy of orcesi and riopastazae with verrucigerus is given below.

Werner (1901:601) based his description of  $Hyla \ vertucigera$  on an adult, stated to be a female having a snout-vent length of 51 mm; he stated that in addition to the adult he had one "halbwuchsiges." Insofar as is known, the material of the several species that Werner discussed in the paper in which he described H. vertucigera is in the Zoologisches Museum in Berlin. However, careful examination of the herpetological catalogues

in that museum and a diligent search of the collection by us in July 1969, failed to reveal the adult specimen. An immature male (ZMB 16589) is labelled as the type of H. *verrucigera* and is so indicated in the catalogue. Entries on the same page of the catalogue include types of other species named by Werner in the same paper. Consequently, we conclude that the only extant type of H. *verrucigera* is ZMB 16589.

The type has a snout-vent length of 32.0 mm. It is slightly soft and faded; the dorsum is pale brown with faint darker brown transverse bars on the limbs and three irregular dark brown spots on the dorsum. Structurally, the type is nearly identical with a juvenile (KU 123186) from the Cordillera del Dué having a snout-vent length of 29.8 mm. The dorsal tubercles and supernumerary tubercles on the hands and feet are absent or barely evident in the type, whereas they are distinct in KU 123186; these differences almost certainly are due to the soft condition of the type. The similarities of the juvenile from the Cordillera del Dué and the extant type of H. verrucigera and the agreement of the recently collected adults with Werner's description strongly support the usage of H. verrucigera for the population in the Cordillera del Dué.

The holotype of *Hyla riopastazae* (NHRM 1960) is a gravid female having a snout-vent length of 64.7 mm. The skin on the dorsum is smooth. The dorsum is pale brown (faded ?); indistinct darker brown transverse bands are barely evident on the limbs. The throat, chest, and belly are cream with brown spots and mottling. The holotype agrees in details of structure and coloration with KU 123176 and 123185 and UMMZ 92095.

The holotype of Hyla orcesi (CAS-SU 13150) is an adult male having a snout-vent length of 52.6 mm. The dorsum is heavily tuberculate. The dorsum is dark brown; faint transverse bands are barely visible on the forearms and tarsi. A faint creamy tan suborbital mark is present. The venter is creamy brown. The holotype agrees in all aspects of structure and coloration with the males from the Cordillera del Dué, except that most of the latter have noticeable dark brown flecks and mottling ventrally, whereas this coloration is absent in the holotype of orcesi. The mottling is absent on all males except those from the Cordillera del Dué; males from other localities have been preserved for 30 years or more. The intensity of the ventral mottling in the males from the Cordillera del Dué has diminished after one year in preservative. Thus, it seems reasonable to assume that the males from other localities, including the holotype of H. *orcesi*, had mottled venters in life. Funkhouser (1956:78) cited a paratype in the collection of Gustavo Orcés-V, at that time housed in Quito, Ecuador, and subsequently acquired by the U. S. National Museum. Together with James A. Peters we searched unsuccesfully for the paratype among the specimens in the Orcés collection.

Funkhouser (1956:78) noted the similarity between *H. orcesi* and *Hyla britti* and erroneously stated that *orcesi* had "an internal vocal sac instead of two external sacs behind the angles of the jaw." The structure of the vocal sacs is essentially the same in both species, as based on observations of calling males and preserved specimens. The sacs are definitely paired; each begins as a short subgular tube extending from the posteromedian part of the throat to a point behind the angle of the jaw; from there when the sac is inflated it expands into a lateral balloon-like structure.

# **GENERIC STATUS**

Although we are currently preparing a revision of the genus Osteocephalus, we consider it necessary here to justify our placement of *H. verrucigera* in Osteocephalus, a genus that has been variously recognized by workers on South American frogs.

Goin (1961:13) diagnosed Osteocephalus as follows: "Males with paired vocal pouches, one at each angle of the jaw; derm of head not co-ossified with skull but roof of skull exostosed." Goin included taurinus, leprieuri, britti, buckleyi, and pearsoni in the genus and suggested other nominal species that possibly were synonyms of those included.

Cochran and Goin (1970) recognized taurinus, leprieuri, and orcesi as Colombian members of the genus but placed buckleyi and pearsoni in Hyla, although Boulenger (1882:363) in the type description of buckleyi stated: "Male with two vocal vesicles, each being situated behind the angle of the mouth; . . ."

