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A REVIEW OF THE SOUTH AMERICAN IGUANID LIZARD GENUS PLICA

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SYNOPSIS

The nomenclatorial history, taxonomy, distribution, and external morphology of the iguanid lizard genus Plica are reviewed, and the genus is compared with related iguanid genera. Plica plica and Plica umbra are recognized as the only valid species. Geographic variation in Plica umbra is discussed, and two races are recognized: the nominate form in Venezuela and the Guianas, and P. u. ochrocollaris Spix in the Amazonian basin of northern Bolivia, Peru, Ecuador, Colombia, and northern Brazil. Use of the generic name Uranoscodon Boie is discussed, and Lacerta superciliosa is designated as its type species.

INTRODUCTION

Plica plica and Plica umbra are among the most abundant, widespread, and earliest known lizards of South America. Their range includes most of northern South America east of the Andes as far to the south as northern Bolivia, and save for the northern parts of Venezuela and Trinidad, from which P. umbra is absent, they are often to be found in the same locale. Both species are conspicuous, arboreal insectivores, and they are exceedingly similar in choice of habitat, diet, movements, and general reactions.

In physical appearance the two species are quite different, and they are easy to distinguish in the field. Plica plica has small dorsal and ventral scales, tufts of spines on the sides of the neck, and a colour pattern of dark brown bands or marbling on a background of light to olive green, a white chin with a black throat and a narrow, black collar. Plica umbra has large dorsal and ventral scales, no spiny scales on the neck, and a colour pattern that is highly variable as well as metachromatic, consisting basically of wide bands or blotches of red, brown, or yellow on a background in some shade of green. Another curious distinction is the colour of the lining of the mouth: white in plica, and deep violet in umbra.

The nomenclatorial history of Plica and related genera has been long and extremely confused. Two other species are now incorrectly recognized: P. tuberculatum Andersson (1918: 2), and P. stejnegeri Burt & Burt (1930: 24), and two currently recognized species of Tropidurus, T. holotropis Boulenger (1912: 420), and T. uncinatus Werner (1899: 480) are actually synonyms of Plica umbra. The genus Plica itself has never been adequately characterized or diagnosed, and in most European museums it is still catalogued under the name Uraniscodon Kaup.

In this study the history of the nomenclature of Plica is presented, the genus is defined and diagnosed, its species are redescribed and accompanied by synonomies, and geographic variation in Plica umbra is discussed.
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The following abbreviations are used:

B.M.N.H. British Museum (Natural History), London.
C.A.S. California Academy of Sciences, San Francisco.
F.M.N.H. Field Museum of Natural History, Chicago.
L.A.C.M. Los Angeles County Museum, Los Angeles.
M.C.Z. Museum of Comparative Zoology, Harvard University, Cambridge.
N.M.W. Naturhistorischen Museum, Wien.
N.R.M.S. Naturhistoriska Riksmuseet, Stockholm.
S.M.F. Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt a.M.
S.N.M. Stanford Natural History Museum, Stanford.
Z.M.B. Zoologisches Museum der Humboldt Universität, Berlin.
Z.M.H. Zoologisches Staatsinstitut und Zoologisches Museum, Hamburg.

HISTORICAL REVIEW

Linnaeus (1758) described the two valid species currently referred to the genus Plica as Lacerta Umbra (pg. 207) from "Meridionalibus," and Lacerta Plica (pg. 208) from "Indiiis." Although Linnaeus made no reference to it a figure of plica had been included by Seba (1734: II.65.5), a figure which later formed the basis for Laurenti's (1768: 48) Iguana chalcedica from "Gallaccia."

Latreille placed umbra in the genus Iguana (1802a: 263), and plica in the genus
Stellio (1802b: 27). Later that same year Daudin (1802) employed the combinations Agama umbra and Agama plica. However, his characterization of Agama umbra, based upon specimens from Cayenne and Surinam, is clearly that of Linnaeus’ Lacerta plica, while his reference to Agama plica is based solely on the authority of Linnaeus. Merrem (1820: 54), and Wied (1825: 125) also included these species in Agama.

