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STUDIES ON SOUTH AMERICAN ANOLES
ANOLIS TRANSVERSALIS A. DUMÉRIL

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INTRODUCTION

In the second volume of Boulenger's Catalogue of Lizards (1885) two species of *Anolis* — *A. transversalis* and *A. buckleyi* — were placed consecutively with the implication that they were closely related.

The provenance of the first of these species was for a time placed in doubt by the author of the name. *A. transversalis* was initially described (A. Duméril, 1851) with no better locality than "Amérique méridionale". Even when Duméril redescribed the species in 1856 with a color figure (his plate XIX) he gave no better information than "Brésil". Fortunately Guichenot (1855) reporting on all the reptiles obtained by Castelnau, who had collected the unique type of *transversalis*, had already given the place of collection as Sarayacu, Peru.

The locality for the two syntypes of *A. buckleyi* has a curiously similar history. Given by the original describer (O'Shaughnessy, 1880) as only "Ecuador", it was corrected by Boulenger in his catalogue to Canelos, Ecuador.

Though coming from two different countries and strikingly different in described coloration, these nominal species were exceedingly similar in structure, as Boulenger's standardized descriptions very clearly showed.

Yet in the long interval since these descriptions the distinctness of these two taxa has never been questioned. Shreve, indeed, in 1941, when confronted by specimens from Ecuador colored somewhat like *transversalis* (with which, however, he did not compare them), pronounced these Ecuadorian individuals to be females of *A. buckleyi*. In this he was quite correct; he should, however, have gone somewhat further. Examination of the types of the two species and of additional material from Peru, Ecuador,

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Colombia and Brasil shows that only one species is involved, the male having received the name *buckleyi* O'Shaughnessy, 1880, the female the name *transversalis* A. Duméril, 1851. The latter is thus the name that must be used.

SPECIES DESCRIPTION

We provide below a standard description of *A. transversalis* somewhat fuller than any previously available and citing the few significant variations.

Head. Head scales smooth, 4-8 scales across snout at level of second canthal. A moderate to slight frontal depression, the scales within the depression as large as adjoining scales, 5-10 scales bounding rostral posteriorly. Anterior and ventral nasal scales in contact with rostral, 4-8 scales between supranasals.

Supraorbital semicircles usually broadly in contact, sometimes separated by one row of scales, each separated from the supraocular disk of its side by one row of scales. Supraocular disk poorly defined, separated from the supraciliary margin by 2-4 rows of granules. Supraciliary scale elongate but short, extending only 1/3 to 1/2 orbital length, continued posteriorly by granules. Canthus blunt, of 6 scales, the second largest. Loreal rows 4-5.

Temporal scales granular, smooth. A more or less distinct line of enlarged scales separating temporal from supratemporal scales. Supratemporal scales subgranular, abruptly separated from the enlarged scales surrounding the interparietal by the ridge bounding the interparietal depression. Interparietal equal to or smaller than ear, rarely slightly large, in contact with the supraorbital semicircles or separated from them by 1-2 (rarely 3) scales. Scales anterior and anterolateral to interparietal quite large, larger than those posterior and posterolateral to it; these again abruptly larger than the supratemporal or dorsal scales.

Suboculars broadly in contact with supralabials, 6-9 supralabials to center of eye.

Mentals wider than long, in contact with 4-5 scales arranged in a forward pointing arch between the enlarged sublabials,¹ 3-4 sublabials in contact with infralabials. Central throat scales granular, smooth.

Trunk. Middorsal rows granular, smooth, not or hardly larger than flank scales. Ventrals larger, smooth, juxtaposed, squarish, arranged in transverse rows.

Gular fan. Large in males, very small in female. Scales smooth, smaller than ventrals, in lines separated by wide areas of naked or weakly scaled skin.

Limbs. Largest scales on forelimbs small, much smaller than ventrals; larger scales on hindlimb, approximately equal to ventrals; scales on both fore and hindlimbs smooth or very weakly keeled. Supradigital scales obscurely multicarinate, 22-27 lamellae under phalanges ii and iii of fourth toe.

1. See fig. 1. This arrangement — scales between sublabials in a strong forward arch — is highly diagnostic of this species.

Tail. Compressed. A double row of scales middorsally, these lightly keeled, vericels obscure. Lateral scales smooth, slightly smaller. Ventral scales larger, keeled. Enlarged postanals in male. Scales under base of tail smooth.

Size. Syntype of *buckleyi*, snout-vent length 98 mm.