Trueb (1970a) based her definition of Osteocephalus on cranial characters, as follows: "Skull broader than long; snout in

dorsal view broad, truncate; canthal ridges distinct, not anteriorly concave; surface configuration of dermal roofing bones consisting of poorly developed ridges; prenasal absent; alary processes of premaxillaries exposed, not co-ossified, not anteriorly inclined; internasal absent; palatines present, poorly developed; vocal sacs paired, lateral, behind angles of jaws." Trueb's definition was based on the type species of the genus, *O. taurinus.* 

Currently four genera of Neotropical hylids having paired lateral vocal sacs behind the angles of the jaws are recognized. Argenteohyla (Trueb, 1970b) has an exostosed skull, no cranial-integumentary co-ossification, skin on dorsum smooth in both sexes, prevomerine teeth situated on transverse ridges, and reduced webbing on the hands and feet. Phrynohyas has thick glandular skin and extensive parotoid glands; the skull is neither exostosed nor involved in cranialintegumentary co-ossification, and the prevomerine teeth are situated on transverse ridges. Osteocephalus and Trachycephalus lack the thick glandular skin and extensive development of the parotoid glands characteristic of Phrynohyas, and both genera have prevomerine teeth situated on angular ridges. The skull of Osteocephalus is well ossified, but there is no modification of the premaxillaries, maxillaries, or squamosals. The lateral edges of the frontoparietals are elevated and form a pair of longitudinal interorbital ridges, which are usually evident externally in large adults. In Trachycephalus the skull is more extensively ossified and is casqued; the premaxillaries, maxillaries, and squamosals are involved in integumentarycranial co-ossification. The dermal roofing bones have a pattern of radiate ridges, which are visible externally in the co-ossified skin.

The presence of paired lateral vocal sacs behind the angles of the jaws unequivocably places verucigerus in the Phrynohyas-Argenteohyla-Osteocephalus-Trachycephalus series. The presence of transverse prevomers and absence of extensive development of the parotoid glands eliminates the consideration of Phrynohyas. The absence of co-ossification of the premaxillaries, maxillaries, and squamosals and the absence of radiate ridges on the dermal roofing bones precludes inclusion of the species in Trachycephalus. The presence of extensive webbing on the feet and angular prevomerine ridges precludes inclusion of the species in Argenteohyla. The characters of the well-ossified skull with lateral ridges on the frontoparietals include the species in Osteocephalus.

# NATURAL HISTORY

All observations reported herein were made at an elevation of 1150 m on the south slope of the Cordillera del Dué, Provincia Napo, Ecuador, on 2-4 August 1968. The Cordillera del Dué is an eastern spur of the eastern Andean range; the site of our field work was on a ridge north of the Río Coca (500 m below) and east-northeast of Volcán Reventador at approximately 00° 02' S and 77° 33' W. In this area the vegetation consists of lower humid montane forest. There are many large trees, but the canopy is incomplete. A few tree ferns and some bromeliads are present. Mosses and small ferns are abundant, and a thick layer of leaf litter is present. Individuals of O. verrucigerus were found in a broad, shallow ravine, in which there is a small stream having its origin in a spring on the north slope of the ridge. This stream is part of the Río Azuela drainage; eventually the Río Azuela flows into the Río Coca.

Males of O. verrucigerus were observed calling from low bushes (less than 1 m above surface) and rocks along a pool in the stream. Individuals were heard between 1915 and 0100 hr, during which time temperatures ranged from 19° to 20° C. The call consisted of a series of well-pulsed, low guttural notes. Recordings of two individuals provided the following data. On KU Tape No. 677 the frog produced notes at a rate of 5.7/min; the duration of a typical note is 0.2 sec, and the note is composed of eight pulses. The dominant frequency is at about 1400 hz. (Fig. 5). On KU Tape No. 678 the frog produced notes at a rate of 10.3/min, with five of those in one 17-sec period. The second individual produced notes like the first, except that some notes were followed by one or two short "clucks."

One female was found on a tree limb about 2 m above the ground and about 10 m away from the pool where males were calling. An amplectant pair was found on the base of a bush adjacent to the pool on the night of 3 August. The pair was placed in a large plastic bag half filled with water. The following morning a clump of about 200 eggs



Fig. 5. Audiospectrogram of the mating call of Osteocephalus verrucigerus (KU Tape No. 677), recorded at Cordillera del Dué, Provincia Napo, Ecuador, on 4 August 1968; air temperature 19° C.

was present in the bag. The disposition of eggs under natural conditions was not ascertained, but those deposited in the bag were loosely adherent and had individual envelopes. Average measurements of 10 eggs are: embryo (yolk plug stage) 2.0 mm, vitelline membrane 3.4 mm, and outer envelope 4.3 mm.

Tadpoles were raised from the eggs and also were found in a quiet silt-bottomed pool in the stream. The pool was about  $1.5 \times 2.5$ m and had a maximum depth of 22 cm; it was covered by dense bushes and showed no evidence of flow. The tadpoles buried themselves in silt on the bottom.

Tadpoles in developmental stages 25–37 are available. The smallest tadpole in stage 25 has a body length of 5.7 mm and a total length of 16.2 mm. The two upper and first and second lower tooth rows are well formed, but the third lower row is incomplete, and the fourth and fifth lower rows are absent. The largest tadpole in stage 37 (KU 124209) having a body length of 14.6 mm and a total length of 40.8 mm forms the basis for the following description.

