## ON THE TAXONOMIC RANK OF THE YELLOW-BILLED TOUCANET (Aulacorhynchus calorhynchus)

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Among congeneric toucans (Ramphastidae) there is often more difference in bill color and pattern than in plumage color. Because of this it has been generally thought that the appearance of their conspicuous bill may be of primary importance in species recognition. Under this concept Aulacorhynchus calorhynchus, a yellow billed, small green toucanet that inhabits the mountains of western Venezuela and northeastern Colombia, has been invariably considered specifically distinct from the neighboring, but allopatric, red billed Aulacorhynchus sulcatus (Groove-billed Toucanet), although in plumage color and pattern and in size the two are practically identical.

Nominate sulcatus has a dark red bill and is limited to the mountains of northcentral Venezuela. Erythrognathus, a brighter red billed form found in the mountains of northeastern Venezuela, is currently considered a subspecies of A. sulcatus. Acoustical evidence suggests that calorhynchus, too, should be treated as conspecific with A. sulcatus rather than as a separate species. This treatment is further justified by the existence of populations intermediate in color and configuration of the bill.

#### VOCALIZATIONS

Certain terms used in the following discussion are here defined, based on BONDESEN and DAVIS, 1966.

figure: sound which produces a single, complete and dis-

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tinct impression — usually represented on a sound spectrogram as a continuous trace.

- motif: a group of figures that has a special rhythmic or melodic character.
- pattern: the arrangement of sound energy in time, particularly as seen on a spectrogram or other visual representation of the sound; also applicable to the aural impression.

Toucanets (Aulacorhynchus) in general produce a number of vocal sounds that can be characterized as growls, grunts and barks (yelps). These may be used or combined in various ways that presumably have certain meanings in certain contexts. However, each species has a standard, stylized vocalization that may be considered homologous to primary song in other avian groups and is probably the vocalization most used in species recognition. In this "song" a more or less standard sound, either a single figure or a motif, is repeated over and over again (succession) with a regular tempo. It would appear that the species recognition information is contained in the pattern of the individual figures and probably to some extent in the tempo of the song. The idea of this can be grasped from Fig. 1, which presents portions of "song" by four different species.

In A. prasinus (Fig. 1, a and b) the individual figures are quite short (less than 0.10 sec). Each figure begins with organized sound that is inflected to a sharp peak and terminates with a "rattle" of somewhat less organized sound; the figure may be said to begin with a bark and end with a growl, differences very probably perceptible to the birds although not to most humans who hear the sound as a slightly graty "churt". The tempo is about two figures per second. The species A. prasinus, as currently recognized, ranges from eastern montane Peru north to Mexico, extending eastward in northern South America to the Merida Andes of Venezuela. The portions of song illustrated in Fig. 1 are of A. p. albivitta, recorded in Venezuela. In the Cornell Laboratory of Ornithology phonograph record "Mexican Bird Songs" (L. Irby Davis recordings), near the end of Band 1, Side 1, can be heard

460

some typical "song" of this species, presumably by A. p. stenorhabdus of Chiapas. A spectrogram of this recording shows the tempo of the song to be the same as in A. p. albivitta. The basic pattern of the figures is also the same, differing only in that the initial bark is proportionately longer and the terminal rattle shorter, the total length of figure being essentially the same. The similarity of song confirms that these widely separated populations are properly considered conspecific.

A. haematopygus as a species ranges from western Venezuela in the Perijá Mountains, through the three Andes ranges in Colombia, south to western Ecuador. Recordings of the nominate form (Fig. 1 d) were made in southwestern Tachira, where the Colombian Cordillera Oriental penetrates somewhat into Venezuela. The figures of this song begin with a bark and end with a growl as in A. prasinus, but they are longer (mostly over 0.20 sec) and lower pitched; in this case the slowly inflected first part and the rattle are perfectly distinguishable to the human ear. The tempo of the song is somewhat slower than in A. prasinus.

The figures of A. derbianus derbianus (Fig. 1 c: recorded in the Cerros del Sira, Dept. Huánuco, Peru, by John S. Weske) are somewhat similar to those of A. haematopyqus (from western Venezuela) but do not have the final part modulated into a rattle (the lighter tracing that follows after the dark second harmonic is no doubt echo and not part of the primary sound); also the song's tempo is slower, being only about one figure per second. That the pattern and tempo of the song as shown in Fig. 1 are probably typical of the Andean populations was determined by comparison with a spectrogram made from another recording by Weske from a distant population in the Apurímac Valley, Dept. Cusco, Peru. A. d. derbianus ranges from southwestern Colombia (probable) south along the eastern slope of the Andes to northwestern Bolivia. Some distant populations inhabiting the Guiana Shield region (mountains of Guyana and southern Venezuela, including the tepuis of the Gran Sabana; also adjacent northern Brazil) are presently considered geographic races of the species A. derbianus. There is no acoustic information available for these populations that could confirm or question their presumed relationship to A. derbianus.