Coloration. ♂ = *buckleyi*. O'Shaughnessy (1880): "Brownish or greenish with black spots or punctations on the back and sides and a black network on the upper surface of the head on the sutures of the scales; fine oblique white or bluish lines down the sides of the body, with rows of black dots between; ventral surface pale bluish, dotted with black; gular appendage bright saffron yellow, with black longitudinal streaks and spots".

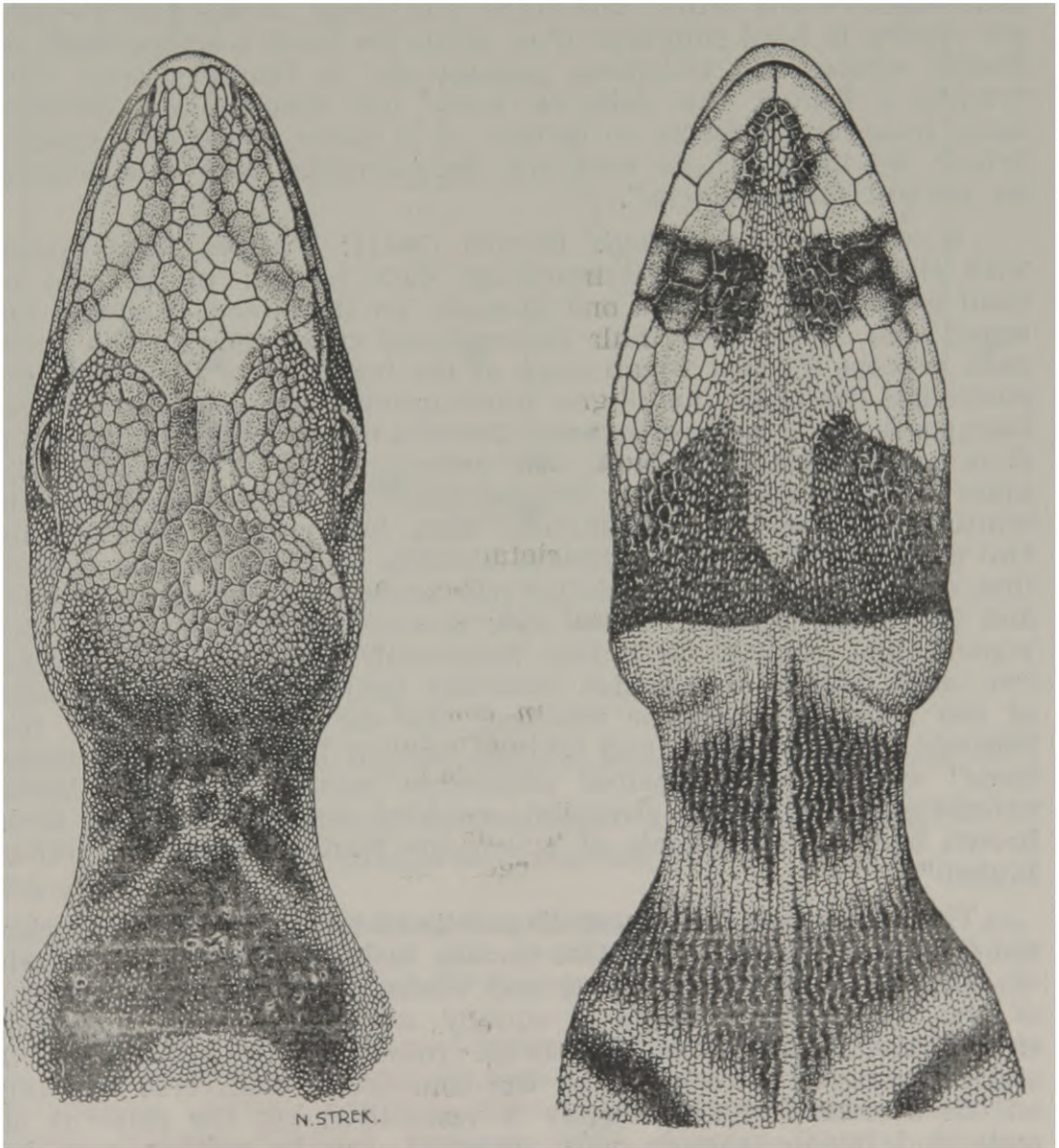


Fig. 1: *Anolis transversalis* ♂, CNHM 42507. Dorsal and ventral views of head.