Body broader than deep, broadest posteriorly; snout in dorsal profile bluntly rounded, in lateral profile round. Eyes small, widely separated, directed dorsolaterally; nostrils directed anterolaterally about midway between eyes and tip of snout. Spiracle sinistral, directed posterodorsally just below midline at about midlength of body; anal tube short, dextral. Caudal musculature moderately slender, terminally curved dorsally; caudal fins about equal in depth on anterior three-fourths of tail, terminating in a blunt tip. Depth of musculature at midlength of tail slightly less than depth of either fin; dorsal fin not extending onto body (Fig. 6).

Mouth moderately small, directed anteroventrally. Median third of upper lip bare; rest of mouth bordered by two rows of short, blunt, closely packed labial papillae. A shallow lateral labial fold containing additional papillae. Beaks slender and smooth; upper beak forming a broad arch with long slender lateral processes; lower beak broadly Vshaped. Two upper and five lower rows of teeth; fifth lower row shorter than others, which extend laterally nearly to labial papillae; second upper and first lower rows narrowly interrupted medially; other rows complete (Fig. 7).

In life small tadpoles are grayish brown, except the dorsal part of the body, which is black. Large tadpoles have a black body with a bluish sheen to the venter. A ventral



Fig. 6. Tadpole of Osteocephalus verrucigerus (KU 124209). × 3.



Fig. 7. Larval mouth parts of Osteocephalus vertucigerus (KU 123209).  $\times$  15.

crescent-shaped area is nearly devoid of pigment. The fins are dark gray, and the caudal musculature is brownish black. Pigment is present on the lips and labial papillae. The iris is black with faint gold flecks and a golden bronze ring around the pupil.

One tadpole metamorphosed on 10 November, 89 days after the eggs were laid. The recently metamorphosed young had a snout-vent length of 8.9 mm. The dorsum was silvery white with a grayish brown triangular mark extending from the eyelids to the middle of the back. The flanks were dark gray; distinct gray transverse bands were present on the limbs. The same pattern is evident, but the colors are different in a juvenile taken at Cordillera del Dué on 3 August. The specimen (KU 123186) has a snout-vent length of 29.8 mm. In life the dorsum was pale olive-green with a dark brown triangular mark extending from the eyelids to the middle of the back. Five dark brown spots were present posteriorly on the dorsum. The flanks, posterior surfaces of the thighs and transverse bands on the limbs were dark brown. The throat and belly were white. A creamy white suborbital mark was present. Evidently this species undergoes considerable ontogenetic change in coloration, which consists principally of an increase in dark pigment and the subsequent obliteration of the juvenile pattern. We are not implying chromatophore expansion, but increase in number.

Although the collection of anurans from the Cordillera del Dué is small (178 specimens of 18 species), some ecological associations are evident from the field observations. The pool where *O. verrucigerus* was found was the only still water observed. Several *Bufo typhonius* and one *Osteocephalus* 



Fig. 8. Distribution of Osteocephalus verrucigerus.

*leprieuri* were found at the pool, whereas along the stream below the pool four other anuran species were observed—an undetermined species of the Hyla bogotensis group, *Centrolenella cochranae*, *Eleutherodactylus cornutus*, and an unidentified species of *Colostethus*. Other hylids taken in the ravine (*Hemiphractus proboscideus* and *Gastrotheca weinlandi*) do not utilize the pool or the stream for breeding.

The only other reported observations on the breeding behavior and life history of *Osteocephalus* were made by Bokermann (1964), who described the wariness of breeding *O. taurinus* and noted that the eggs were deposited in a film on the surface of a pond.

At the present time O. verrucigerus is known from eight localities from southern Colombia (2° N lat) to central Peru (12° S lat). All but three of the 33 specimens are from Ecuador (Fig. 8). Except for the Colombian locality in the upper Río Magadalena drainage, all localities are on the lower Amazonian slopes of the Andes or on the western fringe of the Amazon Basin. The altitudinal range is from 600 m (Río Cotapino, Ecuador) to 1840 m (Baños, Ecuador); most specimens have been found at elevations between 1000 and 1200 m.

### SPECIMENS EXAMINED

COLOMBIA. Departamento de Huila: Acevedo, Río Suaza, FMNH 69709-10. ECUADOR. No specific locality, ZMB 16589. Provincia de Napo: Avila, UMMZ 90413; Cordillera del Dué, KU 123176-88, 123189 (skeleton), 124209, 124211 (tadpoles), 124210 (young), 124208 (eggs); Río Pacayacu, tributary of Río Cotapino (Suno drainage), CAS-SU 13150. Provincia de Pastaza: Abitagua, FMNH 25791, 27619, UMMZ 90414, 92092; Mera, UMMZ 90412 (4). Provincia de Tungurahua: Baños, Río Pastaza, NHRM 1960. PERÚ: Departamento de Ayacuche: La Mar, Sivia, Río Apurimac, FMNH 39853.

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