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MIOCENE LIZARDS FROM COLOMBIA, SOUTH AMERICA

By RICHARD ESTES1

Numerous fossil vertebrates were collected by the 1949 University of California field expedition to the upper Magdalena Valley, Huila, Colombia, South America. Among these, the lower vertebrates include bony fishes, lepidosirenid lungfish, a bufonid frog (identified as ?Leptodactylidae by Savage, 1951), turtles, crocodiles, snakes, and lizards. The lizards are described in the present paper.

I am indebted to Dr. Wann Langston for bringing these specimens to my attention, and to Mr. C. M. Bogert, American Museum of Natural History, Dr. Ernest E. Williams, Museum of Comparative Zoology, Harvard University, and to Dr. Alan Leviton, California Academy of Sciences, for the use of com-

parative material in their collections.

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for numerous helpful suggestions.

The sequence and distribution of the fossil faunas of the Magdalena Valley has been discussed by Stirton (1953, see especially figures 1, 2). Fossil lizards have been found only in the Upper Oligocene Coyaima fauna, and the Upper Miocene La Venta fauna.

Abbreviations. A.M., American Museum of Natural History, Department of Vertebrate Paleontology. U.C., University of California, Museum of Paleontology.

¹ Department of Biology, Boston University, and Research Associate, Department of Vertebrate Paleontology, Museum of Comparative Zoology, Harvard University.

COYAIMA FAUNA Family TEIIDAE cf. Tupinambis sp.

Referred specimen. U. C. no. 56303, maxillary fragment. Locality. U. C. loc. V-4411, Coyaima, Colombia, South America.

Age. Late Oligocene.

Description. The fragment is the posterior end of a right maxilla, which bears one complete tooth and the bases of three others. The complete tooth has a strongly wrinkled crown surface, and in occlusal view is circular. No anteroposterior crests are present.

Discussion. The tooth closely resembles posterior maxillary teeth of Recent Tupinambis teguixin. It differs from comparable teeth of Dracaena in not being dorsoventrally flattened.

LA VENTA FAUNA Family TEIIDAE TUPINAMBIS cf. T. TEGUIXIN

Referred specimen. U. C. no. 38856, left dentary and splenial, with parts of the coronoid, angular and surangular; the symphysis region missing. Collected by Dr. José Royo y Gomez.

Locality. U. C. loc. V-4526, Lower Red Beds, Honda group, Huila, Colombia, South America.

Age. Late Miocene.

Description. The maximum length of the specimen is forty-three millimeters. The dentary is robust, and has a heavy shelf external to the tooth row. Three inferior alveolar foramina are preserved. Posteriorly a large re-entrant notch contains a fragment of surangular. The latter, and part of the dentary anterior to it, is prominently depressed for muscle insertion. The splenial is large, and deep anteriorly as in most teiids. There are two foramina in the splenial, the posterior one smaller. The anterior process of the angular inserts between the splenial and dentary, and reaches only as far forward as the level of the penultimate tooth. The coronoid is represented only by the interior dentary process, which is inserted into a notch between splenial and dentary. The teeth are bulbous and have slightly crenulated surfaces. Immediately posterior to the broken anterior end of the specimen a pit is present for a replacement

tooth. The subsequent teeth (referred to here by numbers 1-8) form a slightly curved series when viewed dorsally, and the line of occlusion viewed laterally has a slight dorsoposterior curve. Tooth one is slightly bulbous and smaller than tooth two.

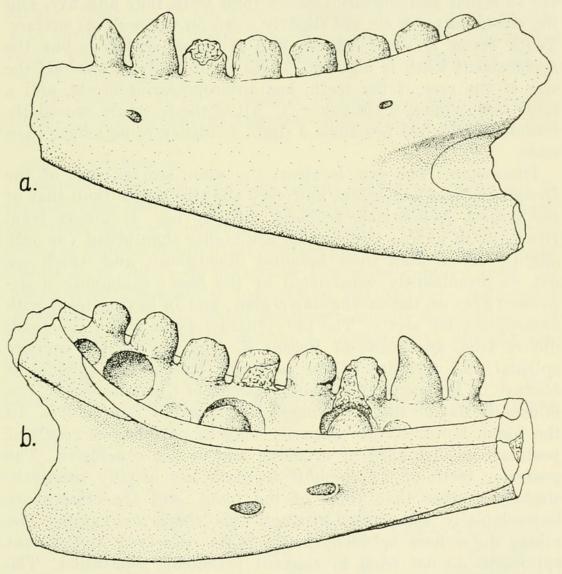


Figure 1. a. *Tupinambis* cf. *T. teguixin*, U. C. no. 38856, labial view of left dentary, x 2. b. The same, lingual view.