♀ = *transversalis*. A. Duméril (1856) p. 515: "La teinte générale, qui semble être un gris violacé, est un vert clair, comme le montre un dessin fait d'après le vivant par M. le comte de Castelnau. Sur la tête, il y a de nombreuses vermiculations brunes. Les épaules sont couvertes par une grande tache de la même nuance, qui se prolonge en une pointe sur le cou et s'étend en arrière et en bas jusque sur les bras. Trois autres taches, larges de 0^m,10 au milieu, et irrégulièrement angulaires comme la précédente, se voient sur le tronc; leurs angles postérieurs descendent obliquement d'avant en arrière, le long des flancs, et se rejoignent presque sur le ventre, dont le couleur est un peu plus claire que celle des régions supérieures.

La mâchoire inférieure, tout à fait en avant, porte une petite tache transversale brune; une autre, plus large, occupe tout l'espace qui sépare le bord inférieur d'un orbite du bord correspondant de l'autre orbite; une troisième, passant sur le fanon, s'étend d'un tympan à l'autre. Au delà, en avant des épaules, une dernière tache transversale forme un collier. A la queue, il y a des anneaux bruns; les membres ne sont que demi-annelés, leur face interne ne portant aucune tache".

♀ = as ♀ of *buckleyi*. Shreve (1941): "Above light brown with the under-mentioned markings dark brown: upper side of head extensively marked and spotted; an ill-defined band on the upper side of the neck; four rather broad crossbands on the back, each (except the last which stops at the insertion of the hindlimb) encircling the body, but for an interruption on the median ventral line; speckling is present between the crossbands, but in the juvenile it is restricted to the back, not extending to the sides. Limbs more or less spotted and crossbanded; tail crossbanded. Below whitish, chin with a semi-divided dark brown spot, followed by two pairs of prominent, transverse blotches separated on the median line, or the much larger posterior pair sometimes slightly in contact and projecting upward to the eye; dewlap, particularly along the ventral line, whitish with fine horizontal blackish lines forming two dark brown or blackish band-like projections into each side of the neck, the anterior reaching the ear (the dewlap in the juvenile is undeveloped and whitish, but on the neck the "projections" appear as two paired transverse spots); belly and limbs extensively (slightly in juvenile) speckled and spotted with dark brown between crossbands of which the first crossband is rather broken".

The color characters most diagnostic of the male of this species are the black edging to the flat smooth scales of the dorsal surface of the head and the speckled and obscurely patterned coloration of the trunk. The female is equally unmistakable by the very characteristic pattern of the throat (described by both Duméril and Shreve, see above) and by the bold broad transverse banding on the dorsum. In detail there is variability, but the patterns of male and female, though very different, can in neither case be confused with the patterns of any other species.

DISTRIBUTION

Western Amazonian region from Loreto in Peru through Ecuador and Colombia to the Rio Solimões in Brasil. In Ecuador known to extend up certain river valleys an undefined distance into the foothills of the Andes.