The song of A. coeruleicinctis (Fig. 1 e: recorded in Dept. Cusco, Peru, by Weske) differs from all those mentioned in being composed largely of a succession of motifs. These consist of a long and a short figure. The sound of the long figure is rather unor. ganized and is modulated into a more or less well defined throaty rattle; some figures are initiated with a short bark of organized sound. The majority of short figures are in the form of a short bark of organized sound which tends to break down in the final part: occasionally a short figure consists almost entirely of less organized sound. The tempo is slightly slower than one motif per second but a bird may fairly frequently interrupt this song pattern by repeating several times in succession either of the figures that comprise the motif. A. coeruleicinctis is limited to the Andes of eastern Peru and northwestern Bolivia. I have no information on the voice of A. huallagae of northeastern Peru (Libertad), which, on morphology and distribution, may be nearest to A. coeruleicinctis.

It is readily apparent from Fig. 2 that A. sulcatus is vocally as distinct as each of the four species already considered, and that the voice of calorhynchus (a) is practically identical with that of nominate sulcatus (b) both in pattern of figure and in tempo. In normal song the sound is organized (voiced sound appearing in definite frequency bands), although it is not unusual for it to break down at times; a tendency to do so can be noted in the peaks of the figures in b, e and f. In certain contexts —I have noted it especially in the squawks of distressed birds the sound may be completely unorganized (random frequencies over a wide spectrum, "noise), or may alternate abruptly between organized and unorganized.

In many bird species there may occur an alteration in vocal pattern and characteristics when a bird is highly excited by territorial conflict, a condition that can be simulated by playing to a bird a recording of vocalizations of its own species. As in some species I have found that a bird so excited may "escape" from the genetic template that governs its normal vocalizations and produce sounds that appear to reflect more primitive or ancestral relations, I analized some sounds produced in such context by both *calorhynchus* and *sulcatus*. Spectrograms of two different



Sound spectrograms of portions of "song" by four species of toucanet. Aulacorhynchus prasinus albivitta: a and b, respectively west central Mérida and central Táchira, Venezuela; A. derbianus derbianus: c, Cerros del Sira, Dept. Huánuco, Perú (recording by J. S. Weske); A. haematopygus haematopygus: d, southwestern Táchira, Venezuela; A. coeruleicinctis: e, Cordillera Vilcabamba, Dept. Cusco, Perú (recording by J. S. Weske).



Sound spectrograms of portions of "song" by Aulacorhynchus sulcatus. A. s. calorhynchus: a, c and e, southern Táchira, Venezuela; A. s. sulcatus: b, d and f, northern Aragua, Venezuela. The figures c-f were recorded after song playback.



Bill pattern. (Top) yellow billed Aulacorhynchus sulcatus calorhynchus from southeastern Lara; (bottom) red billed A. s. sulcatus from northern Aragua; (center) two specimens from Cerro Platillón, northern Guárico, representing opposite extremes of that intermediate population.



The presently known distribution in northcentral Venezuela of Aulacorhynchus sulcatus calorhynchus (yellow-billed), A. s. sulcatus (red-billed), and two intermediate populations. Meaning of symbols: inverted black triangles = localities of specimens shown in Fig. 3; point enclosed in circle = site of city of Barquisimeto. Present interpopulation environmental conditions: W = wet, D = dry or lowlands ecologically unsuitable, ED = extremely dry. Double-pointed arrows indicate probable paths of interchange during a presumed past period of secondary contact between the yellow-billed and red-billed forms. sounds are shown and it is seen that even in such context the voice of *calorhynchus* (c and e) is quite the same as that of *sulcatus* (d and f).

The song of *erythrognathus* is the same as illustrated for nominate *sulcatus* and *calorhynchus*. Thus, the acoustic evidence indicates that these three allopatric forms are conspecific.

