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THE GENUS *DRACAENA*, WITH A BRIEF CONSIDERATION OF MACROTEIID RELATIONSHIPS (SAURIA, TEIIDAE) (3)

P. E. VANZOLINI (1)
J. VALENCIA (2)

INTRODUCTION

One species of the genus *Dracaena* Daudin, 1802, of very large and strinkingly-looking, teiids, has been known since pre-Linnean days. Adequate descriptions of the genotype, *D. guianensis*, were available early in the nineteenth century. However, specimens of the second form, *D. paraguayensis*, were first reported as late as 1904, by Peracca, and even then under the erroneous assumption that they belonged to *guianensis*. No comparative study has been published; the only good modern figures of *guianensis* are habitus and ethological ones, and no figures of *paraguayensis* have come to our attention.

It seems to us that the genus deserves a better treatment than so far it has received. Not only the habits are very peculiar (Vanzolini, 1961) and apparently related to striking morphological adaptations, but the relationships between the two known forms are very interesting because of their geographical distribution. Having had access to both forms, it seemed to us worthwhile to present detailed descriptions, illustrations and comparisons, as well as some pertinent comments. This has necessitated a brief excursion into the general systematics of the macroteiids, for which the senior author is responsible.

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(1) Departamento de Zoologia, Secretaria da Agricultura do Estado de São Paulo, Brasil.

(2) Departamento de Anatomía, Universidade Católica, Santiago, Chile. At the time of preparing this paper, on a Fellowship of the "Associação de Defesa da Flora e da Fauna", São Paulo.

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sidade de São Paulo; dr. C. M. Bogert, American Museum of Natural History, New York; Miss Alice G. C. Grandison, British Museum (Natural History); and to the authorities of the Instituto e Museo di Zoologia, Universitá di Torino, Italia.

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LITERATURE

The history of *D. guianensis* Daudin, 1802, far antedates the publication of this first nomenclatorially valid name.

There are many references by pre-Linnean authors (e.g. Seba, Wormius), but it seems that a great deal of confusion existed between *Dracaena* and *Varanus*, doubtless due to the presence of molariform teeth and of a double tail crest in both genera. Thus, Lacepède (1788:243,245) states that Seba had a *Dracaena;* Shaw's figure (1802: 218, pl. 67), specifically said to be a copy of Seba's, shows that this belongs to a *Varanus*, probably *V. bengalensis*, as said by Duméril & Bibron (1839: 55).

One single specimen is cited in all the literature before Boulenger's Catalogue (1885). It was in the Paris Museum, then "Cabinet du Roy", a skin sent from Cayenne by Delaborde, who also provided interesting ecological data. It was first described and figured, under the vernacular name "La Dragonne", by Lacepède (1788). The description is relatively good, but the two figures, one of the animal at rest, and a smaller one climbing a tree trunk, drawn by de la Seve and engraved by Haussard, are very poor. These figures were subsequently copied several times.

Bonnaterre (1789: 36, pl. 3: 2-3) repeated Lacepède's data, mentioning the same specimen and reproducing the figures, but omitting the names of painter and engraver. He still adhered to the vernacular "Dragonne".

Shaw (1802) reproduced again Lacepède's data, adopting a mistaken name, *Lacerta bicarinata* L.; his references, however, to the Paris specimen and to Delaborde's notes, are unambiguous. As noted above, his figure is that of a *Varanus*.

Daudin (1802: 421, pl. 28) first gave an acceptable binominal to the species; his description is good, but the figure is only a copy of Lacepède's resting specimen. De la Seve is credited with the drawing, but the engraver was Hubert.

Cuvier (1817: 26) gave an adequate diagnosis, under the vernacular "Dragonne" and was the first to remove the genus from the crocodilians to the lizards. Undoubtedly he had seen the old Paris specimen. Duvernoy (1836-49: 40, pl. 10 bis) simply repeated Cuvier's diagnosis but gave fine figures: a colored painting of the whole specimen, a palatal view of the skull and a lingual view of the mandible.

Duméril & Bibron (1839: 51 *seq.*) gave an exhaustive and (for them) unusually to-the-point description of the same specimen, besides an excelent historical resumé. They adopted the generic name *Thorictes*, an amendment of *Thorictis*

Wagler, 1830, created because *Dracaena* was thought to be preoccupied by a plant name. Finally Duméril & Duméril (1851: 111) simply mentioned again the type specimen in their catalogue of the Paris collection.

Griffith & Pidgeon, in the former's edition of Cuvier's Animal Kingdom (1831: 203, pl.) state that they used a specimen in the British Museum to describe and figure the form, which they called *Ada guianensis*, after Gray (1825). In the "Synopsis" appended to that book, Gray (1831: 28) assembled *D. guianensis* and *Crocodilurus lacertinus* in the subgenus *Ada* of the inclusive genus *Teius*. Gray himself does not mention a British Museum specimen, either in the "Synopsis", or in the "Catalogue" (1845), in which he raises *Ada* to full generic rank, for the only species *guianensis*. Miss Alice G. C. Grandison was kind enough to inform us that there are no records of the specimen allegedly seen by Griffith & Pidgeon.

There is also, in this early period, a number of wholly nomenclatorial references. Thus Oppel (1811: 34-35), in his classification, diagnosed the genus *Dracaena*, monotypic, with the only species *gujanensis*. Merrem (1820: 62) repeated older data, using the name *Teius crocodilinus*, but not giving any reason for the change. Fitzinger (1826: 21-22) remarked that *Dracaena* was preoccupied by a plant name, and preferred *Crocodilurus* Spix, a sounder nomenclatorial expression of Gray's (1825) concept. Wagler made the same remark (1830: 153), and proposed a new name, *Thorictis dracaena*, listing as synonyms several specific names, beginning inadequately with *Lacerta bicarinata* Linné. Wagler's change was accepted by Duméril & Bibron *(supra)* and by Fitzinger (1843: 20), who adopted *Thorictis dracaena*.

The treatment which summed up the past and afforded, as usual, a firm basis for subsequent work was Boulenger's (1885: 337-339), with an adequate description of *D. guianensis*, based on 4 specimens of both sexes, including one half-grown.

Goeldi (1902: 541) gave a color description and some ecological notes of the animal in Pará.

Peracca (1904: 2) was the first herpetologist to mention specimens from the Paraguay basin. The statement, if one takes into account his usual accumen, is a very confusing one:

"Due femmine adulte di Carandasinho (Mato Grosso).

Uno degli esemplari é perfettamente normale e corrisponde esattamente alle descrizioni. Il secondo exemplare presenta una curiosa anomalia, assai rara nei Teiidi, consistente nella divisione presso a poco simmetrica della maggior parte degli scudi cefalici.

Io ho avuto recentemente occasione di esaminare gli esemplari del Museo Britannico di Storia Naturale e potei constatare che le Dracene del bacino del Paraguay non differiscono affato delle Dracene finora esclusivamente trovate nel bacino delle Amazzoni e nella Guiana".

This very definite statement, from such a competent herpetologist as Peracca, proved very difficult to interpret. We obtained photographs of the actual specimens (Plate II, figs. 3-4), through the courtesy of the Director of the Zoological Museum of the University of Torino; they are clearly recognizable as *D. paraguayensis.*

Burt & Burt (1930: 32) cited one specimen of *D. guianensis* in the U. S. National Museum, with no more definite locality than "South America"; this is to us a doubtful reference, as the Burts were not able to discern the two forms in the American Museum collection (see below). They also mistakenly cited as type – locality the "Saint-François River, Brazil".

This error – which is curious in view of the repeated mentions of Delaborde's specimen in the literature — is certainly due to a misunderstanding of the older authors, who used to cite, as a synonym of "La Dragonne", a lizard, the "Ignarucu", described by travelers as inhabiting the Rio São Francisco, "Saint-François" in French. Amaral (1950: 282) has remarked that this is a misspelling of "Iguanuçu", and believed the animal to be actually a *Dracaena.* This is probably the reason why he cites (1937: 189) the species for northeastern Brasil; we were unable to find any references to actual specimens south of Pará; one of us (PEV) has seen skins in São Luis, Maranhão. We find *Iguana* a more probable guess, as it is common in the São Francisco valley.

In their following paper, Burt & Burt (1931: 330) mentioned nine specimens of *guianensis*, eight obtained from zoological gardens, and one from Mato Grosso (Leo Miller leg.); the latter is actually *paraguayensis* (C. M. Bogert, personal communication). They still adhered to the error in the type-locality, which was further maintained in the Check-List (1933: 61).

Crawford (1931: 23) mentioned *D. guianensis* (with a short diagnosis) in a key to the lizards of British Guiana, as did Amaral in his list of the lizards of Brasil (1937: 189) and of the state of Pará (1949: 111). In 1950 Amaral described *D. paraguayensis,* on 3 Mato Grosso specimens, founding the species on the type of head scutellation and on the number of abdominal scale rows.

Conant (1955) presented some extremely fine pictures of *guianensis* feeding on snails. Several authors referred in abridged or semi-popular accounts to the lizard's appearance and mode of feeding. Thus, Buddenbrock (1956: 395) and Oliver (1951). Vanzolini (1961) commented on the color pattern and behaviour of zoo specimens kept in Pará in quasi-natural conditions, and on the habitat of the species in the island Marajó. Finally, Cunha (1961) presented a description, from the literature, of *guianensis.*

Dracaena Daudin, 1802

Dracaena Daudin, 1802: 421. Type species *D. guianensis* Daudin, 1802, monobasic.

Dracaena, Oppel, 1811: 34.

Teius (*part.*) Merrem, 1820: 60. Type species *Lacerta teyou* Daudin, 1802 (= *Teius viridis* Merrem) by tautonimy.

Ada Gray, 1825 (not seen).

Crocodilurus (not of Spix), Fitzinger, 1826: 21-22.

Thorictis Wagler, 1830: 153. Type species *Dracaena guianensis* Daudin, 1802 (= *Lacerta bicarinata,* not of Linné, Wagler, *loc. cit., in errore*).

Teius (*Ada*) (*part.*) Gray, 1831: 28. Type species not indicated.
Thorictes, Duméril & Bibron, 1839: 51.
Thorictis, Fitzinger, 1843: 20.
Ada, Gray, 1845: 25.
Dracaena, Boulenger, 1885: 337. Burt & Burt, 1933: 61. Amaral, 1937: 189.

DIAGNOSIS

Large macroteiids, snout to vent length reaching 45 cm. Limbs well developed, strong, with five clawed digits. Dorsal lepidosis heterogeneous, with small scales and large tubercles. Ventral scales with low keels. Tail one and half times as long as the body (Graph 1), laterally compressed, with flat upper surface bounded on each side by one crest. Dorsal and ventral scales with lenticular sense organs. "Cushion" scales on limbs. Fingers laterally compressed, with rows of small keeled scales on the palmar surface. Tall prismatic scales on plantar surface of toes. Abdominal and femoral pores. Anterior teeth chisel-like to conical, changing posteriorly into broad molariforms with basis embedded into a lattice-work of bone.