Two is taller and slimmer than the succeeding teeth and is slightly recurved and concave posteriorly. Tooth three is being replaced, its crown is broken, and its thin eroded base has been crushed ventrally so that the tooth appears lower than it actually was; measurement of the replacement tooth indicates that it would be intermediate in height between the preceding and succeeding teeth. The replacement pits under the first and second teeth are in the interdental position. Teeth four and five are subequal; four has a faint anterior and posterior crest near

the crown. The crown of tooth five is worn smooth. The large, fully formed replacement tooth below it has a slightly crenulated surface near its apex, and its anteroposterior crests are connected to the central point of the crown. Teeth six and seven are subequal and slightly smaller than teeth four and five, and the crests on tooth six are slightly worn on the occlusal surface. Tooth seven is worn smooth and is being replaced, but the replacement tooth is missing. Tooth eight is about one-half the size of the rest of the teeth, has anteroposterior crests, and a large replacement crypt below it. All of the teeth are essentially round, but the last few show a slight tendency to be longer than wide.

Discussion. The jaw is about the same size as that of the Dracaena described below, and very slightly larger than that of the largest Tupinambis teguixin seen by me. It differs from Dracaena in having teeth which are higher than broad (or only slightly lower than their broadest dimension), and which are not as prominently constricted at the base; in having a depressed area on the surangular region; and in having teeth with anteroposterior crests. The only characters in which the fossil differs from specimens of Recent T. teguixin are the concave splenial and the size of the posterior teeth. The splenial is concave in Dracaena and in some species of Cnemidophorus, but is usually flat or slightly concave to convex in Tupinambis. In the fossil, however, the concavity may in part be the result of postmortem shrinkage or crushing and is not conclusive. The posterior teeth of Tupinambis teguixin are usually relatively slightly smaller than those of the fossil, and are often more linguolabially compressed, though this character varies. minor differences between the fossil as preserved and Recent specimens do not seem to warrant taxonomic separation. The other Recent species, T. nigropunctatus, has higher crowned, smooth, and prominent cuspate teeth, and is smaller than T. tequixin.

Rovereto (1914a) described several fossil species of *Tupinam-bis* from the Pliocene of Argentina. Their validity is difficult to determine at the present time, but they seem to resemble *T. teguixin* most closely.

Dracaena colombiana n. sp.

Type. U. C. no. 39643, complete right dentary, collected by Dr. R. W. Fields.

Referred specimens. U. C. no. 40277, distal and proximal ends of a left femur, catalogued as float from ?Cerbatana gravels. U. C. no. 37899, sacrum and associated first caudal vertebra, collected by Dr. José Royo y Gomez from U. C. loc. V-4517, Monkey Unit. U. C. no. 38927, posterior half of right maxilla, with bases for three teeth, from U. C. loc. V-4528, Upper Red Beds. The four localities occur within an area about six kilometers in diameter.

Type locality. U. C. loc. V-4536, San Nicolás, near Villavieja, Huila, Colombia, South America. San Nicolás clays, Honda group.

Age. Late Miocene.

Diagnosis. Differs from the Recent Dracaena guianensis in the following characters: dentary larger and more robust; tooth row more strongly curved upward posteriorly; tooth outline round or suboval; tooth number fifteen. From the living D. paraguayensis it differs in possessing five more dentary teeth. It differs from Tupinambis teguixin in having more posteriorly expanded cheek teeth, which are larger, basally constricted, and wider than high, and in lacking a depression in the exterior notch for the surangular.

Description. The dentary is 60 millimeters long. The Meckelian fossa is widely open. The robust symphysis has a rugose

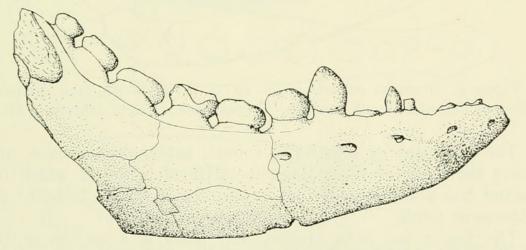


Figure 2. Dracaena colombiana, n. sp., U. C. no. 39643, type specimen, Miocene, Colombia, South America. Labial view of right dentary, x 1.5.

articular surface, and is separated from the main body of the dentary by a linguolabial constriction. There are five inferior alveolar foramina, and the dentary is rugose labially near the symphysis, probably for the genioglossus muscle. A broad shelf

is present labial to the tooth row. The labial coronoid notch is prominent, and reaches as far forward as the anterior border of the last tooth. There are fifteen subpleurodont (or subacrodont) teeth, of which all but six are preserved. Teeth one through five are missing; six and seven are conical and slightly striated. The eighth is missing, but the base shows that it was molariform. Teeth nine to fifteen are molariform, and the ninth projects well above the preceding and succeeding teeth. Beyond the ninth, the teeth are flattened, button-like, and have finely striated, round or suboval crowns, which increase in diameter to the twelfth tooth and then decrease posteriorly. Most of the molariform teeth have occlusal attrition facets, especially tooth twelve. Teeth seven through fifteen have replacement pits at their bases, and several of these pits (eight, ten, twelve, fourteen) contain almost full term replacement teeth. The tooth replacement is directly successive, and apparently alternate.