#### MORPHOLOGY

All toucans of the genus *Aulacorhynchus* are mountain birds, living in forested regions of the cool, humid subtropical zone (some range down to the upper tropical, others up to the lower temperate zones). They do not differ greatly in size and all share a general green color; in plumage the various forms differ mainly in color of throat, presence or absence of a contrasting hue on upper or under tail-coverts, and in extent or absence of chestnut tail tipping.

The forms here considered races of A. sulcatus are alike in gray throat, green (non-contrasting) upper and under tail-coverts, and blue-feathered orbital area; in lacking any chestnut tipping to the tail they differ from all other taxa of Aulacorhynchus except A. derbianus osgoodi (Acary Mountains, Guyana), which is unique among the forms currently assigned to the species A. derbianus in lacking chestnut tail tipping (and, to be emphatically redundant, is the only taxon outside the species A. sulcatus to lack this). As plumage differences among the populations of A. sulcatus are very small they will not be discussed in this paper.

A. calorhynchus and A. erythrognathus were originally (and concurrently) described as species. That only calorhynchus has been maintained as a distinct allopatric species has apparently been due principally to the difference in bill color (yellow vs. red) from nominate A. sulcatus. However, the red bill of erythrognathus is in some ways more different from that of nominate sulcatus than is the yellow bill of calorhynchus.

In calorhynchus and nominate sulcatus the bill is crossed diagonally by an area of black that is somewhat irregular in outline but fairly consistent in gross pattern (see Fig. 3). In sulcatus the color of the maxilla anterior to the black area varies from wine red to reddish brown, usually deepening in tone distally. In calorhynchus this area is yellowish ivory or pale greenish yellow proximally, changing gradually to yellow distally; occasional individuals have a slight reddish wash along the culmen. In calorhynchus the tip of the mandible is yellow; it is brownish to blackish red in sulcatus. On the lateral surfaces of the mandibular rami, posteriorly from the black area there is a lighter area which is pale greenish to whitish yellow in calorhynchus and variable in sulcatus from wine red to ivory. Bordering the base of the bill, beginning at the nostril and continuing downward to curve around the base of the mandible, there is a narrow but prominent white band in calorhynchus; in sulcatus this mark is less prominent, frequently being almost obsolete.

There is also some difference in the relief of the maxilla. In *sulcatus* the culmen is essentially flat in the proximal region but usually rounded distally. Further, the sides of the maxilla are usually pronouncedly depressed (pinched in) directly below the culmen in the proximal region. In *calorhynchus*, however, the culmen tends to be rounded throughout. In some individuals the sides of the maxilla slope outward slightly from the curve of the culmen; in others there is a slight depression below the rounded culmen but in a continuous, smooth curve with it.

The bill of erythrognathus differs from both sulcatus and calorhynchus in having the black patch much less extensive to obsolete. Distally, and on the upper part of the maxilla, the color is dark red to reddish brown as in nominate sulcatus; however, the proximal lateral quarter to third of the bill, from the nostril down, is bright scarlet orange with some tendency toward a brownish hue. In lacking even a trace of white band bordering the base of the bill, erythrognathus differs again from the other two forms. The shape of the maxilla is much like that of calorhynchus, although some individuals are similar to sulcatus in having the proximal region of the culmen somewhat flattened and the sides of the maxilla depressed.

Recent collections by personnel of the Estación Biológica de Rancho Grande, under the direction of Dr. GONZALO MEDINA P.,

disclosed that on Cerro Platillón, a mountain peak in the hills south of the central Cordillera de la Costa. there is a population of the toucanet in question that is intermediate between calorhunchus and sulcatus both in bill color and relief of the maxilla. The color of the maxilla varies from vellow with a dull reddish wash to dull vellowisch red and tends to be darker proximally, approaching sulcatus, but lighter distally, approaching calorhyn chus. The overall shade is lighter or darker, as seen in Fig. 3, depending upon the greater or lesser presence and extent of reddish hue. The tip of the mandible is similar to that of the maxilla and the light area on the mandibular rami is buffy to yellowish ivory: the white line bordering the base of the bill varies between the extremes indicated for sulcatus and calorhunchus. Similarly. the form of the maxilla varies from the round-culmened condition found in calorhynchus to the flat-culmened character of sulcatus. All 12 specimens of the Cerro Platillón population in the Rancho Grande collection as well as four additional specimens subsequently obtained at the same location by the Phelps Collection are similar in the above respects.