Spix (1825: 10) described Lophurus ochrocollaris from “in sylvis fluminis Amazonum,” and on the following page described Lophurus Panthera from “sylvis ad pagum Ecágá.” The types of both forms, formerly in the Zoologische Sammlung des Bayerischen Staates, München, were destroyed during World War II. However, it is clear from the descriptions and coloured figures of Spix that ochrocollaris was based upon a sombre coloured adult of Plica umbra, and panthera was based upon a brightly coloured juvenile of Plica plica.

At this point the nomenclatorial history of Plica becomes confused with that of two unrelated genera, Enyalus and Uranoscodon. Kaup (1825: 590) described the genus Uranoscodon, based upon Linnaeus’ (1758: 200) Lacerta superciliosa, although he included as well both plica and umbra. Boie (1825: 1090), in commenting upon Kaup’s work, indicated that Agama catenata (Wied, 1821: 247), and Agama picta (Wied, 1925: 125) should be included in the same genus with superciliosa, for which he suggested that either his own name Ophryessa, or Uraniscodon (emended from Kaup’s Uranoscodon) might be used. Boie specifically excluded plica and umbra from this genus. In the following year Kaup (1826: 89) adopting Boie’s spelling of Uraniscodon, gave a more detailed description of the genus, to which he referred eight species. In addition to superciliosa, plica, and umbra he included Lophurus rhombifer (Spix, 1825: 9), Lophurus margaritaceus (Spix, 1825: 10), Agama picta, Agama catenata, and Agama hispida (Spix, 1825: 12). L. rhombifer and L. margaritaceus are synonyms of Agama catenata, and both catenata and picta are currently referred to as Enyalus (Etheridge, 1969). Agama hispida Spix is now regarded as a species of Tropidurus. Later that year Boie (1826: 119), in dealing with most of the same species, placed in the genus Ophryessa the species superciliosa, catenata, margaritaceus, ochrocollaris, panthera, and auronitens. As pointed out above, margaritaceus is a synonym of catenata, ochrocollaris a synonym of umbra, and panthera a synonym of plica; auronitens, as recognized by Kaup (1826: 90) is a synonym of superciliosa.

Most of the same species were referred to by Fitzinger (1826: 48), who recognized Boie’s Ophryessa, in which he included superciliosa, catenata, margaritaceus, and umbra. In the genus Echphymotes Fitzinger placed plica, undulatus, pictus, and acutirostris. Kaup (1827: 612) then proposed the subdivision of Uraniscodon into three subgenera: Uraniscodon, containing Agama hispida; Pneustes, containing picta, umbra, and plica; and Ophryessa, containing superciliosa, catenata, and margaritaceus.

Wagler (1830: 150) described the genus Hypsibatus, including in it the species plica, umbra, and picta. Wiegmann (1835: 289) replaced Hypsibatus with Hypsibolus, pointing out that the former was preoccupied by Hypsibates Nitzsch (1827: 150), a genus of birds.¹

¹ Under Article 56 (a) of the current edition of the International Code of Zoological Nomenclature Hypsibatus Wagler and Hypsibates Nitzsch would not now be considered homonyms, but under Article 23 (b) Hypsibatus Wagler is to be considered a nomen oblivum.
Gray (1827: 208) described Lophurus agamoides, which he later (Gray, 1831: 41) recognized as a synonym of Plica plica. Gray (1831: 40) described Plica as a subgenus of Ophiessa (an emendation of Ophryessa Boie), including in the subgenus brasiliensis, picta, and plica. Brasiliensis is unrecognizable from its description, but probably is a synonym of Enyalius catenatus (Etheridge, 1969: 244). The characterization of Ophiessa (Plica) picta is clearly that of Plica umbra, although Gray lists as its synonyms Agama picta Wied, Lophurus ochrocollaris Spix, and L. panthera Spix. The characterization of plica is that of Plica plica, and listed as its synonyms were Lacerta plica Linnaeus, Agama plica and Agama umbra of Daudin, and Lophurus agamoides Gray.

The confusion between Wied's Agama picta (= Enyalius pictus fide Etheridge, 1969) and Plica umbra was continued by Schinz (1833: pl. 25; 1835: 86) who figured Wied's species of Enyalius under the name Calotes pictus, and referred to its synonymy Lophurus ochrocollaris and L. panthera of Spix.