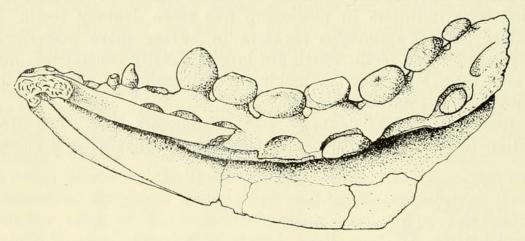


Figure 3. Dracaena colombiana, n. sp, U. C. no. 39643, type specimen, Miocene, Colombia, South America. Lingual view of right dentary, x 1.5.

The fragment of maxilla is robust, externally concave, and bears the bases of three large molariform teeth, of which the second has a replacement pit containing a large, flattened replacement tooth.

The femur has been broken, and there is a section of the diaphysis missing. It has been restored to a length of 75 millimeters, by analogy with femora of *Dracaena guianensis*. It is large, but not especially robust, and the patellar groove and muscle attachment scars are prominent. A small U-shaped notch separates the head from the trochanter major.

The sacrum is composed of two co-ossified vertebrae, which have prominent zygosphene-zygantrum articulations. The maximum length of the sacrum from center of cup to tip of ball is

20 millimeters. The greatest width from the centers of iliosacral articulation is 45 millimeters. The first caudal vertebra has a perfectly hemispherical cup and ball, and a prominent zygo-sphene-zygantrum articulation. It is 16 millimeters long from center of cup to tip of ball.

Discussion. The distinctive specialization of the teeth of Dracaena has long been known. Owen (1845) figured a specimen, and Peyer (1929) discussed the form and function of the teeth. Amaral (1950) has described another Recent species, D. paraguayensis, but I have not seen a specimen.

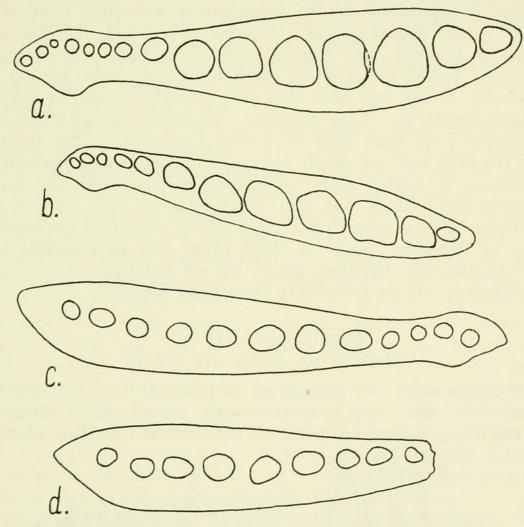


Figure 4. a. Outline of occlusal view of right dentary, Dracaena colombiana, U. C. no. 39643, Miocene, Colombia. b. The same, Recent D. guianensis. c. The same, left dentary, Recent Tupinambis teguixin, A. M. no. 62545. d. The same, Tupinambis cf. T. teguixin, U. C. no. 38856, Miocene, Colombia. a.-d. x 1.5.

The principal differences from the Recent D. guianensis are as follows: (1) The fossil is more subpleurodont in tooth implantation, resembling other teids, whereas the Recent species

tends to be subacrodont. (2) *D. colombiana* has fifteen dentary teeth, *D. paraguayensis* has ten (fide Amaral) and *D. guianensis* twelve. (3) The anterior teeth, as far as they are preserved, are less bulbous than in the Recent species. (4) The occlusal outline of the tooth crowns is round or suboval in the fossil and suboval or subrhombic in *D. guianensis*. (5) The crown surface of the molariform teeth is more flattened, and the dorsoventral compression of the entire tooth is less in the fossil.