HABITS

Dracaena guianensis has been known, since the very beginning of herpetology, to be a shell crusher. Delaborde, in the notes that accompanied the type specimen, remarked that it was a swamp dweller. Goeldi (1902) noted its occurrence in the swampy areas of the island Marajó, at the mouth of the Amazonas. One of his captive specimens accepted chopped fish, after a rather long period of fasting. In the same island of Marajó one of us (Vanzolini, 1961) obtained the species; the habitat is in fact swamp sparsely covered with low trees and bushes, and it is remarkable that the lizard feeds in the water, on shells, but spends most of its time on low trees. The color pattern is procryptic for both situations. Vanzolini photographed captive specimens kept in conditions very much resembling natural ones.

Dracaena paraguayensis apparently has the same habits, as stated by Amaral (1950) and as we have heard from persons who have seen it in nature in the "pantanais" of the Paraguay valley. Actually, the physiognomy of the latter region very closely resembles that of Marajó.

In describing the two forms of *Dracaena* we'll start with *D. paraguayensis*, apparently more primitive, in the sense of more closely approaching the norm of the macroteiid group of genera. Since both forms are very similar, *guianensis* will be described in terms of differences from *paraguayensis*.

Dracaena paraguayensis Amaral, 1950

Plate I: 2. Plate II: 2-4. Plate III: 1,4. Plate V: 1-5.

Dracaena guianensis, not of Daudin, Peracca, 1904: 2; two specimens from Carandásinho, Mato Grosso (Borelli), Torino Museum.

Dracaena guianensis (*part.*), Burt & Burt, 1931: 330; one specimen from Mato Grosso (Leo Miller), American Museum of Natural History.

Dracaena paraguayensis Amaral, 1950: 283; type from São Lourenço, Mato Grosso, Faculdade de Filosofia, Ciencias e Letras, Universidade de São Paulo; paratypes from Carandazal and Corumbá, Mato Grosso, Instituto Butantan.

DIAGNOSIS

No post-nasals: naso-frontal in contact with upper nasals (Plate II, figs. 2-4). Parieto-temporal edge formed by a series of regular scales (Plate III, fig. 4) Two pairs of enlarged gulars in contact on the midline (Plate III, fig. 1). Body tubercles in rather regular longitudinal and especially transverse rows (Plate I, fig. 2; Plate IV, fig. 1). Thirty four to thirty nine transverse rows of ventrals.

DESCRIPTION

Head (Plates II, fig. 2-4; III, 1, 4) pyramid-shaped, with plane top and sides. Canthus rostralis distinct but rounded, continuing into a sharp superciliary edge, which also continues backwards, as an obtuse edge, to the level of the tympanum, which is round. Nostrils superior, not valvular.

Rostral high, rounded, visible from above, frequently broken at the lower corners. Nasals double; the superior in contact with its fellow on the midline; nostril on the (rather irregular) suture between upper and lower nasals; upper nasal in contact with the rostral, with the anterior corner of the first labial, and with the fronto-nasal; lower nasal in contact with the first and second labials, with the frontonasal (narrowly) and with the anterior loreal. Frontonasal large, hexagonal, variable. Two transverse rows of prefrontals; the anterior one formed by two large scales, meeting laterally the loreals and the upper preocular; the posterior row of prefrontals has four scales, the outermost of which practically belongs to the supraocular series; the two median scales are squarish. Frontal large, roughly hexagonal. Two fronto-parietals. Parietals and inter-parietal very irregular, with a tendency toward splitting. Occipital region with two rows of irregular polygonal scales showing splittings and fusions; they are separated from the temporo-parietal series by small and irregular scales. Supra-ocular series with four scales (outer prefrontal not included), decreasing backwards; sometimes a small fifth scale, poorly differentiated. Small irregular scales between the large median head scales and the supra-oculars.

Canthus rostralis following the internasal suture and then the suture between the scales on the top and side of the snout. Superciliary series numerous, in two longitudinal rows, whose suture forms the supercilium. Behind this a series of 4 large scales, forming the rounded parieto-temporal edge. Six large upper labials, squarish, reaching the vertical of the middle of the eye. From this point backwards a series of small scales progressively less differentiated. Two large polygonal loreals, higher than long. Infraorbital semicircle formed by largest scales inferiorly, where it meets the labial series; in front separated from the loreals and prefrontals by small scales, which might be termed preoculars. Eyelid scaly. Between the loreals, labials and the infraorbital semicircle, an area of irregular scales, with an upper patch of smaller and a lower series of larger elements. Temporal region with irregular polygonal scales, larger behind. Border of tympanum well-differentiated in front, much less so behind.

Symphysial small, anvil-shaped, separated by a straight transversal suture from a large, pentagonal post-symphysial. On each side, starting on the lateral sutures of the symphysial, a deep groove, covered with small scales, almost granular anteriorly. Lateral to this sulcus, the infralabial series, with ten scales, the fourth and fifth largest, decreasing posteriorly; this series diverges backwards from the sulcus, from which it is separated by, successively, one, two and three rows of small scales. Median to the groove, a "V" of enlarged gulars with the post-symphysial at the vertex; the scales of the first two pairs meet on the midline. The space between the two branches of the "V" is filled with flat polygonal scales; these are larger on the sides; towards the throat they become progressively arranged into more or less regular transversal rows of sub-hexagonal scales. A very definite sulcus, lined with granules, uniting the angles of the mandible and extending obliquely to the back edge of the ear. Gular region with polygonal scales, smooth, imbricate; a second sulcus, revetted with small granules, at the level of the tympanum; a pronounced sub-cervical fold, and another, very broad ("collar"), at the height of the shoulder girdle.

Back (Plate I, fig. 2; IV, 1) with large striated tubercles and small scales. On the neck the tubercles are flattened, interspersed with smaller tubercles and granules.

The dorsal tubercles are arranged into transverse rows, fifteen between limbs. These are separated by one (often locally or completely duplicated) row of small narrow scales, irregular in length, shape and degree of keeling. Similar scales, some of them sub-tubercular, separate the tubercles of the same row, 2-3 scales to a tubercle. These are elongate, keeled, ending behind into a point, blunter on the anterior half of the body. In a very large specimen the tubercles are flattened, oval, but still keeled, striated and pointed.

There are four to six dorsal tubercles on each side of the midline, which remains free of them. They are loosely arranged into four to six longitudinal rows, the two median ones joining each other at the root of the tail.

The flanks are covered with irregular, sub-imbricate scales. On the depression into which fits the adpressed forelimb there is a series of arcuate folds, sub-parallel, irregularly spaced.

Belly with regular transverse rows of low-keeled scales; on the breast they are one and one-half times as long as wide; further back they become narrower, with rounded or obtusely pointed hind margin. Scales on the lower belly smaller; a broad patch of preanal scales. Thirty-four to thirty-nine rows of ventrals anterior to the preanals.

Antero-dorsal aspect of forelimb with leaf-shaped keeled scales; they are very thick, resting on and separated by soft granules, which form a sort of cushion. Ventral aspect of arm, fore-arm and hand with similar but smaller, keelless, "cushion" scales.

Scalation of fingers rather complex. One single dorsal row of thick and very convex scales. Sides of fingers high, with two rows of small irregular scales, reducing to one row near the tip. Palmar surface with transverse rows of 4 to 6 small, sharply-pointed scales, the row away from the axis of the hand largest, especially on the pollex, whose proximal scales are very thick. Distally the volar elements become fused, only the central one remaining separate, as a sharp leaf-point at the base of the claw.

Scalation of thigh (Plate V, fig. 1), leg and tarsus similar to that of the forelimb. Dorsally the toes show irregular proximal elements, the distal ones becoming similar to those of the fingers. Scalation of sides and plantar surface of toes (Plate V, fig. 3) similar to that of fingers, but the enlarged lateral rows are enormously thick, especially on toes I to IV, where the scales are actually prismatic, forming a tall serrated palisade.

Tail with flat upper surface, laterally bounded by a continuous serrated crest, which continues the longitudinal tubercle rows of the back. Sides of tail (Plate V, fig. 2) with long narrow keeled scales, alternately one and two to each crest tubercle. Ventrally the scales are similar to the laterals, but larger (one row to each tubercle) and with sharper keels.

All scales and tubercles of the dorsal surface of head, trunk, limbs and tail with sense organs. On the head they are lens-shaped, surrounded by more or less distinct areolae; their number per scale varies from a dozen upwards. On the dorsal elements they are apical, prominent, and agree rather well with Scortecci's (1937, 1940) "lenticels". Similar organs are found on the ventral surface (Plate V, fig. 4), from the gulars to approximately the tenth subcaudal row; they are almost always close to the hind edge of the scale, approximately on the midline.

On each side a series of 2 to 4 small femoral pores, continuing along the antero-lateral margin of the pre-anal patch on a series of 4 larger, abdominal, pores.

Alcoholic specimens are dorsally dark reddish brown with lighter head and tubercles. The ventral surfaces are dirty yellow, with dark mottlings. The tail is more or less distinctly barred. These data lead to believe the color in life to be similar to that described by Vanzolini (1961) for *guianensis*.