Duménil & Bibron (1827) used Wagler's name Hyphisatus for two species, H. agamoides, and a new form, H. punctatus, both of which are clearly synonyms of Plica plica. In the same work Duménil & Bibron (1837: 247) proposed the new genus Uperanodon, based on Plica of Gray in part, and Hyphisatus of Wagler in part. Included in Uperanodon were ochrocollarae, with Lacerta umbra listed as its synonym, and pictum, with Lophurus panthera as a synonym.

Fitzinger (1843: 58) included umbra and pictus in the genus Hyphisatus, with umbra designated as type of the subgenus Hyphisatus, and pictus the type of the subgenus Uperanodon. On the following page he included punctatus (of Duménil & Bibron) and plica in the genus Ptychosaurus, designating punctatus as the type of the subgenus Ptychosaurus, and plica as the type of the subgenus Ptychopleura.

Gray (1845: 223) referred two species to Uraniscodon: umbra, based on a specimen from Pernambuco that is clearly Plica umbra, and pictum, based on Wied's description of Agama picta. He then refers to Plica umbra, based on a specimen of uncertain locality and referable to Plica plica, and Plica punctata (p. 224) based on the description of Hyphisatus punctatus.

Cope (1876: 170) described Hyperanodon pelligerus from Peru, another synonym of Plica umbra.

Boulenger (1885: 179–180) did a remarkably good job of untangling the confused history of the genus, correctly recognizing the existence of only two valid species, and erring only in the consideration of Agama picta as a synonym of umbra, and in using the generic name Uraniscodon rather than Plica.

Stejneger (1901: 182) pointed out that Kaup's original description of Uranoscoodon was based upon Lacerta superciliosa, although plica and umbra were included by Kaup in the genus, and that Boie (1825: 1090) specifically excluded plica and umbra from the genus. Although this may not be considered a formal designation of the type species of Uranoscoodon, as Stejneger believed, to do so now would certainly seem to be the desirable course. I therefore designate Lacerta superciliosa Linnaeus (1758: 200) as the type species of the genus Uranoscoodon Kaup (1825: 590). Note that although Fitzinger (1843: 16) designated superciliosa as type of the subgenus
Ophryoëssa (emended from Ophryessa), Boie did not publish the description of Ophryessa until several months after the publication of Kaup's Uranoscodon.

Following the appearance of Boulenger's catalogue, three additional names have been proposed for Plica umbra: Tropidurus uncarinatus from Surinam (Werner, 1899: 480), Tropidurus holotropis from Peru (Boulenger, 1912: 420), and Plica tuberculatum from Bolivia (Andersson, 1918: 2). An additional new species, described as Plica stejnegeri (Burt & Burt, 1930: 24), is a synonym of Tropidurus spinulosus.

A review of the recent literature, and of the catalogues of numerous museums in the United States and Europe indicates that at the present writing Tropidurus holotropis, T. uncarinatus, Plica tuberculatum, and Plica stejnegeri are all considered valid.

**PLICA** Gray, 1831

In Cuvier edit Griffith, The Animal Kingdom, 9: 40. Type species: *Lacerta plica* Linnaeus 1758.


*Uperanodon* Duméril & Bibron, 1837, p. 247. Type species: *Lophurus ochrocollaris* Spix.

*Pythopleura* Fitzinger, 1843, p. 59. Type species: *Lacerta plica* Linnaeus.

*Psychosaurus* Fitzinger, 1843, p. 59. Type species: *Hypsibatus punctatus* Duméril & Bibron.

*Hyperanodon* Agassiz, 1847 (replacement name for *Uperanodon* Duméril & Bibron), p. 190.

**Definiton and Diagnosis.** No adequate characterization or diagnosis of the genus *Plica* has been published. Boulenger (1885: 179), using the name *Uranoscodon*, listed a number of characteristics that the species *umbra* and *plica* have in common, by which, supposedly, they may be distinguished from other iguanids. Most of the characters listed by Boulenger are shared with one or more other iguanid genera. In his key to the genera of iguanid lizards Boulenger (1885: 4) employed the characteristics of "digits strongly bent at the articulations; anterior maxillary teeth longest" to distinguish *Uranoscodon* (that is *Plica* in current usage) from *Tropidurus*: "digits straight; no canine-like teeth." The digits are bent at their articulations to at least some degree in *Tropidurus* and *Uracentron*, and in some species of *Tropidurus*, e.g. *spinulosus*, *pictus*, and *bogerti*, the digits are as strongly bent as they are in *Plica*. The enlargement of anterior maxillary teeth is ontogenetic. Even though they are relatively longer in adult *Plica* than in *Tropidurus*, the condition is approached by some species of *Tropidurus*. Although enlarged anterior maxillary teeth and bent digits will not distinguish *Plica* from other iguanid genera, several other characteristics will.