The referred skeletal elements are somewhat larger than would be expected for a modern Dracaena with a dentary the size of D. colombiana, as the appendicular skeleton is relatively small in the Recent species. If correctly referred, the skeletal elements perhaps came from a larger individual. The sacrum and first caudal vertebra are characteristically teiid, having a perfectly round cup and ball, and strongly developed zygosphene-zygantrum. They resemble comparable bones of Recent Dracaena more than those of Recent Tupinambis. The femur has the deep patellar groove seen in many teiids and resembles Dracaena in having more separation between head and trochanter major than that seen in Tupinambis. The lack of a pronounced fossa posterior to the condyles resembles the condition in Dracaena. Some of these bones may be referable to the Tupinambis described above, but on the basis of present comparisons, all are referred to Dracaena colombiana.

Family IGUANIDAE UNIDENTIFIED GENUS AND SPECIES

A fragmentary left dentary of an iguanid, U. C. no. 39644, from U. C. loc. V-4517, Monkey Unit, shows some similarity to the living *Polychrus*, but lacks the vertical wrinkling of the

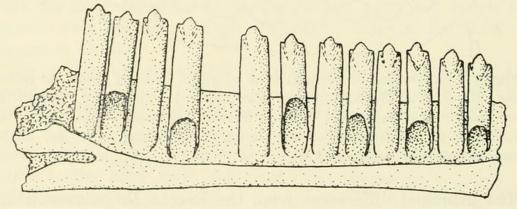


Figure 5. Iguanidae, unidentified genus and species, U. C. no. 39644, Miocene, Colombia, left dentary, broken anteroposteriorly, x 10.

tooth surface found in the latter. Many iguanid genera were compared with this fossil, but close correspondence was not found. It may be new or represent one of the forms not seen, and further identification was thus not attempted.

ECOLOGICAL AND ZOOGEOGRAPHICAL CONSIDERATIONS

Fields (1957, p. 394-395, and 1959, p. 428-429) has described the upper Magdalena Valley area during the late Miocene as a vast floodplain, subject to alternating periods of flooding and drying in a wet-tropical climate. Dry seasons resulted in extensive development of swamps and mudflats, and wet seasons were times of periodic, extensive flooding. The fossil mammalian fauna has a dominantly savannah aspect, but also includes riparian and aquatic types.

Recent Dracaena guianensis is particularly abundant in tidal marshy sections and swamps of the Amazon Valley, and Recent D. paraguayensis (more primitive in scutellation, yet having a reduced tooth count) inhabits drier ground on the fringes of the swamps in southern Brazil and Paraguay. The fossil Dracaena colombiana is found in the Upper Red Beds (playa lake deposit), San Nicolás clays (lacustrine deposit), and the Monkey Unit (sheet floodplain deposit). Tupinambis cf. T. teguixin occurs in the Lower Red Beds (playa lake deposit). These units all reflect a regional marshy floodplain environment. According to Fields (op. cit.) the Magdalena Valley in this region today has a semi-arid climate and is between four and five hundred meters above sea level in the area where these sediments were deposited. Neither Tupinambis nor (especially) Dracaena usually occur at this altitude, for both are humid-tropical types. They are thus in accord with structural and depositional indications in the sediments (op. cit.) for a lower altitude and moister climate in this area during the late Miocene.

These fossils constitute a considerable range extension for the genera involved. *Dracaena* is found today from the Guianas southward to the Amazon, Tocantino, and São Francisco basins, and from the southern Matto Grosso region, Brazil, south to the District of Chaco, Paraguay (Amaral, 1950). *Tupinambis* occurs over much of the forested districts of tropical South America from Trinidad south through the Guianas to Uruguay. Thus, nearly a thousand miles separate the fossils from their nearest Recent representatives. It is apparent that these genera were

once much more widely distributed over northern South America than they are at present, and that their habitat has been restricted both by uplift and by increasing aridity.

The presence of *Tupinambis* in these late Oligocene and late Miocene sediments indicates an early Tertiary origin for this genus, and perhaps also for *Dracaena*. The bufonid frog mentioned in the introduction is closely related to the Recent South American species *Bufo alvarius* and *B. crucifer*, and further heightens the modern aspect of the late Miocene herpetofauna of northern South America. It is clear that modernization of at least part of this fauna took place not later than the Miocene, and quite probably much earlier.

SUMMARY

The teiid lizards *Dracaena colombiana*, n. sp., and *Tupinambis* cf. *T. teguixin*, and an unidentified iguanid lizard occur in the late Miocene La Venta fauna, Colombia, South America. The fossil teiids, found a thousand miles from their nearest modern representatives, indicate a once greater distribution for these genera in northern South America. Their presence corroborates previous interpretation of the La Venta region during the late Miocene as a moist, swampy, lowland floodplain.

A fragmentary specimen from the Coyaima fauna shows the presence of *Tupinambis* sp. in the late Oligocene of the same region.

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