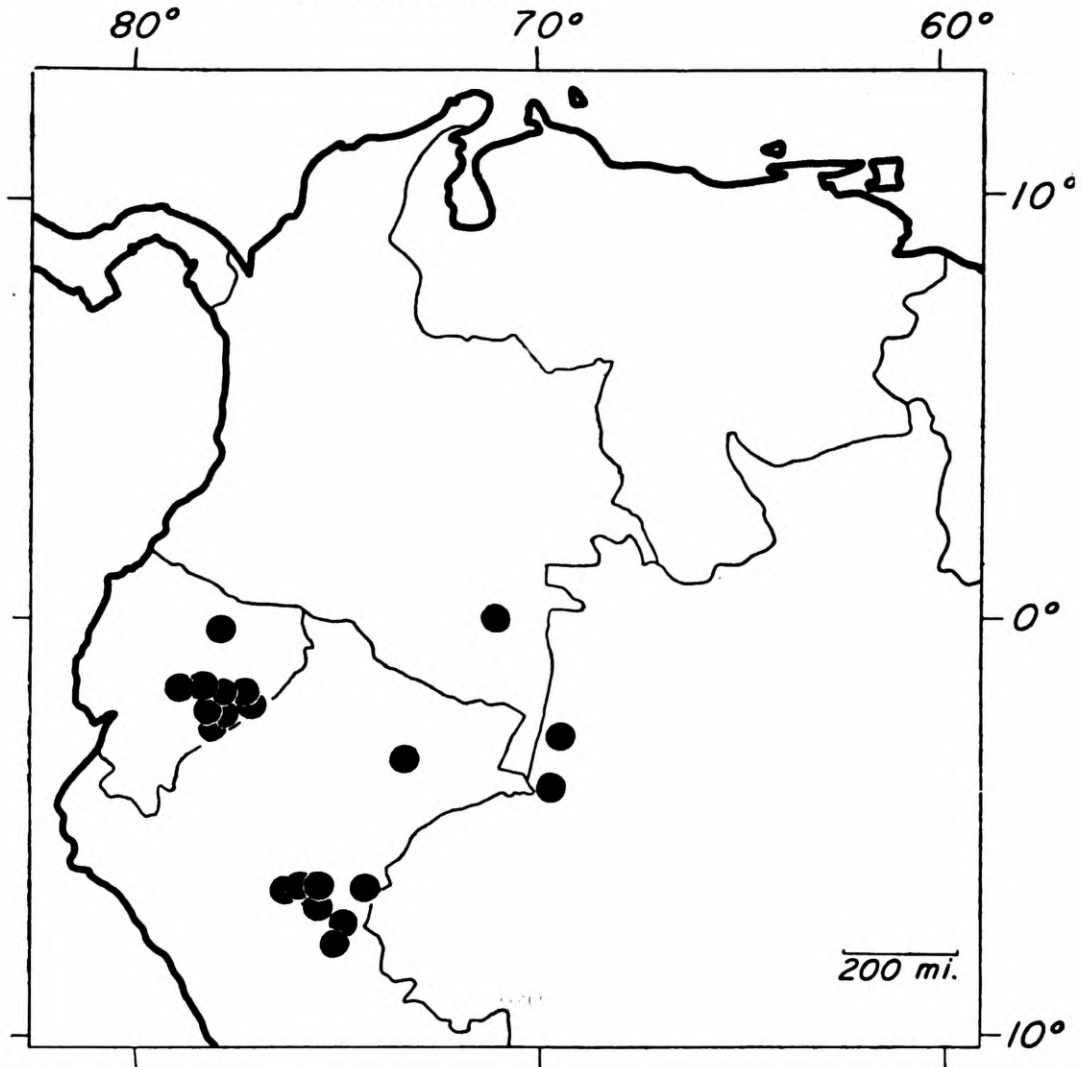


Fig. 2: Geographical distribution of *Anolis transversalis*.

SPECIMENS EXAMINED¹

Ecuador

Napo-Pastaza. Ayacocha, Rio Bobonaza: AMNH 60631-2. Canelos: BM 1956.8.13.18-19 (*A. buckleyi*, syntypes). Montalvo: Orcés 4008. Palanda, SE of Sarayacu, Rio Bobonaza: Orcés 4347-49,

1. For the privilege of examining this material we are indebted to the curators in the following Museums: Academy of Natural Sciences, Philadelphia (ANSP), American Museum of Natural History (AMNH), British Museum (Natural History) (BM), Chicago Natural History Museum (CNHM), Escuela Polytechnica, Quito (Orcés), Museum National d'Histoire Naturelle (Paris), Naturhistorisches Museum, Wien (Vienna), Zoologisches Museum, Berlin (ZMB).

4571-72. Rio Conambo (or Cunambo): Orcés 4586. MCZ 84351.¹
 Rio Llushin, N of Arapicos: Orcés 1749. Lower Rio Payamino:
 Orcés 4404. Sarayacu: MCZ 38529.

Santiago-Zamora. Between Rio Santiago and Rio Pastaza, S
 of Macas and N of Gualaquiza: MCZ 45777, CNHM 42507.

No precise locality: DZ 6708, 6716, 3373, 3384.

Peru

Loreto. Achinamisa, Rio Huallaga: AMNH 56980. Bombo, Rio
 Tapiche Valley: AMNH 56978. Cashiboya, Rio Ucayali: AMNH
 56983. Cerro Azul: CNHM 56099. Iquitos: Vienna 97 a and b.
 Pampa Hermosa, near mouth of Rio Cushabatay, Ucayali River
 Valley: AMNH 56979. Sarayacu, Rio Ucayali: Paris 2449 (*A.*
transversalis type). Tepishca, Contamana Region, Ucayali River
 Valley: AMNH 56982. Utoquinia Region, Ucayali River Valley:
 AMNH 56981.

No precise locality. ANSP 13118.

Colombia

Vaupés. Ginogojé, Rio Apaporis: MCZ 53252.