*Plica* belongs to a group of South American–West Indian iguanids that is distinguished by the presence of a large sternal fontanelle and the absence of femoral pores, the "tropidurines" (Etheridge, 1964: 629). Within the tropidurines *Plica* is a member of that section in which the interparietal scale is very much larger than the adjacent scales, a group which also includes *Tropidurus*, *Uracentron*, *Strobilurus*, and *Uranoscodon*. The characteristics by which *Plica* may be distinguished from *Tropidurus* are as follows:
**Plica**

1. Orbit bordered below by 5 to 7 subequal suboculars; no enlarged preocular.

2. Loreal scales small and numerous; several rows of loreolabials.

3. No enlarged postmentals or lateral gulars.

4. Nostril in the approximate centre of nasal scale, directed anterolaterally.

5. Superciliaries short and broad, forming a sharp crest.

The characteristics by which *Plica* may be distinguished from *Uranoscodon* are as follows:

**Uranoscodon**

1. Upper head scales small, subequal; supraoculars small; supraorbital semicircles not distinct; scales irregularly pyramidal.

2. Interparietal scale about as wide as distance between orbits.

3. Superciliary crest strongly projecting, the last superciliary conspicuously enlarged.

4. Tail long and thick, distinctly compressed, with a serrate middorsal crest.

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**Plica plica** (Linnaeus)

*Lacerta Plica* Linnaeus, 1758, p. 208 (type locality, "Indiis"; here restricted to the vicinity of Paramaribo, Surinam).

*Iguana chalcidea* Laurenti, 1768, p. 48 (type locality, "Gallaccia").

*Agama umbra* Daudin, 1802, p. 375.

*Agama plica* Daudin, 1802, p. 412.

*Stelio plica* Latrielle, 1802b, p. 27.

*Lophyurus Panthera* Spix, 1825, p. 11 (type locality, "sylvis ad pagum Ecgá," Brazil).

*Ecephymotes Plica* Fitzinger, 1826, p. 49.

*Uraniscodon plica* Kaup, 1826, c. 91.

*Uraniscodon (Pneustes) plica* Kaup, 1827, c. 610.

*Lophyurus (Ophyresa) Agamoides* Gray, 1827, p. 208.

*Hypsibatus Plica* Wagler, 1830, p. 150.

*Ophyessa (Plica) Plica* Gray, 1831, p. 40.

*Hypsibatus agamoides* Wiegmann, 1834, p. 15.
Hypsibatus punctatus Duméril & Bibron, 1837, p. 258 (type locality, none given).
Hypsibius plica Wiegmann, 1835, p. 289.
Psychosaurus (Psychosaurus) punctatus Fitzinger, 1843, p. 59.
Psychosaurus (Psychopleura) Plica Fitzinger, 1843, p. 59.
Plica umbra Gray, 1845, p. 223.
Plica punctata Gray, 1845, p. 224.
Hypsibius punctatus Peters, 1877, p. 408.
Plica plica Burt and Burt, 1930, p. 19.

HOLOTYPE. N.R.M. No. KaF 1900 : 112. Linnaeus obviously erred in listing India as the origin of the holotype. Although the ranges of both species of Plica in South America are vast, geographic variation in Plica umbra is sufficient to narrow the origin of the syntypes of that species to the general region of the Guianas. I have elsewhere (Etheridge, 1968 : 51) pointed out that many of the South American species of plants and animals described by Linnaeus were brought to him from Surinam by Carl Gustaf Dahlberg and Daniel Rolander, the latter a student of Linnaeus, and that most of their collections were made in Paramaribo and the nearby countryside. I, therefore, propose the restriction of the type locality of Plica plica to the vicinity of Paramaribo, Surinam.