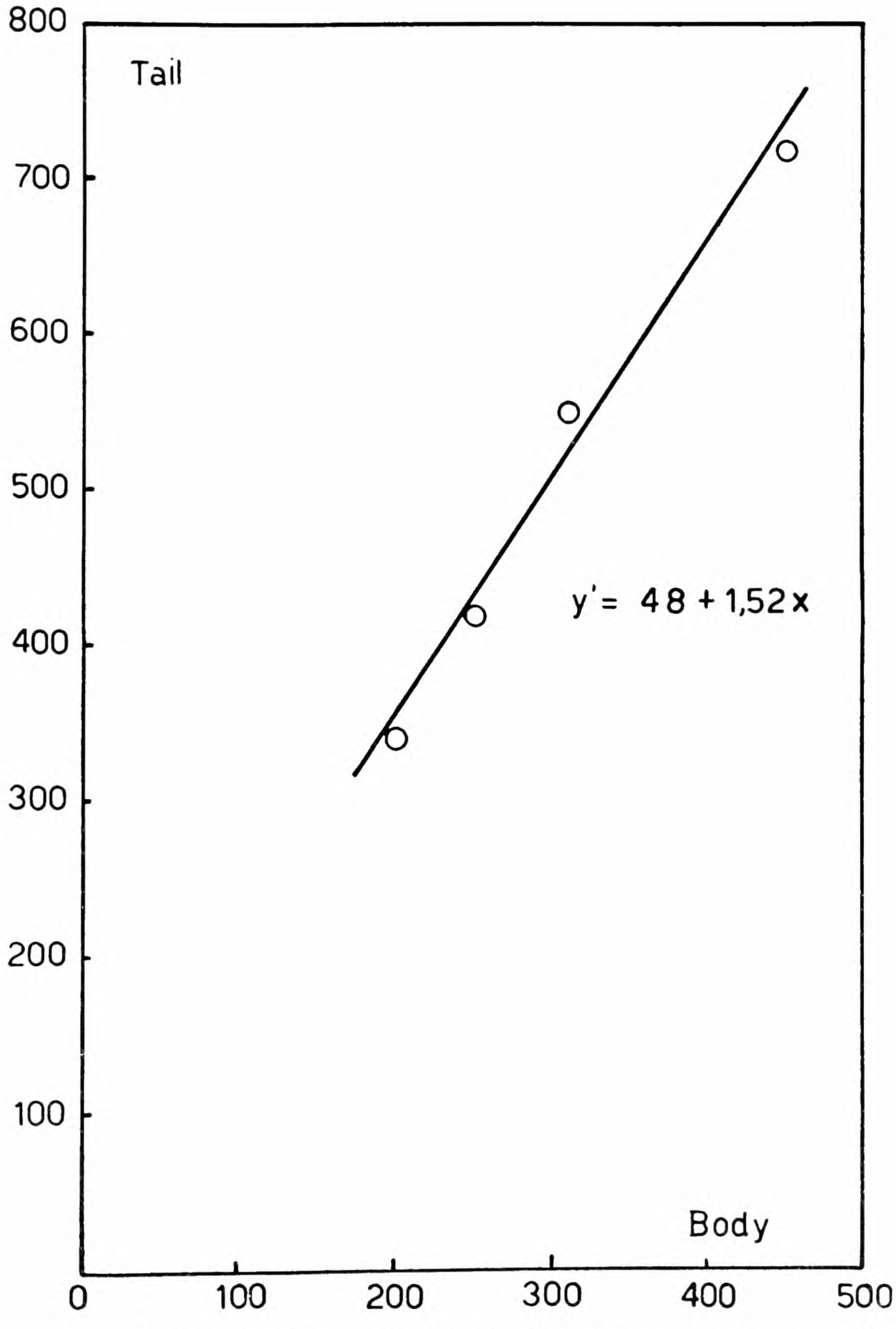
SPECIMENS SEEN

Type, ♀, São Lourenço, Mato Grosso, 270 + *x* mm (broken tail), ventrals 34. In the collection of the Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo.

Instituto Butantan 689, paratype, ♂, Carandazal, Mato Grosso, 250 + 420 mm, ventrals 36.

Instituto Butantan 506, paratype, ♀, Corumbá, Mato Grosso, 210 + *x* mm, ventrals 37.

Departamento de Zoologia 8386, ♀, Rondonópolis, Mato Grosso, 450 + 720 mm, ventrals 39.



Graph 1. Regression of tail length on body length; measurements in millimeters, both species combined. Standard deviation of *a* 45.9 (not significant at the 5% level); of *b* 0.15 (significant at the 1% level).

Dracaena guianensis Daudin, 1802

Plate I: I. Plate II: 1. Plate III: 2. Plate IV: 2.
Plate V: 7.

"La Dragonne", Lacepède, 1788: 243, pl. 16; one specimen from Cayenne (Delaborde), Paris Museum; Bonnaterre, 1789: 36, pl. 3: 2-3; same specimen.

Lacerta bicarinata, not of Linné, Shaw, 1802: 218, pl. 67. After Seba (? Surinam).

Dracaena guianensis Daudin, 1802: 421, pl. 28. One specimen from Cayenne (see "La Dragonne" above). Oppel, 1811: 35; mention.

Teius crocodilinus Merrem, 1820: 62.

Ada guianensis Gray, 1825 (not seen).

Crocodilurus guianensis, Fitzinger, 1826: 21.

Thorictis dracaena Wagler, 1830: 153. New name.

Ada guianensis, Griffith & Pidgeon, 1831: 203, pl.

Teius (Ada) guianensis, Gray, 1831: 29.

Thorictes dracaena Duméril & Bibron, 1839: 56; type described. Duvernoy, 1836-49: 40, pl. 10 bis: 2 a-b; figures presumably of type (dentition).

Thorictis dracaena, Fitzinger, 1834: 20.

Ada guianensis, Gray, 1845: 25

Thorictes dracaena, Duméril & Duméril, 1851: 111

Dracaena guianensis, Boulenger, 1885: 337; specimens from Santarem (state of Pará), Upper Amazons and Cashiboya (Peru), British Museum. Goeldi, 1902: 541; ecological notes, Pará. Burt & Burt, 1930: 32; one specimen, no locality, United States National Museum.

Dracaena guianensis, part., Burt & Burt, 1931: 330; 8 specimens, no locality, American Museum of Natural History.

Dracaena guianensis, Crawford, 1931: 23; mention for British Guiana. Burt & Burt, 1933: 61; check-list, South America. Amaral, 1937: 167; check-list, Brasil. Amaral, 1949: 111; check-list, state of Pará. Oliver, 1951: 151, photos; zoo specimen. Conant, 1955: no page, note on feeding, photos, zoo specimen. Buddenbrock, 1956: 395; mention of mode of feeding. Vanzolini, 1961: 237; bionomy of zoo specimens, Pará; description of Marajó specimens, Dept. Zoologia, São Paulo. Cunha, 1961: 106; mention for Brasilian Amazonia.

DIAGNOSIS

One pair of post-nasals (Plate II, fig. 1). Parieto-temporal edge following the sutures between two series of scales (Plate III, fig. 3). Three pairs of enlarged gulars in contact on the midline (Plate III, fig. 2). Body tubercles irregularly arranged (Plate I, fig. 1; IV, 2). Thirty-two or thirty-three transverse rows of ventrals.

DESCRIPTION

As noted above, we will describe this species with reference to *paraguayensis.* The head (Plate II, fig. 1; III, 2-3) is relatively shorter; its scutellation shows great differences, especially on the top of the snout. There is no large single fronto-nasal; instead, the nasals are met posteriorly by a pair of regular scales. The frontal is placed much forward and sometimes irregularly divided transversely; between it and the pair of post-nasals there is one single central scale, six or seven-sided, which seems to correspond to the frontonasal of *paraguayensis.* On either side of this scale one pair of anterior scales, joining anteriorly the post-nasals and laterally the anterior loreals; these should correspond to the two large anterior prefrontals of *paraguayensis*. Behind them two oblique scales, embracing the anterior edges of the frontal, each followed latero-posteriorly by one scale in continuation with the supra-ocular series; these four scales must be homologous to the second row of prefrontals of *paraguayensis*. The remainder of the top of the head is very much as in the former species. A difference is noted in the supraocular series, whose second scale is very short. In general, the sutures of *guianensis* are much more regular. On the sides of the head there are smaller differences: the anterior loreal is smaller; the anterior half of the infraorbital semi-circle is almost straight; the parieto-temporal edge is not formed by a regular series of scales, but by irregular elements. On the gular region there are three instead of two pairs of enlarged gulars in contact on the middle.

The dorsal tubercles (Plate I, fig. 1; IV, 2) are fewer, flatter, more widely separated; the transverse rows, which are much less regular, are separated at most by a series of granules.

SPECIMENS SEEN

Departamento de Zoologia 7285, ♀, Igarapé Taperebá, Ilha de Marajó, Pará, 200 + 340 mm, ventrals 33.

Departamento de Zoologia 7286, ♀, Igarapé Santa Quitéria, Ilha de Marajó, Pará, 310 + 550 mm, ventrals 32.

INTRA-GENERIC RELATIONSHIPS IN DRACAENA

The question of whether the two forms of *Dracaena* are full species or subspecies must be examined both from the morphological and the geographical angles.

From the morphological viewpoint, the more important differences are found in the scutellation of the head, back and belly.

A first major cephalic difference is the presence in *guianensis* of a pair of dorsal postnasals, with consequent major modifications of the scales of the anterior portion of the top of the head. Then, still on the dorsal norm, there is the matter of the narrow, band-like second supra-orbital of *guianensis*. The condition of the edge between the top and side of the head in the temporal region also differs in the two forms. In general the upper head scutes of *paraguayensis* are more variable.

In the gular region *guianensis* has 3 pars of post-symphysials in contact on the midline, against 2 of *paraguayensis*.

The transverse rows of dorsal tubercles and scales are much more regular in *paraguayensis*.

Finally, there is a difference in the number of transverse ventral rows: 32-33 in *guianensis* and 34-39 in *paraguayensis*.

In the acknowledgedly few specimens seen there are no intermediate conditions. However, one must accept the fact that the differences are, with exception of the dorsal topography of the snout, rather trivial and such as usually seen in geographical races of lizards.

Even in the case of the snout differences, although they are rather drastic, it is not impossible to imagine intermediate steps leading smoothly from the *paraguayensis* to the *guianensis* condition. The series of transformations would begin with a transverse splitting of the upper nasals, the posterior pair becoming large and pushing back the scales of the prefrontal region, which would need to get reorganized.

In our opinion, the cephalic scutellation of *paraguayensis* and the more regular arrangement of its dorsal rows of tubercles and scales are decidedly primitive in contrast with the conditions of *guianensis*.

As for the geographical argument, the area of *D. guianensis* (Map) is extremely wide. It reaches the Atlantic coast from the Guianas to Maranhão; inland it extends to the Upper Amazonas and middle Ucayali.