Brasil

Amazonas. Santa Rita, Rio Solimões: ZMB 30964.

No precise locality. "Amazon": Paris 1820.

DISCUSSION

Anolis transversalis extends from the Upper Amazon to the
 Apaporis and the Ucayali and the neighborhood of the tributaries
 of the latter in the eastern foothills of the Andes. It is quite
 unknown in eastern Amazonia. Its restriction to the western part of
 the Amazonian region is paralleled by that of certain other common
 anoles belonging to quite different species groups, e.g. *A. scypheus*.

A. transversalis is apparently a green anole restricted to forests,
 and in the main area of Amazonia, in the Guianas, and in the
 coastal regions of east Brasil, a relative. *A. punctatus*—as close to
transversalis as any known anole, though perhaps not very close
 — is the common green anole of the forests. In the west, however,
A. punctatus in the Loreto region of Peru overlaps half of the
 range of *A. transversalis*, while *A. boulengeri*, a vicariant or
 subspecies of *punctatus*, differing from it only in having keeled
 rather than smooth ventrals, overlaps the other part in Ecuador
 and Colombia. (We shall discuss *punctatus* and *boulengeri* more
 fully at a later time).

The three ecologically similar, rather closely related² anoles
 — *transversalis*, *punctatus*, *boulengeri* — present an interesting
 geographic and biological puzzle.

1. Female with characteristic throat pattern but with male dorsal
 pattern.

2. Both adjectival phrases are deliberately vague. We simply do
 not know enough about either the ecology or the relationships of these
 species to be precise.

Anolis punctatus extends through the forests of eastern Brasil from S. Paulo northward, then probably skipping the belt of open formations that separates these forests from the Amazon, then in the Amazonian forests and up the Ucayali into the Amazonian portion of Bolivia. It extends north into all three of the Guianas. In this enormous area, though several names have been proposed, it shows only trivial variation. In the foothills of the Andes in Peru and in Ecuador and Colombia it intergrades with *boulengeri*.

Why in western Amazonia and not elsewhere should differentiation occur? Why here should there be a second species — equivalent in size and apparently quite similar in habits? How has this situation originated and how has it been maintained?

It is undoubtedly premature to attempt to trace the history of these species; there is much evidence — systematic, ecological, paleontological and geological — still to obtain. Yet it may be very useful to order our ideas now, the better to frame hypotheses that can be tested.

These are animals of the forests, and it is best to explain their history in terms of the history of forests. From this point of view it is important that tropical South America has, during the later Tertiary and especially the Pleistocene, experienced alternate wet and dry periods, the extremes in both directions going far beyond the conditions of the present¹. It is especially important that during the dry periods there is evidence of wet refugia on the eastern slopes of the Brazilian mountain belts and probably of the Andes. Disjunct areas of this sort would provide excellent theatres for geographic speciation.

Surely *transversalis* and *punctatus* began their separate histories in the disjunct forests of one of the dry periods. It is easiest to suppose that *transversalis* arose in west Amazonia north of the Amazon; this is its stronghold still. In what part of its present range *punctatus* may have arisen is less certain; we postulate only that it was allopatric to *transversalis*, hence south of the Amazon if in western Amazonia, but perhaps north of the river if in eastern Amazonia.

In some wet period *punctatus* then spread into the range of *transversalis*; it is obviously the more vagile species. The contact of the two stocks resulted in *punctatus* in a character divergence or displacement in the area of contact morphologically recognizable as the subspecies *boulengeri*.

Further events may now have been suspended by a dry period. However, with the next wet period — perhaps that just before the present — *punctatus* spread still further, occupying all the rest of its present range (then continuous forest). *Transversalis* at this time spread south of the Amazon and there was able to coexist with, without displacing or being displaced by, typical *punctatus*. (From this we may infer that *transversalis* in its contact with the population that became *boulengeri* was itself displaced so that it could accommodate to sympatry with any *punctatus* populations, even those of the typical race.)

1. We thank Aziz Nacib Ab'Saber, Universidade de São Paulo, for geomorphological information — some of it still unpublished — on Late Tertiary and Quaternary climates.

The final step of the history requires only the very recent dry period which broke the eastern range of *punctatus* into two parts.

This for us is the most probable story. It implies some relatively ancient events but implies also that much of the distribution of both *transversalis* and *punctatus* is extremely recent. This is an intriguing conclusion. It will be interesting to discover how much of the present distributions of South American vertebrates are very recent in their extension or restriction.

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