CHARACTERISTICS. Rostral band-like, about four times wider than high. Nasals convex, above and anterior to canthal ridge, separated from rostral and upper labials by two rows of small scales; nasal opening directed dorsolaterally. Internasals, frontonasals, and prefrontals small, imbricate, irregularly arranged. Supraorbital semicircles moderately distinct anteriorly, scarcely distinct from adjacent parietal scales posteriorly, medially separated by a row of small scales or with one or two scales in contact medially between the orbits. Four to seven large, transversely widened supraoculars, medially separated from supraorbital semicircles by two rows of small scales, laterally separated from superciliaries by several rows of smaller scales. Interparietal much larger than adjacent scales, a third to a fifth as wide as head, separated from supraorbital semicircles by smaller scales, narrowing in front, with a central "eye." Scales of parietal and upper temporal region small, irregularly arranged, imbricate, and sharply keeled. An elongate, sharply keeled canthal, followed by four or five elongate, keeled superciliaries, in turn followed by two similar scales overlapping in the opposite direction; the canthal and superciliaries together forming a projecting crest. About 15 imbricating scales in loreal region, not markedly distinct from adjacent loreolabials and scales of preocular region. Orbit bordered below by a well defined arc of large scales of more or less equal size, each with a sharp keel near the upper margin; no enlarged preocular. Loreolabials in several irregular rows, separating nasals, loreals, and suboculars from upper labials. Temporals small, rhomboidal, imbricate, obtusely keeled; those bordering anterior margin of ear with a laterally projecting spine. Four to six rectangular upper labials. Mental subtriangular. Five or six lower labials similar to upper labials. No enlarged postmental or lateral gulars. Gulars small, imbricate, smooth anteriorly, becoming smaller still and obtusely keeled near the transverse gular fold; a medial row of very slightly enlarged scales along margin of dewlap.

A row of enlarged scales aligned middorsally extending from occiput to proximal
third of tail, forming in adults a low serration on the neck and anterior back. Dorsal nuchals conical, each with a stout central spine, not distinctly imbricate, becoming smaller still on the sides of the neck; three patches of markedly enlarged, spinose scales on side of neck, one posterodorsal to the ear opening, the third posterior to the anterodorsal patch. Dorsal body scales keeled, imbricate, the keels forming oblique lines that converge toward the midline posteriorly, each keel ending in a short, outward projecting spine; dorsolateral body scales becoming gradually smaller until they meet the dorsolateral body fold, the latter provided with slightly larger and more distinctly spinose scales; below the dorsolateral fold scales becoming gradually larger and less strongly keeled, grading into smooth, rhomboidal, imbricate ventrals.

**Fig. 1.** Dorsal view of the head of *Plica plica* (A.M.N.H. 61315).

Two transverse gular folds, the posterior one rising on each side as an antibrachial fold enclosing granular scales, arching above the forelimb insertion, and continuing back as a dorsolateral body fold to end just above the hindlimb insertion. Sides of neck with strong, irregular folds.

Caudal scales anterior to first autotomy segment similar to body scales above and below; autotomy annuli distinct, with five scale rows in the first few segments, six rows in segments of the midportion of the tail, and thereafter seven rows in each segment.
Upper limb scales mostly rhomboidal, keeled, imbricate, those of the proximal limb segments also mucronate; ventral limb scales mostly smooth, imbricate. Supracarpals, supratarsals, and supradigitals keeled, imbricate; infracarpals and infratarsals each with a median keel ending in a stout spine. Infracidental lamellae each with a sharp, median keel ending in a stout spine, flanked on each side by a much weaker keel and spine. Proximal lamellae of first and second fingers, and first, second and third toes somewhat enlarged dorsoventrally.

COLOUR. The pattern is basically one of cross bands or bold, irregular blotches of black, dark brown, or grey on a background of some shade of green. The anterior cross band usually forms a distinct, very dark collar. Upper surfaces of the limbs are similarly patterned. Small individuals are whitish below; adult males have a black throat narrowly bordered with yellow, shading into orange that covers the rest of the ventral surfaces of the body, limbs and tail. In life the epithelial lining of the mouth is white. A detailed description of the colour in life of an individual from Kartabo, British Guiana may be found in Beebe (1944: 204–205). The pattern usually remains distinct even after many years in preservative, with only the background fading to bluish or olive grey.