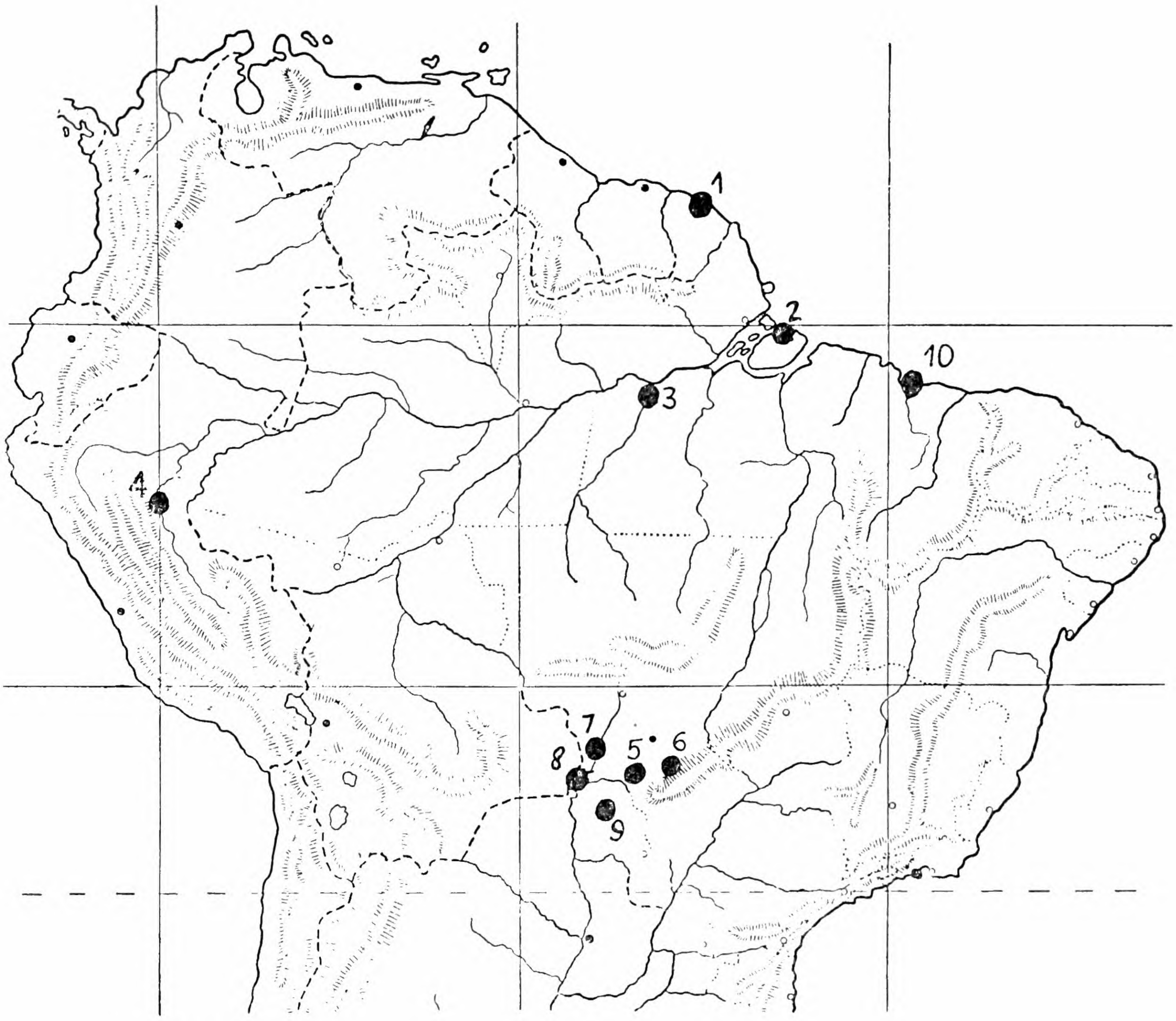
The presently known area of *paraguayensis* is much smaller. All localities are in the seasonally-flooded "pantanais" of the Upper Paraguay.

There is a very broad gap between the two areas. If we accept the premise that *Dracaena* needs a swamp-like environment, it becomes at once apparent that the upper courses of the Centro-Brasilian tributaries of the Amazonas (Tapajós, Xingu and Tocantins-Araguaia) do not offer ideal conditions to the genus. These rivers flow amongst gallery forests encroached upon by dry savanna-like "cerrados". The region between the Cuiabá plain (northernmost locality of *paraguayensis*) and the head waters of the Amazonian tributaries is a dry rolling cerrado.

On the western side of the range conditions are presumably better for geographical continuity. There is a belt of lowlands between the Guaporé (second-order tributary of the Madeira) and the Upper Paraguay.

Thus, while there is no actual evidence indicating that the two forms are races of a same species, the possibility cannot at present be ruled out.

In any case, they are allopatric and, although unmistakably related, well-differentiated. It seems certain that *paraguayensis* is the more primitive form — closer to the macroteiid norm. It seems worthwhile noting that the more primitive form has a narrower, extra-Amazonian distribution, while the more specialized one is widely distributed throughout the Guiano-Amazonian region. We have encountered this same pattern of distribution in *Amphisbaena fuliginosa* (Vanzolini, 1951) and in the gekkonid genus *Coleodactylus* (Vanzolini, 1957).



Localities of *D. guianensis:* 1, Cayenne. 2, Igarapés Taperebá and Santa Quitéria (northern coast of Marajó). 3, Santarem (lower Tapajós). 4, Cashiboya (middle Ucayali).

Localities of *D. paraguayensis*: 5, S. Lourenço region. 6, Rondonópolis. 7, Carandásinho. 8, Corumbá. 9, Carandazal.

Possible locality of *D. guianensis:* 10, S. Luis.

RELATIONSHIPS OF THE GENUS

Dracaena belongs among the macroteiids, a formally undefined but very convenient term which has crept into the literature, as applied to group A of Boulenger's key to the family in his Catalogue (1885). Nine genera are usually included in this assemblage: *Cnemidophorus, Ameiva, Teius, Kentropyx, Dicrodon, Callopistes, Crocodilurus, Tupinambis* and *Dracaena.*

Our notes on the group are founded on the following materials:

Ameiva ameiva, numerous specimens from all the range. *A. auberi,* 1 specimen from Cuba. *A. b. bifrontata* and *A. b. divisa,* several specimens from Venezuela, Colombia, Peru and Brasil. *A. dorsalis*, 3 specimens from Jamaica. *A. edracantha*, several specimens from Ecuador and Peru. *A. festiva*, 1 specimen from Nicaragua. *A. septemlineata*, several specimens from Ecuador. *A. lacertoides*, several specimens from Uruguay and Brasil.

Milstead (1961) places the latter form in the genus *Cnemidophorus*. Actually, the shape of the tongue seems to be intermediate between *Cnemidophorus* and *Ameiva*. The other characters cited by Milstead are not relevant.

Callopistes maculatus: several Chilean examples.

Cnemidophorus murinus, 1 specimen from Surinam. *C. l. lemniscatus*, many specimens from all the range; *C. l. nigricolor*, 1 specimen from Los Roques. *C. ocellifer*, many specimens from all the range. *C. sexlineatus*, several specimens from the southern United States.

Crocodilurus lacertinus, 3 specimens from Pará.

Dicrodon heterolepis, 1 specimen from Peru. *D. guttulatum*, 1 paratype of *D. barbouri*.

Kentropyx: at the present time we do not wish to attach names to our specimens of this genus; we have seen abundant materials from all the range but Argentina.

Teius teyou, many specimens of both races, *teyou* and *cyanogaster*, from Uruguay, Brasil and Bolivia.

Tupinambis nigropunctatus and *T. teguixin*, many Brasilian examples, from all the range. *T. rufescens*, one stuffed specimen.

With regard to the forms not or insufficiently represented in the collections of the Departamento de Zoologia, we had recourse to the literature, as follows:

Ameiva: Barbour & Noble's (1915) revision, in spite of many obvious mistakes, contains sufficient information for our purposes. Boulenger (1885) has data on *A. multilineata*. Burt's (1931) revision was used for *Cnemidophorus*, supplemented by Smith's (1946) handbook.

Data on *Callopistes flavipunctatus* were gotten from the original description (Duméril & Bibron, 1839: 72, pl. 51) and from that of its synonym *Tejovaranus brannickii* Steindachner, 1878.

On *Dicrodon holmbergi*, Schmidt's (1957) original description.

Gallardo (1962) has recently described a new species, *Kentropyx lagartija*, from Argentina, which we have not seen.

Additional data on *Tupinambis rufescens* were taken from Boulenger (1885: 335) and especially from Günther's (1885) fine figures. *T. duséni* remains to us an enigmatical form, which we prefer not to comment at the present time.

In the following notes species are not cited individually unless there is significant intra-generic variation. Of course the published information on the forms we have not seen is not always complete, and thus a certain degree of omission should be expected.

We have prepared a table summarizing the argument, which faces page 30 and may be unfolded in order to be constantly available while reading.

DISTRIBUTION

The macroteiids are a typically South American group, and several of the genera are very widely distributed in the continent, two of them extending beyond its limits.

Cnemidophorus ranges from Wisconsin in the United States to the 15th parallel in Brasil. It seems, however, to be absent from western Amazonia.

Ameiva does not reach beyond Tamaulipas in Mexico to the north; it is, however, widely distributed throughout the West Indies and the Bahamas and goes as far south as Mendoza in western and Bahia Blanca in eastern Argentina.

Tupinambis, *Kentropyx* and *Dracaena* extend from the Guianas south: the first to Mendoza, the second to Tucuman and the latter to southern Mato Grosso.

Crocodilurus is limited to the Guiano-Amazonian region. *Teius* is a southern enclave (Province of Buenos Aires to eastern Bolivia) in the territory of *Ameiva* Finally, *Callopistes* and *Dicrodon* are trans-Andean; the former extends from Peru into central Chile and the latter from Ecuador into Peru.

With regard to habitat, *Dracaena* lives in swampy regions, feeding on mollusks and spending much of its time on low trees (Vanzolini, 1961). *Crocodilurus* prefers small rivers ("igarapés"), swimming very well and digging extensive burrows in the muddy banks (Goeldi, 1902).

Cnemidophorus, *Ameiva*, *Teius*, *Tupinambis* and *Callopistes* are terricolous and prefer open country; even in the Amazonian forest they are found along trails, in clearings and other exposed situations. They use existing burrows or dig their own. *Dicrodon* (Holmberg, 1957), lives in burrows in the sand.

The southern forms of *Kentropyx* are also terricolous, open-country lizards. With regard to the northern forms, there is some doubt. Beebe (1945) has found both *K. calcarata* and *intermedia* in the jungle; one of us (PEV) has collected one specimen in the dense forest of the Acre. On the other hand, *Kentropyx* was quite common in open country in the island Marajó, in the same habitat as *Ameiva*, at the edge of the swamp where *Dracaena* was collected.

HEAD SCUTELLATION

There is a general pattern of upper head scalation from which few forms deviate. The rostral is high and pointed, partly (as an anomaly, completely) separating the nasals. These meet on the midline; there is no internasal. Behind the nasals are found one fronto-nasal, an arched prefrontal series, a frontal, a pair of fronto-parietals and a parietal group of usually 3 scales, surrounded by granules.

In *Callopistes flavipunctatus* there is no regular pattern of enlarged scutes; the scalation resembles that of the iguanids. In *C. maculatus* the parieto-occipital region is as in the remainder of the genus, but the anterior part is disorganized as in *flavipunctatus.*

In *Dracaena guianensis* there is one pair of scales between the upper nasals and the prefrontals, a unique character.

The ventral aspect of the head presents a series of interesting features. The limit between throat and chest is always marked by a strong skin fold. In *Kentropyx* there is a single row (a "collar") of prominent scales; in all other genera the fold is formed by a narrow granular area between two patches of enlarged flat scales.

In all genera but *Kentropyx* there is another, almost identical fold, halfway between the posterior one and the level of the tympanum.