A review of specimens in the Phelps Collection disclosed that the toucanet population of the hills "El Cerrón" and "El Cogollal" in western Lara, presently assigned to the form *calorhynchus* (PHELPS and PHELPS, 1958: 251), is also intermediate between *calorhynchus* and *sulcatus*; it differs from the Platillón population in having the reddish area of the maxilla less extensive and the white basal line more consistently defined, being thus closer to *calorhynchus*.

### DISCUSSION

It is interesting that in neither of the intermediate populations are there specimens that correspond to *calorhynchus* or to *sulcatus* in all characters; they are consistently intermediate. They are also apparently completely isolated at the present time from all red billed and yellow billed populations. The origin of these intermediate populations might be variously explained: proto-A. *sulcatus* could have evolved more or less contemporaeously in different sites of isolation into red billed, red-yellow billed and yellow billed forms; or it may originally have been red-yellow billed and the present intermediate populations are relicts. However, the particular locations of the separate intermediate forms and the characters peculiar to each of them suggest another hypothesis.

Various authors have suggested that animal distribution and evolution have been influenced by climatic changes. HAFFER (1967-1970) has developed this idea to a considerable extent with regard to the Neotropical avifauna, suggesting that alternating climatic cycles of the Pleistocene and post-Pleistocene have caused or permitted recession or expansion of vegetation types, hence of biotopes, and that birds isolated in refugia so created have frequently evolved away from the ancestral stock to different degrees of speciation. Many examples from my own investigations support Haffer's hypothesis. I would emphasize the importance of minor, as well as major, climatic cycles and the secondary influence of topographical features, such as mountains, that may cause relatively local conditions within the macro-condition of climatic cycles, resulting in local refugia. This would appear an appropriate basis to explain the case of these toucanets.

Fig. 4 shows the presently known distribution within the critical area of nominate *sulcatus* (red billed), *calorhynchus* (yellow billed), and the intermediate forms. It can be seen that all of the forms are presently separated from each other by ecologically unsuitable lowlands or regions that are dry to extremely dry due to "rain shadows", caused primarily by mountain formations lying in the path of the prevailing easterly winds. We may assume that the colonizing of extreme northern South America by the ancestral form took place during some favorable, presumably wet-cool, major climatic cycle and that during some ensuing dry-warm phase of major cycle this population was divided into isolated populations which evolved (or retained) red or yellow bill as the case may be.

It may be impossible to determine the sites where the yellow billed and red billed forms that are today *calorhynchus* and nominate *sulcatus* evolved. Those refugia may have been quite small, but during the development of a later wet-cool climatic period the two forms may have expanded gradually through the areas presently covered, resulting in the establishment of substantial gene pools of "red bill" to the north (east) and "yellow bill" to the south (west).

With a continued increase of appropriate conditions during a major climatic cycle these two toucanet forms may have expanded further until they came into secondary contact. Although by that time they had become quite different in bill color they retained the same vocalizations. There is ample evidence that voice is of primary importance in species recognition and pair formation in many avian species, and it is probable that the vocal similarities sufficed to facilitate extensive interbreeding of the two allied forms.

The region just west of Barquisimeto is an extremely dry, virtually vegetationless desert. Its aspect is such as to indicate that it has long remained dry, even during major climatic cycles when other presently dry areas probably developed a vegetation related to a more humid condition. This and other conditions suggest that the contact between the two toucanet forms took place in an east-west direction between the northeastern tip of the Andes and the hills and mountains to the east, and also in a north-south direction between the northwestern tip of the Andes and the hills of the Cerrón-Cogollal region, concurrent with an east-west contact between there and the hills to the east. As a major climatic cycle would likely encompass a relatively long period of time, there probably developed broad zones with a thorough red and yellow gene mixture.

The particular geographic situation of both the Platillón and the Cerrón-Cogollal mountains is such that the effects of a climatic change back toward drier conditions would be quickly reflected in the lowlands surrounding those two regions, assuming that the prevailing winds were easterly as they are today. This would have left populations of intermediate birds isolated on those ecological mountain islands, where a thorough red-yellow gene mixture persists even today. The greater similarity of the Platillón population to red billed *sulcatus* and of the Cerrón-Cogollal population to yellow billed *calorhynchus* suggests that those links were stronger and/or persisted longer; such possibility is consistent with the geography-climate effect that one might predict. Elsewhere, however, the red-yellow gene mix was gradually swamped out in the substantial reservoirs of red "genes" to the north and east and yellow "genes" to the south (west), although the presence of a reddish wash on the culmen of an occasional yellow billed bird and of a strong tendency toward buffy at the base of the mandibular rami in red billed birds may indicate that there remains a slight influence from the former contact.