GEOGRAPHIC VARIATION. Unfortunately the poor state of preservation of most of the specimens examined does not permit a useful analysis of geographic variation in Plica plica. The most deviant sample I have seen is from Puerto Ayachucu on the Orinoco River, between Venezuela and Colombia. Specimens from this locality differ from others in having a more acuminate snout, larger dorsal snout scales, slightly smaller dorsal body scales, less well developed lateral neck spines, and a less densely spotted throat in males. Specimens from the vicinity of Esmeralda, Venezuela also have large dorsal snout scales but are otherwise typical. Specimens from northern Venezuela, Trinidad, and the Guianas appear to reach the greatest maximum size, and because of greater development of scale mucrons have overall a more spiny appearance.

RANGE. (Text-fig. 2.) Trinidad and northern South America east of the Andes, including northern Brazil, British Guiana, Surinam, Cayenne, northern Bolivia, eastern Peru, eastern Ecuador, eastern Colombia, and Venezuela except in the northwest.


**Fig. 2.** Map of northern South America showing localities for *Plica plica.*

**Plica umbra** (Linnaeus)

*Lacerta Umbra* Linnaeus, 1758, p. 207 (type locality, " Meridionalibus " ; here restricted to the vicinity of Paramaribo, Surinam).

*Iguana umbra* Latreille, 1802a, 263.

**Agama umbra** Merrem, 1820, p. 54.

**Lophyrus ochricollaris** Spix, 1825, p. 10 (type locality, " sylvis fluminis Amazonum, " Brazil).

**Ophryessa Umbra** Fitzinger, 1826, p. 48.

**Uranisodon Umbra** Kaup, 1826, c. 91.

**Uranisodon (Pneustes)** umbra Kaup, 1827, c. 612.

**Hypsibatus umbra** Wagler, 1830, p. 150.

**Uperanodon ochrocollare** Duméril & Bibron, 1837, p. 247.

**Hypsibatus (Hypsibatus)** Umbra Fitzinger, 1843, p. 58.

**Uranisodon umbra** Gray, 1845, p. 223.

**Hyperanodon peligerus** Cope, 1876, p. 170 (type locality, Peru).

**Hyperanodon umbra** Peters, 1877, p. 408.
Hyperanodon panthera Peters, 1877, p. 408.
Uraniscodon umbra Boulenger, 1885, p. 179.
Tropicurus unicarinatus Werner, 1899, p. 602 (type locality, Surinam).
Tropicurus holotropis Boulenger, 1912, p. 420 (type locality, Alipayaca, Rio Pastaza, Ecuador).
Plica tuberculatum Andersson, 1918, p. 2 (type locality, San Fermin, Bolivia).

Syntypes. N.R.M. No. 1900 : 111 (2 exs). The syntypes exhibit those characteristics of scalation that are typical of individuals from the region of the Guianas (see discussion of geographic variation below). The reasons applied to the restriction of the type locality of Plica plica are equally applicable to this species, and I therefore propose the restriction of the type locality of Plica umbra to the vicinity of Paramaribo, Surinam.

Characteristics. Rostral strap-like or subtriangular. Nasals moderately large, convex, above and anterior to canthal ridge, separated from rostral and anterior upper labials by one or two small scales; nasal opening directed dorsolaterally. Scales of internasal, frontonasal, and prefrontal region moderately large, more or less symmetrically arranged. Supraorbital semicircle scales large, usually three pairs in broad contact medially between the orbits. A row of large, transversely widened supraoculars, usually four in number, medially separated from supraorbital semicircles by two rows of small scales, laterally separated from superciliaries by two rows of smaller scales anteriorly; posterior enlarged supraocular in broad contact laterally with posterior superciliary. Interparietal scale large, a third to half as wide as head, narrowing anteriorly, in broad contact with posterior scales of supraorbital semicircles, with a central "eye." Posterior parietals bordering interparietal small to large, slightly to very strongly convex. A single, elongate canthal, followed by four or five elongate, overlapping superciliaries, in turn followed by three superciliaries overlapping in the opposite direction, the last much the longest; canthal and superciliaries together form a continuous, projecting crest. Scales of loreal region small, juxtaposed, scarcely distinct from loreolabials or scales of preocular region. Orbit bordered below by an ill defined arc of slightly enlarged, strongly keeled scales of nearly equal size. Loreolabials in several irregular rows, separating loreals and suboculars from upper labials. Temporals small, subimbricate, weakly and obtusely keeled, those bordering the ear anteriorly scarcely projecting. Upper labials four or five, more or less rectangular. Mental subtriangular. Lower labials five or six, similar to upper labials. No enlarged postmentals or enlarged lateral gulars. Gulars small, imbricate, becoming a little smaller, feebly keeled, and bluntly mucronate posteriorly as they approach the transverse gular fold.