These two folds are all that is found in *Cnemidophorus, Teius, Ameiva* and *Dicrodon.* In *Callopistes* and *Crocodilurus* there is one sulcus (not quite a fold, but a row of granules) between the tympani. This row is lacking in *Tupinambis,* which has, however, a similar one uniting the angles of the lower jaw. Finally, in *Dracaena,* both latter sulci are present.

DORSAL SCALES

The dorsal lepidosis is composed of more or less irregular rows of small, pointed granules in *Cnemidophorus, Ameiva,* and *Teius.* In *Callopistes* and *Dicrodon* the granules are relatively larger, flattened and arranged in more regular transverse rows. In at least one species of the latter genus *(heterolepis)* the granules grow in size posteriorly, the transition to the large dorsal caudals being smooth. In *Tupinambis* one observes the transition from oval flattened large granules to rectangular scales. In *Crocodilurus* there are regular transverse rows of small rectangular, keeled, mucronate scales. In *Dracaena* are seen the characteristic tubercles; the intervening scales resemble those of *Crocodilurus,* but in the latter genus there are no apical sense organs.

Some forms of *Kentropyx* have dorsal granules similar to those of *Ameiva.* Others are distinctly specialized in having sharply dimorphic dorsal scutellation, with granules and large keeled scales in different longitudinal arrangements.

VENTRAL SCALES

The ventrals are squarish or rectangular in all genera but *Kentropyx,* where they are phylloid, sharply keeled.

They are arranged in transverse and longitudinal rows.

The transverse rows are regular in all forms. Immediately behind the collar they are arcuate or actually V-shaped, but can be counted. The posterior limit is always clear, being the anterior edge of the preanal patch.

The longitudinal rows are also definite in *Cnemidophorus*, *Dicrodon*, *Kentropyx*, *Teius* and *Ameiva*. The transition between lateral granules and flat, enlarged, shiny ventrals is usually sharp, or includes at most one ambiguous element. In these genera the longitudinal arrangement is very regular.

In the genera *Callopistes*, *Crocodilurus*, *Tupinambis* and *Dracaena* the transition between lateral granules and ventral scales is much less sharp — differences of 3 or 4 elements being found on one side in adjacent rows of ventrals. For this reason we have not used this character in the taxonomic treatment, and the figures listed below are only approximate. The linear arrangement is also much less precise.

Differences between the two groups of genera are also apparent in the number of rows. In Table 1 and Graph 2 we present a rough preliminary study of the question.

TABLE 1

Ranges of counts of transverse and longitudinal rows of ventral scales and of femoral pores.

		Ventrals		
		Transverse	**Longitudinal**	**Pores**
1.	Cnemidophorus	26 - 42	8 - 12	5 - 45
2.	Dicrodon	28 - 35	8	10 - 21
3.	Kentropyx	32 - 35	14 - 16	7 - 22
4.	Teius	32 38	8 10	15 21
5.	Ameiva	25 38	6 - 18	10 39
6.	Crocodilurus	36 - 40	24 - 26	2 6
7.	Callopistes	39 - 44	24 - 29	0
8.	Tupinambis	34 - 40	27 - 40	2 18
9.	Dracaena	32 - 39	37 - 45	2

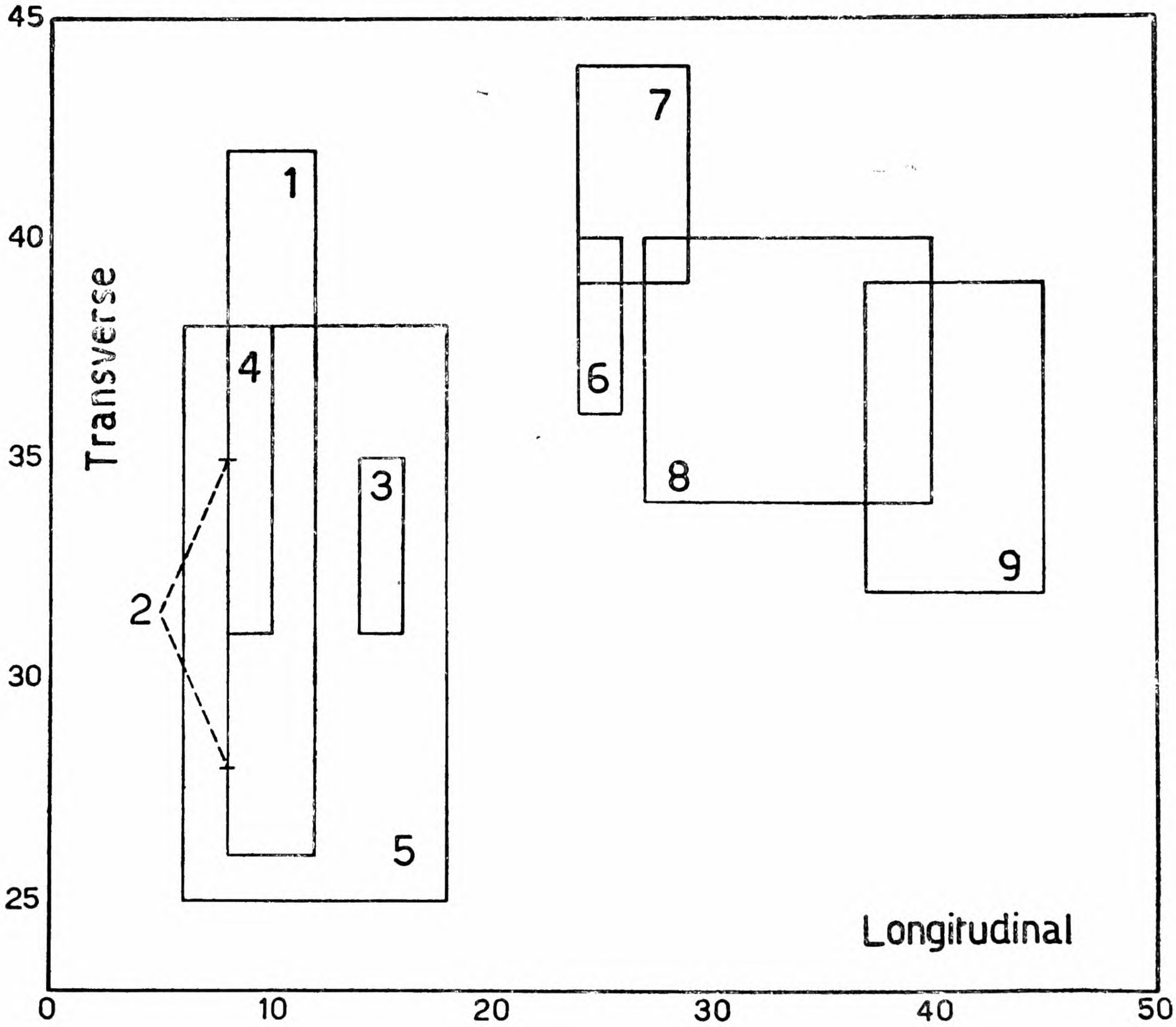
In the table we have listed the genera in approximate order of increasing body size. This involves some difficulty in the case of *Cnemidophorus* and *Ameiva*, large genera whose species vary considerably in size. We have placed these genera according to their mainland South American representatives.

The figures for numbers of rows of scales of *Cnemidophorus*, *Dicrodon*, *Kentropyx*, *Teius* and *Ameiva*, which are very easy to count, have been culled from the literature, after some spot-checking convinced us that there was no bias between published data and our own observations. In the case of *Crocodilurus*, *Callopistes*, *Tupinambis* and *Dracaena*, we resorted only to our own counts, as pronounced divergences were found with published data. These are apparently due to the different morphology of the anterior- and posteriormost rows in the transverse counts and, of course, to the difficulties in reading the transition between flank and belly scales.

We have examined 3 *Crocodilurus lacertinus*, 6 *Callopistes maculatus*, 15 randomly-selected *Tupinambis* of the *teguixin-nigropunctatus* kreis and the specimens of *Dracaena* included in this paper.

We fully acknowledge the heterogeneity of the data. Thus, some genera (as *Cnemidophorus*) are represented by literally thousands of specimens belonging to as many as 25 forms, strongly varying in size, while others are represented by a few specimens of one single form.

On the other hand, in drafting Graph 2, we have ignored the possibility of correlation between transverse and longitudinal rows, both within and among species. Thus, the rectangles depicted, which have as base the range of longitudinal rows and as height the range of transverse rows, represent a maximum of combinations possible for the whole genus.



Graph 2. Range of the number of transverse and longitudinal rows of ventral scales. 1, *Cnemidophorus;* 2, *Dicrodon;* 3, *Kentropyx;* 4, *Teius;* 5, *Ameiva;* 6, *Crocodilurus;* 7, *Callopistes;* 8, *Tupinambis;* 9, *Dracaena.*

In spite of these drawbacks, the data quite clearly point out two groups of genera. *Cnemidophorus, Dicrodon, Kentropyx, Teius* and *Ameiva* cluster together, with a lower number of both longitudinal and transverse rows. On the other extreme are *Crocodilurus, Callopistes, Tupinambis* and *Dracaena.* These have on the average more transverse rows; however, the difference is much more pronounced when it comes to longitudinal rows.

As a result of this broad analysis, it is possible to say that the larger-bodied genera tend to have narrower ventral scales, in less well arranged longitudinal rows and less sharply differentiated from the flank scales.

SCALE SENSE ORGANS

Dracaena has very evident scale sense organs in practically all head, trunk and limb scales, and in the basal region of the tail. These organs are apparently of the type called lenticular by Scortecci (1937, 1940). They are constant on the head of teiids (see, for instance, the photograph of *Ophiognomon abendrothi* in Vanzolini, 1962). On the trunk, however, they seem restricted to *Dracaena* among the teiids.

In other families they seem also to be scarce. We are indebted to Prof. E. H. Taylor for calling our attention to organs seemingly very similar in the xantusiid genus *Lepidophyma* (Taylor, 1956). Underwood (1959) has also described multiple scale organs, very different from those of *Dracaena,* in the trunk scales of New World anguids.

Dr. A. S. Rand, examining one freshly-preserved specimen of *Gymnophthalmus multilineatus,* discovered, on the ventrals, some curious sub-epidermal round spots, for which we have at present no explanation, and which are not visible in older preserved specimens.

CUSHION SCALES

A curious type of scales is found, in some genera, on the upper surface of the limbs, and especially evident on the thigh. The usual leaf-shaped scales or enlarged granules are surrounded and partially underlaid by small swollen granules. For these we propose the name "cushion scales".

This feature is rather prominent in *Tupinambis* and *Dracaena,* even in young specimens.