A. sulcatus is very much confined to forest; from all I have observed it does not make relatively long flights accross open country as do some ramphastid species. This probably explains the stability of the different forms in spite of their relative proximity — the Platillón region is scarcely 50 km distant from the nearest red billed population and no more than 70 km separate calorhynchus from sulcatus; in both cases the lower country between is totally unsuitable ecologically.

Some red billed populations are today effectively isolated from each other, a fact manifest in small mensural differences among them, but as the country they occupy is directly exposed to prevailing winds blowing from the sea, it would require no more than minor climatic change to permit periodic contact and reinforcement of the red bill character among them. However, it would require a greater change to bring the red billed populations again into contact with the intermediate and the yellow billed populations or to permit contact between the last two. If this were to occur, as they all still have the same voice I believe the different forms would again freely interbreed. Hence, in my opinion, they should be treated as one species, A. sulcatus.

HAFFER (in litt.) has pointed out that "hopping" to the isolated mountain "islands" by occasional individuals of the red billed and yellow billed populations could theoretically result in essentially the same situation as now exists, but he agrees that this explanation is unlikely from what we know about the birds in question. However, even if "hopping" should be the explanation it would lead to the same general conclusion respecting conspecificity.

## RELATIONSHIP OF A. SULCATUS TO OTHER SPECIES

HAFFER (1970b) suggests that A. derbianus. A. sulcatus and A. calorhynchus are members of a superspecies and that the latter two evolved progressively from derbianus or proto-derbianus in a dispersal eastward from the main South American Andes to the table mountains (tepuis) of the Guiana Shield, thence northward to the coastal mountains of Venezuela and westward along them to the mountains of western Venezuela and northeastern Colombia. We have already seen that *calorhynchus* should really be considered conspecific with A. sulcatus. I once thought that derbianus, too, might prove conspecific with A. sulcatus, for although there are some pronounced morphological differences there is also considerable similarity and all races of both complexes are allopatric. However, having learned the song of nominate derbianus through the opportune supply of tape recordings from eastern Peru by John S. Weske, I believe that both vocal and morphological differences require treating A. sulcatus and A. derbianus as distinct species. They may comprise a superspecies as Haffer suggests.

Acoustic evidence does not argue against the derivation of A. sulcatus from A. derbianus (sensu stricto), for although their "songs" are quite distinct both in pattern of figures and in tempo, and thus would presumably be of reproductive isolating importance today, I believe the one song could relatively easily have evolved from the other. The slower, somewhat simpler song of A. derbianus may represent the ancestral form. Incidentally, it should be pointed out that although the difference in fundamental pattern is real, the difference in harmonic content seen in the spectrograms of the two species could be an artifact resulting from different recording techniques.

It is not clear what may be the relationship of the previously mentioned Guiana Shield populations presently assigned to the species A. derbianus; these are considerably isolated from nominate A. derbianus of the main Andes as well as from A. sulcatus to the north. We lack vocal and other behavior information relative to the Guiana Shield birds which could help clarify this, and possibly lend support to, or detract from, Haffer's suggested dispersal route leading to A. sulcatus. Several alternate hypotheses can be offered to explain the origin of A. sulcatus but it seems futile to speculate further until we have more complete information available, some of which should not be difficult to obtain. It may be of special relative and intrinsic interest to obtain behavior, especially acoustic, information about the southeasternmost taxon, A. derbianus osgoodi. The need is basic for this information for A. d. whitelianus (once considered specifically distinct), and/or the not very different neighboring race, duidae.

As I have not studied them all morphologically I am not prepared to discuss properly the probable relationships among other species of Aulacorhynchus. Haffer is concluding such a study. No indubitable relationships are suggested by the acoustic information available to me. There is certainly a striking difference in the song pattern of A. coeruleicinctis of eastern Peru in comparison with the other species. But it is conceivable that the patterns of the figures of A. haematopygus and A. prasinus are merely refinements of, for example, the second long figure and the first short figure, respectively, of A. coeruleicinctis. It could also be that the figure of A. prasinus is a shortening of that of A. haematopyqus, or the latter a prolonging of the former. In synthesis, about all that can be said is that the voices of the species of Aulacorhynchus appear to be closely related to each other; and I might add that they are quite distinct from the voices of the other small ramphastids known to me (species of Pteroglossus and Selenidera).

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474

## SUMMARY

Vocal similarities considered together with the existence of intermediate populations indicate that the yellow-billed form, A. calorhynchus, of small, green, norhern South American toucanet should be theated as a subspecies of Aulacorhynchus sulcatus, the two previously recognized races of which have red bills.

The bioacoustical, morphological and zoogeographic evidence to justify this treatment is presented and an explanation offered for a probable past secondary contact between the yellow billed and red billed forms which resulted in two isolated, intermediate populations.

Possible relationships among the species of *Aulacorhynchus* and their vocalizations are considered briefly but no conclusions are offered.

## RESUMEN

Entre las especies congenéricas de los tucanes (familia Ramphastidae) el color y su distribución en el pico son en muchos casos más distintivos que el color del plumaje. Por ésto se ha pensado que la apariencia de su pico grande y conspicuo pueda ser de importancia primordial para el reconocimiento específico. Bajo este concepto el Pico de Frasco Andino (Aulacorhynchus calorhynchus), un pequeño tucán verde, con pico amarillo, que habita las montañas de Venezuela occidental y Colombia nororiental, ha sido considerado invariablemente como especie distinta a la vecina, pero alopátrica, especie Aulacorhynchus sulcatus de pico rojo. Ambas formas son prácticamente idénticas en el color del plumaje y en tamaño.

La forma nominativa de A. sulcatus está restringida a las montañas de la región norcentral de Venezuela y su pico es de color rojo obscuro. Otra forma vecina, erythrognathus, restringida a las montañas de Venezuela nororiental, también tiene el pico rojo pero se diferencia por tener la región proximal del pico de color anaranjado rojizo vivo (con leve matiz parduzco); esta forma se trata corrientemente como subespecie (raza geográfica) de A. sulcatus.

En vista de que el canto de la forma Andina, calorhynchus, es similar al de sulcatus nominativo y erythrognathus, y como se han encontrado poblaciones intermedias entre calorhynchus y sulcatus en las cuales el pico muestra intergradación de color, se recomienda que calorhynchus también sea tratado como subespecie de A. sulcatus y no como especie distinta como se ha venido haciendo.

Se expone la evidencia bioacústica, morfológica y zoogeográfica que justifica el tratamiento taxonómico recomendado y se ofrece una hipótesis sobre un probable contacto secundario entre la forma de pico amarillo y la de pico rojo, del cual resultaron las dos poblaciones intermedias actualmente conocidas.

Se consideran, sin proponer conclusiones, posibles relaciones entre las especies de *Aulacorhynchus* y sus vocalizaciones.

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# SOCIEDAD VENEZOLANA DE CIENCIAS NATURALES BOLETIN

TOMO XXIX - MARZO 1972 - NUMERO 122/123

SUMARIO	Pág.	
EDITORIAL	413	
PALEONTOLOGIA		
Nueva especie de Ave Fósil ( <b>Strigiformes: Tytonida</b> e) del Pleis- toceno Superior de Cuba. Por Oscar Arredondo	415	
ORNITOLOGIA		
Observaciones acerca de algunas aves y su proceso de nidifica- ción. Por E. RutkisOn the taxonomic rank of the yellow-billed toucanet ( <b>Aula-</b>	432	
<b>corhynchus calorynchus</b> ). Por Paul Schwartz Notas sobre hábitos alimenticios y comportamiento reproductivo	459	
del zambullidor <b>Podilymbus podiceps</b> (Aves), en Colom- bia. Por José Ignacio Borrero H	477	
BIOLOGIA		
Locomoción y musculatura de las regiones glútea y femoral en los cebidos de Venezuela. Por Roberta Bodini Aporte al estudio de los Corales ( <b>Coelenterata</b> ) de la Bahía de	487	
Mochima, Estado Sucre. Por Régulo A. Campos Villarroel On Atelopus oxyrhynchus boulenger (Amphibia, salientia) with description of a new race and a related new species from	545	
the Venezuelan Paramos. Por Juan A. Rivero	600	
PARASITOLOGIA		
Comportamiento de <b>Tripanosoma vivax,</b> cepa desorwitz, en ani- males de laboratorio y en rumiantes. Por Carlos Díaz-Ungría	613	
ESPELEOLOGIA		
Les troglodytes de la science. Por Jacques Chabert	622	
BOTANICA		
Morfología y anatomía de las semillas de la familia Melastoma- taceae. Por Lila Parisca	633	
FORO NACIONAL SOBRE RECURSOS VIVOS DEL MAR. Informe final	641	
ACTIVIDADES DE LA SOCIEDAD	707	

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