In other forms there is a sort of rudimentary indication of this condition: small granules interspersed among the larger ones. This in the case in *Ameiva edracantha, ameiva* and *festiva,* but not in *auberi, b. bifrontata, bifrontata divisa, dorsalis, septemlineata* and *lacertoides.* In some *Kentropyx* (western Amazonian), in *Teius* and in *Callopistes* the rudimentary condition is present. In the examined *Cnemidophorus* (*l. lemniscatus, l. nigricolor, m. murinus, ocellifer* and *sexlineatus*), in *Dicrodon* and *Crocodilurus* the scutellation is homogeneous.

NUMBER OF DIGITS

All genera of macroteiids have well-developed limbs. There are five fingers in all. Toes are also five, but there is a tendency to deemphasize toe V, which is inserted quite a ways from the others, more basally. In *Cnemidophorus*, *Kentropyx*, *Callopistes*, *Crocodilurus*, *Tupinambis* and *Dracaena* it reaches beyond the hallux; in *Ameiva* and *Dicrodon* it is shorter and very weak; finally, in *Teius* it is reduced to a stump.

PALMAR SURFACE OF HAND

The palm of the hand furnishes also some interesting characters. The simplest pattern is that of *Callopistes*, *Cnemidophorus*, *Ameiva*, *Teius*, *Dicrodon* and *Kentropyx*, which have single ventral lamellae on the fingers. The basal lamellae tend to be verrucose. There is a transverse row of carpal tubercles, usually incomplete in the middle, united by enlarged scales on the tenar (on the side of finger I) and hypotenar (on the side of finger IV) regions to the lamellae of the respective fingers. In *Tupinambis* and *Crocodilurus* carpal tubercles are lacking, and the basal lamellae of the fingers are split into coarse granules. In *Dracaena*, finally, the ventral lamellae are substituted by rows of small sharp scales; carpal tubercles are also absent.

TOE LAMELLAE

The ventral lamellae of the toes show tall prominent tubercular projections in all genera. In *Crocodilurus* these projections are arranged as a double lateral fringe; in *Kentropyx* as a single fringe. In *Dracaena* they form the tall palisades of prismatic scales figured in Plate V. In the remaining genera this condition is hinted at, but never quite reached. These projections are always found on the side of the toe farther away from the midline of the foot.

PORES

In all macroteiids but *Callopistes* femoral pores have been reported in the literature. Some interesting phenomena, however, seem to have been missed.

Thus, contrary to what is frequent, if not the rule, among microteiids, there seems to be no sexual dimorphism.

Secondly, in some genera (*Crocodilurus*, *Callopistes* and *Dracaena*) the femoral series continues proximally beyond the groin on the abdominal surface, parallel and anteriorly to the pre-anal patch. They vary in number from 2 to 6.

Finally, there is some pattern in the variation of the femoral pores proper. The data on Table 2 have been obtained in the same way as those for ventral scale counts. *Crocodilurus*, *Callopistes* and *Dracaena* have low numbers. The other genera show ample ranges, with high upper limits. It is to be noted that these broad ranges are composites of the much narrower and well-differentiated ranges of the individual forms; femoral pore number is an useful character in the taxonomy of macroteiids. In the case of *Tupinambis*, the only large-bodied genus with high counts, our preliminary survey shows that there is pronounced geographical variation of the character.

PRE-ANAL SPURS

These structures are present: in males of seemingly all species of *Kentropyx*, in some *Cnemidophorus* and in *Ameiva edracantha*. In the first named there are two (occasionally three) very strong spines; in the second only one, weak spur; in the third there is a bunch of 5-7 definitely spinose scales.

TAIL

The tail is usually rounded and, except for the base, dragged when the animal walks, leaving a characteristic trail. Only in *Crocodilurus* and *Dracaena*, active swimmers, it is laterally compressed, with a double row of serrated scales.

The scutellation offers some curious phenomena. In *Cnemidophorus*, *Ameiva*, *Teius*, *Dicrodon* and *Kentropyx* the caudal scales are arranged into regular annuli.

In *Tupinambis* and *Crocodilurus* every other annulus (except at the base of the tail) is composed of one row of scales on the ventral half to which correspond two rows dorsally. In *Callopistes* there are two single rows after every double one. This same scheme obtains in *Dracaena*, with the further complication that the doubling occurs only on the sides of the tail; to each scale of the serrated edge correspond one dorsal and one ventral row, but on the sides alternately 1 and 2 rows, as shown on Plate V.

COLOR PATTERN

The dorsal color pattern of *Cnemidophorus*, *Ameiva*, *Teius* and *Kentropyx* is fundamentally linear, although in some forms this is effaced with age.

Callopistes, *Crocodilurus*, and *Dicrodon* have dorsal spots, smaller or larger.

Tupinambis has either a transversely barred pattern (*teguixin*, *nigropunctatus*) or a fairly homogeneous one (*rufescens*). *Dracaena* tends to this type of dorsal pattern: head and tubercles lighter, red or at least much more rufous than the general greenish bronze ground color.

As to the belly, it is normally immaculate in *Cnemidophorus*, *Ameiva*, *Teius*, *Kentropyx* and *Dicrodon*. *Callopistes*, *Crocodilurus* and *Tupinambis* have a light belly more or less spotted with black. *Dracaena* has, as described by

Vanzolini (1961), a mottled belly, especially procryptic when the animal is perching on low trees. There is definite seasonal variation of the color of the lower belly of *Ameiva* and *Kentropyx* males, but present materials are insufficient for analysis.

DENTITION

The dentition of *Ameiva, Cnemidophorus, Callopistes, Kentropyx* and *Crocodilurus* is of the insectivore pleurodont type: the anterior teeth are conical or chisel-shaped and the posterior ones laterally compressed, with a tricuspid crown.

In *Teius* and *Dicrodon* the posterior teeth are bicuspid, transversely instead of laterally compressed. *D. holmbergi* adults are phytophagous (Holmberg, 1957), but the other forms are insectivorous (Schmidt, 1957).

In *Tupinambis*, a voracious and large omnivore, there is a strong tendency towards molarization of the hind teeth, with a degree of acrodoncy. In *Dracaena* this tendency is extreme, leading to the formation of pseudo-alveoli which give the molariforms the needed support for their shell-crushing function.

TONGUE

Boulenger (1885) uses the condition of the hind margin of the scaly portion of the tongue to classify the macroteiid genera. *Tupinambis, Dracaena, Kentropyx* and *Ameiva* would have that portion "not or but feebly emarginate posteriorly, frequently retractile into a basal sheath". On the contrary the condition in *Cnemidophorus, Callopistes, Dicrodon, Teius* and *Crocodilurus* would be "arrow-headed, bifid and not retractile posteriorly".

We find it difficult to judge the matter of retractility in usual collection specimens, but a fair assessment can be made of the condition of the posterior margin.

Examination of our specimens shows that in *Tupinambis, Dracaena* and *Ameiva* (with the exception of *A. lacertoides*) the hind margin is certainly entire. In *Cnemidophorus, Dicrodon, Teius* and *Callopistes* that portion is widened and has a very deep median rounded emargination, the whole resembling very much the shape of an aroid leaf.

In *Crocodilurus* and *A. lacertoides,* however, the condition is not extreme, the emargination being shallow.

In some *Kentropyx* the tongue is shallowly emarginate; in others the margin is entire. In at least one specimen from eastern Brasil there is a deep emargination.

SUMMARY

From the above elements and keeping in mind that no osteological, splanchnological or hemipenial information has been used, it is possible to present a preliminary assessment of relationships within the macroteiid group and especially of *Dracaena.*

A group of 5 genera — *Cnemidophorus, Ameiva, Teius, Kentropyx* and *Dicrodon* — seems to have some important characters in common.

The joint presence of a large series of well-developed femoral pores and the absence of abdominal pores is shared by these five genera and by no other. The same may be said of the simple scutellation of the caudal annuli and of the absence of gular sulci at the tympanic and angular levels.

These five genera (with the exception of the larger forms of *Ameiva*) are decidedly smaller-bodied than the remaining four — *Callopistes, Crocodilurus, Tupinambis* and *Dracaena* — and perhaps related to this is the smaller relative size (and consequent larger number of rows) of the ventral scales. Their teeth are either tricuspid and longitudinally compressed or bicuspid and transversely compressed — no instances of molarization are known. Carpal tubercles are present in all, and only in *Callopistes* among the larger-bodied genera. In two of them there are pre-anal spurs in the male. There are no well developed cushion scales.

Characters shared by both groups (smaller and larger-bodied) are the presence of enlarged flattened dorsal granules, keeling on the ventrals, and of emargination of the posterior margin of the scaly portion of the tongue.

Among the five genera of smaller macroteiids *Cnemidophorus* seems to occupy a central position. It has pointed granular dorsals, large smooth ventrals in regular longitudinal rows, one collar and one gular skin fold but no gular sulci, no cushion scales, well-defined carpal tubercles, large femoral and no abdominal pores, rounded tail with simple annuli, longitudinally compressed tricuspid teeth and notched tongue.

Very close to *Cnemidophorus* — so close, in fact, that the relationship needs much more detailed investigation — is *Ameiva.* The alleged main difference is the absence of a notch on the posterior margin of the scaly portion of the tongue. We have seen this is a weak character.

Teius is at once characterized by its transversely compressed teeth, otherwise present only in *Dicrodon.* The matter of the obsolescense of toe V has already been considered as trivial. The tongue is distinctly notched.

Dicrodon also has transversely compressed teeth. The dorsal granules are enlarged, oval, flattened, arranged in well-defined transverse rows, in apparent transition to a more typical scale. Otherwise agreement with *Cnemidophorus* is perfect.

Finally, *Kentropyx* is the most differentiated genus in this assemblage. As unique characters it has phylloid keeled ventrals, only one skin fold (the collar) and heterogeneous dorsal scutellation. The condition of the tongue is rather peculiar, but tends more towards the *Ameiva* type. The presence of pre-anal spurs tends to link this genus to *Cnemidophorus* of the *lemniscatus* group.

Among the larger-bodied teiids, we cannot decide for a centrally-placed genus, although it is tempting to consider *Tupinambis* so.

Callopistes is well defined by the complete absence of pores. The dorsals are (as in *Tupinambis*) enlarged flat oval granules arranged into transverse rows. Carpal tubercles are present (a unique character in the sub-group) and the tongue is frankly emarginate.

Some of the characters of *Dracaena* are peculiar and not even approached by other macroteiids. Such are the presence of dorsal tubercles, of scale sense organs in the dorsals and ventrals and the scutellation of the fingers.

It has been suggested that the presence of dorsal tubercles in *Neusticurus* might indicate some sort of relationship. It is our belief that *Neusticurus* is a good microteiid, at least from the viewpoint of head and body scalation, and that the presence of tubercles is due to convergence.

The massive presence of single scale sense organs in *Dracaena* seems to us to be unparalleled among teiids of other South American lizards, and comparable only to what is found in *Lepidophyma.*

The presence of ventral scale sense organs has been known at least since Boulenger (1885). The conspicuous "pits" on the dorsals apparently had not been noticed till now. The meaning of both remains enigmatical to us. The ventral "pits" might be explained as a network of pressure receptors, especially useful for an animal that rests on tree branches with little if any help of the legs. In order to estimate the probability of such a hypothesis, we examined other lizards which also frequent tree branches over open water (*Crocodilurus, Basiliscus, Iguana, Uranoscodon*) or even other iguanids which do the same over dry land (*Anolis,* some 12 species, *Polychrus, Plica*). In no one of these forms did we find the desired scale organs, and thus the proposed explanation finds no analogical support.

Table 2

Summary of characters studied

	Cnemidophorus	Dicrodon	Kentropyx	Teius	Ameiva	Crocodilurus	Callopistes	Tupinambis	Dracaena
1. Upper head scalation	A	A	A	A	A	A	C	A	A,B
2. Throat sulci	O	O	O	O	O	I	I	II	I II
3. Dorsal scalation	A	B,C	A,F	A	A	D	B	B	D,E
4. Ventrals' shape	A	A	D	A	A	B	B	B	C
5 transv rows	26 42	28-35	32 35	32 38	25 38	36 40	39-44	34-40	32-39
6. long. rows	8 12	8	14-16	8 10	6 18	24 26	24 29	27 40	37-45
7 Cushion scales	O	O	O,A	A	O,A	O	A	B	B
8. Finger lamellae	A	A	A	A	A	B	A	B	C
9. Carpal tubercles	+	+	+	+	+		+		
10. Toe lamellae	A	A	B	A	A	C	A	A	D
11. Femoral pores	5-45	10-21	7 22	15 21	10 39	2 6	O	2 18	2
12. Abdominal pores	O	O	O	O	O	2 4	O	3-6	2-4
13. Pre-anal spurs	+,-		+		+,-				
14. Tail annuli	A	A	A	A	A	B	C	B	D
15. Dentition	A	B	A	B	A	A	A	C	C
16. Tongue	C	C	A,B,C	C	A,B	B	C	A	A

1. Upper head scalation
A, general pattern
B, post-nasals present
C, disrupted pattern

2. Anterior throat sulci

O, none
I, inter-tympanic
II, inter-angular

3 Dorsal scalation

A, small pointed granules
B, large oval flat granules
C, as in B, growing posteriorly
D, rectangular scales
E, tubercles
F, large keeled scales and granules, in longitudinal strips

4 Ventrals' shape

A, smooth, regular longitudinal rows
B. smooth, less regular
C, as in B, keeled
D, phylloid, keeled

5, 6. Ventrals, transverse and longitudinal rows

Actual range

7 Cushion scales

O, absent
A, indicated
B, well developed

8 Finger lamelae

A, simple, basal lamellae verrucose
B, basal lamellae granular, distal simple
C, rows of small sharp scales

9. Carpal tubercles
Present (+) or absent (—)

10. Toe lamellae

A, with some tubercular projections
C, single fringe
C, double fringe
D, palisade of prisms

11. Femoral pores

Actual ranges

12. Abdominal pores

Actual range

13. Pre-anal spurs

Present (+) or absent (—)

14. Tail annuli

A, simple
B, Dorsally alternate single and double rows
C, dorsally alternation of 2 single and 1 double row
D, as in C, but doubling only on sides of tail

15, Dentition

A, pleurodont, tricuspid, longitudinally compressed
B, as in A, transversely compressed
C, molariform, with tendency to formation of pseudoalveoli

16. Tongue

A, entire
B, shallowly emarginate
C, frankly emarginate

The morphology of the volar surface of the fingers (transverse rows of small pointed and keeled scales) strikingly differs from everything that is known not only in the macroteiids but in the whole family. We take it as an adaptation of a large lizard to the needs of rapid climbing — a situation without parallel in the family.

Other characters of *Dracaena*, although peculiar to it, are approached, but not shared, by other genera.

The larger macroteiids have sulci (or rows of granules) anterior to the two usual skin folds on the throat. *Dracaena* has one such sulcus at tympanum level and another joining the mandibular anguli. The latter is present in *Tupinambis;* the former in *Callopistes* and *Crocodilurus*. It would seem that such sulci are related to the strengthening of the mouth floor in relation to the ingestion of bulky prey. The anterior sulcus, especially, is probably concerned in some way with the crushing function of the molariforms.

The dorsal scales of *Dracaena* are rectangular, keeled. The condition is approached by *Crocodilurus*. The transition between small pointed granules and rectangular scales can be easily seen in *Tupinambis, Callopistes* and *Dicrodon*.

The condition of the toes of *Dracaena* is an extreme development of the general macroteiid tendency towards tuberculization of the ventral lamellae. It is more closely approached in *Tupinambis*. *Crocodilurus* has fringed toes, which are probably used for swimming or perhaps walking on the water, after the fashion of *Basiliscus*. *Dracaena* has been seen (Vanzolini, 1961) not to use its feet for swimming, only the tail.

An interesting character for which we have no mechanical explanation is the peculiar scutellation of the tail. The situation in *Dracaena* is extreme, in that a tail annulus is one scale wide on the dorsal and ventral portions, but on the sides, there is alternation of one double and one single rows. In *Tupinambis, Crocodilurus* and *Callopistes*, each caudal annulus is divided into two parts, ventral and dorsal. For every ventral row there may be one or two dorsal rows. In *Tupinambis* and *Crocodilurus* single and double dorsal rows alternate; in *Callopistes maculatus* there are two single for every double row. Thus, the condition of *Dracaena* could be derived from that of *Tupinambis* and *Crocodilurus*.

The dentition of *Dracaena* is again extreme in the degree of molarization. The only near approach is *Tupinambis*. This is beyond doubt an omnivore: insects, fishes (A. S. Rand, obs. in our laboratory), amphibians, reptiles and mammals are usual in its diet. Milstead (1961) has reported large snails in the stomach contents of Rio Grande do Sul specimens of *T. teguixin*. *Dracaena* is, at least predominantly, molluscivorous.

Finally, with regard to color pattern, that of *Dracaena* is well adapted to its mode of living (Vanzolini, 1961), but easily derivable from that of the large-bodied macroteiids.

Some characters of *Dracaena* are common to it and to few other genera. Those are the presence of cushion scales, the absence of carpal tubercles, the shape of the tail and of the tongue, and the presence of abdominal pores.

Cushion scales are found in *Tupinambis* and somewhat approached in *Ameiva, Teius, Kentropyx* and *Callopistes.* They are definitely absent in *Crocodilurus.*

The absence of carpal tubercles is shared by *Tupinambis* and *Crocodilurus.* This character might be thought to be related to the aquatic habits of *Dracaena* and *Crocodilurus,* but the tubercles are absent even in large specimens of *Tupinambis,* a robust digger.

The shape of the tail, laterally compressed and crested, is common to *Crocodilurus* and doubtlessly related to swimming.

The shape of the tongue is very similar to that of *Tupinambis* and *Ameiva,* and not too different from that of *Crocodilurus.*

It seems obvious that *Tupinambis* is the closest relative of *Dracaena.* All characters that the latter shares with other genera are found in *Tupinambis,* and some of them are seemingly important in indicating relationship. Thus the shape of the tongue, the presence of cushion scales, the absence of carpal tubercles, the molarization of the teeth, the morphology of the tail annuli and the distribution of pores.

On the other hand, practically all the differences between *Dracaena* and *Tupinambis* are directly ascribable to the former's peculiar mode of life: dorsal tubercles, scutellation of fingers and toes, color pattern. The matter of scale sense organs remains to us unexplained.

Crocodilurus also approaches *Dracaena* in some important characters, such as the shape of the non-tuberculate dorsal scales, the absence of carpal tubercles, the shape and scalation of the tail and the distribution of the pores.

It is thus to be seen that *Dracaena* is closely related to *Tupinambis* and, next, to the other large macroteiids, *Crocodilurus* and *Callopistes,* in the order named, and that the smaller-bodied genera form a rather homogeneous ensemble, with probably *Cnemidophorus* as a central stock.

This conclusion is in frontal divergence with Burt's (1931: 253) diagram of teiid evolution. He begins by dividing the whole family on the basis of general tails shape (crested against cyclo-tetragonal). We believe this to be such a fundamental flaw — as a swimming tail is probably one of the easiest things to acquire in evolution — that we feel that there is no point in proceeding with a comparison of the two schemes.

A KEY TO THE GENERA OF MACROTEIIDS

1.	Femoral pores absent	*Callopistes*
1'.	Present	2
2(1')	Abdominal pores present	3
2'.	Absent	5
3(2)	Dorsal tubercles present	*Dracaena*
3'.	Absent	4
4(3')	Tail crested	*Crocodilurus*
4'.	Not	*Tupinambis*
5(2)	Ventrals keeled	*Kentropyx*
5'.	Not	6
6(5)'.	Posterior teeth transversely compressed, bicuspid	7
6'.	Longitudinally compressed, tricuspid	*Ameiva* and *Cnemidophorus*
7(6).	Toes four, fifth obsolete	*Teius*
7'.	Toes five	*Dicrodon*

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Plate I

1, *Dracaena guianensis*, DZ 7286. 2, D. *paraguayensis*, DZ 8386.

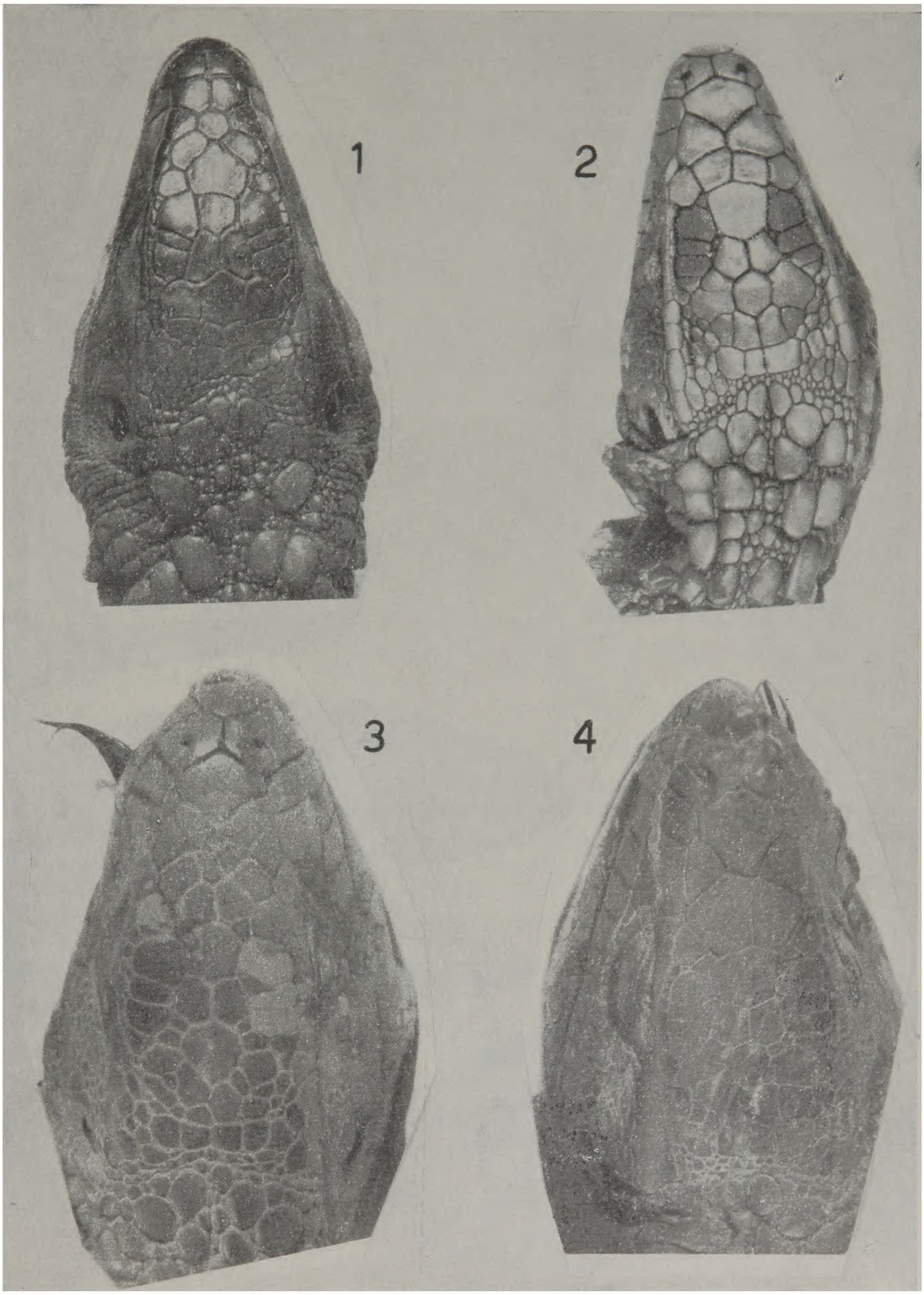

Plate II
1, *Dracaena guianensis*, DZ 7286. *D. paraguayensis*: 2, IB 689; 3,4, Peracca's specimens.

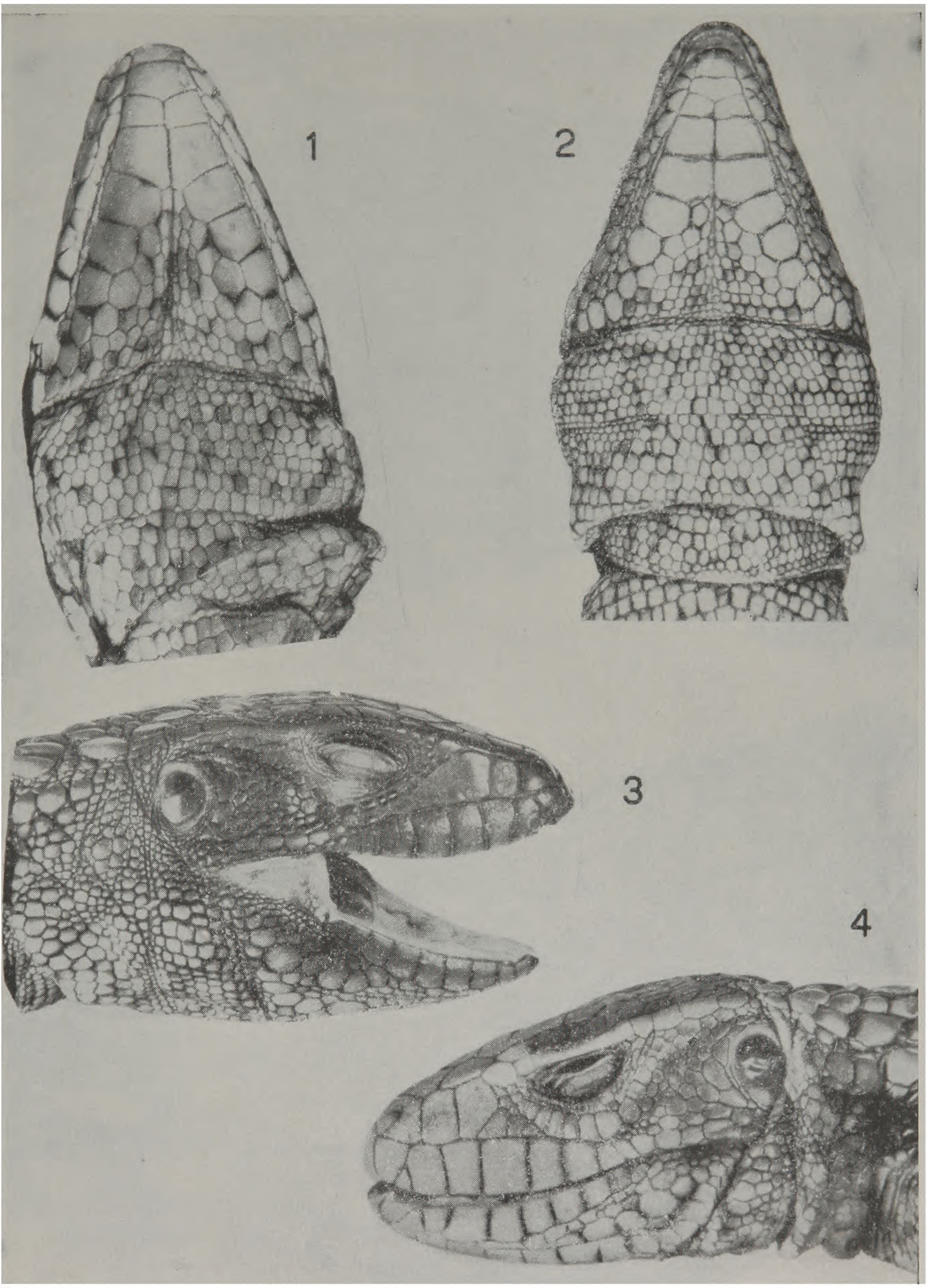

Plate III
1,4, *Dracaena paraguayensis*, IB 689. 2,3, *D. guianensis*, DZ 7286.

Plate IV
1, *Dracaena paraguayensis,* DZ 8386. 2, *D. guianensis,* DZ 7286.

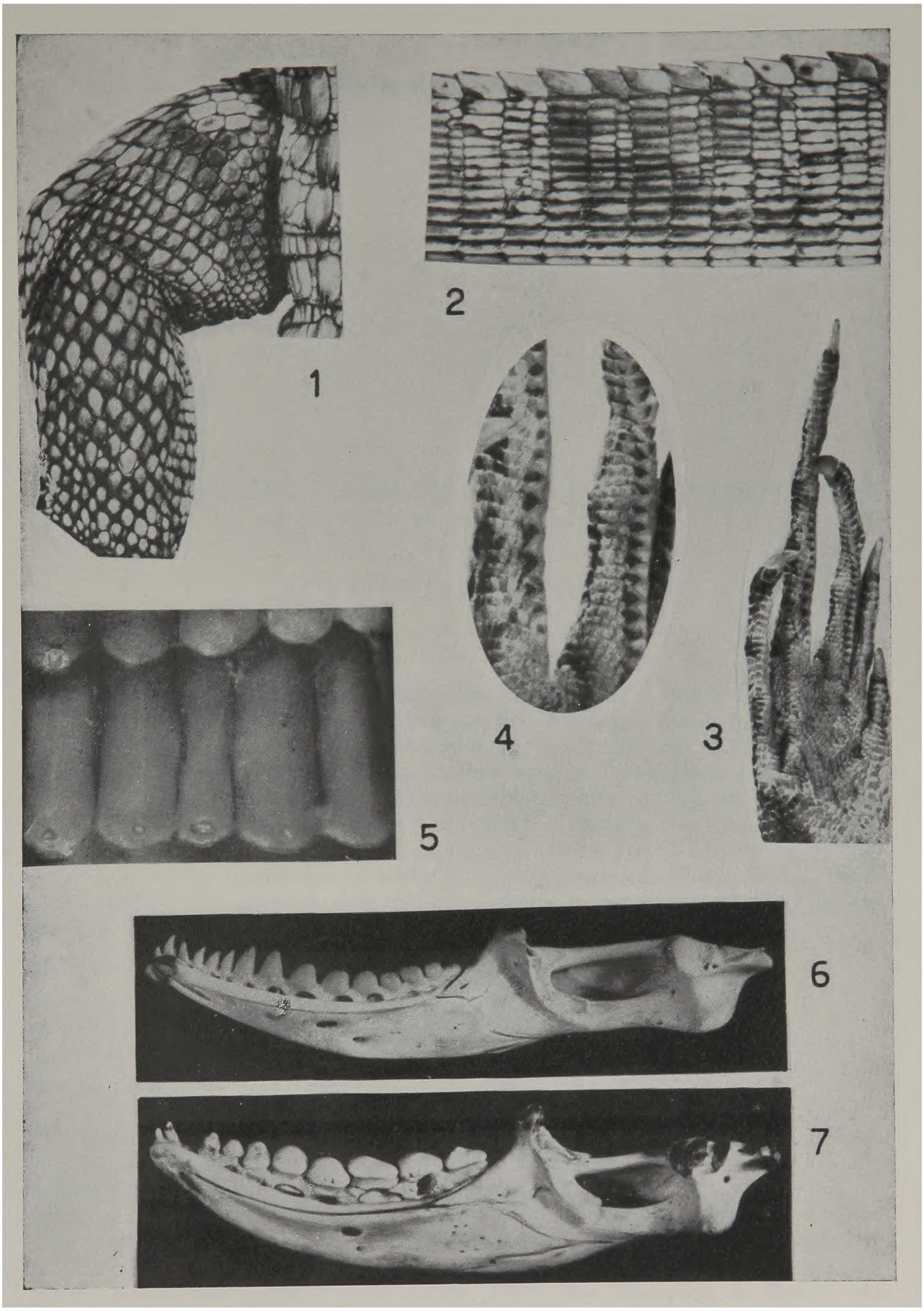

Plate V

D. paraguayensis, DZ 8386: 1, cushion scales; 2, lateral view of tail, middle third; 3, left foot, ventral view; 4, detail of fig. 3, toes II and III; 5, ventral scale sense organs. 6, *Tupinambis nigropunctatus* and 7, *Dracaena guianensis*, DZ osteological collection, not numbered: mandible, lingual view.