A row of scales aligned middorsally beginning at the occiput and extending to the lumbar region, or past the sacral region and onto the tail; middorsal scales of neck and anterior body distinctly enlarged, forming a denticulate crest. Dorsal scales of body and neck rhomboidal, imbricate, with a blunt posterior keel and a short, blunt mucrone, the keels forming oblique rows that converge toward the midline posteriorly. Lateral neck scales, except those within skin folds, smaller, but otherwise similar to dorsal neck scales; lateral body scales similar to dorsals, grading into distinctly
keeled and mucronate ventrals. Dorsal, lateral and ventral body scales about equal in size, save the anterior laterals which are a trifle smaller.

Strong antibrachial folds containing granular scales, terminating dorsally about halfway between forelimb insertion and median crest, and joining a very strong transverse gular fold ventrally. No lateral body folds and no other lateral neck folds other than antibrachial and gular; no patches of enlarged scales on sides of neck.

Caudal scales anterior to first autotomy annulus similar to body scales both above and below; median crest disappears before first autotomy annulus. Autotomy annuli distinct, four scale rows in the first few annuli, five in those of the midportion of the tail, and thereafter six rows. Males lack enlarged postanal scales.

Forelimb scales equal to or a little smaller than body scales, imbricate and keeled, except for proximal postbrachials which are smooth, the keels forming lines more or less parallel to long axis of limb; postantibrachials more sharply keeled and more strongly mucronate than other forelimb scales. In males, a patch of smooth posterior infrafemorals three or four scale rows wide and about 20 scale rows long; all other hindlimb scales (as well as all posterior infrafemorals in females) keeled, imbricate, a little larger to a little smaller than body scales. Infraarpals and infratarsals each with a single, stout mucrone. Supradigitals unicarinate; subdigital lamellae with a strong median keel and mucrone flanked on each side by a much weaker keel and mucrone.

Scale counts are given in Table I. Maximum snout–vent lengths and body–tail proportions of both sexes are given in Table II.

**Colour.** The colour is highly metachromatic, and the pattern exceedingly variable. The pattern is basically one of wide, dark cross-bands or blotches on the body, limbs, and tail, light coloured on the throat and belly, with or without streaks of darker colour, and very dark colour within the antihumeral fold. The background is usually some shade of green, ranging from yellowish-green, to bright green, bluish-green, olive, or olive brown; the bands and blotches are usually some shade of brown. yellowish-brown, black, red, or orange. In adult males the centre of the throat may be orange, and there is a patch of yellowish colour anterior to the vent and on the lower surface of each femur. In life the epithelial lining of the mouth is deep violet. Beebe (1944: 207–8) has provided us with a most excellent and detailed description of the colour and pattern of four living animals at Kartabo, British Guiana, and Spix's (1825: pl. 12, fig. 2) illustration of Lophyurus ochrocollaris is a good representation of an adult. In preservative specimens usually become dark purplish brown with still darker markings, although the paler markings of the head and neck frequently persist.

**Geographic variation.** The very great majority of specimens may be readily identified as one of two distinct types. One of them occurs in the Guianas, the other in the Amazonian Basin of Brazil, Colombia, Ecuador, Peru, Bolivia, and in southern Venezuela. Specimens from intermediate localities are unavailable so that the question of whether two subspecies or two distinct species are involved cannot be
resolved with certainty. Tentatively, however, the two forms may be considered subspecies. The syntypes of *Plica umbra* are of the form that occurs in the Guianas. The oldest name available for the Amazonian form appears to be *Lophurus ochrocollaris* Spix.

![Dorsal view of the head of Plica umbra ochrocollaris (L.A.C.M. 49140).](image)

The two forms may be compared as follows:

**ochrocollaris**

1. Vertebral scale row prominent from occiput to base of tail, forming a distinct denticulation on the neck.

2. Dorsal head scales swollen, with blunt, irregular surface.

3. A pair of large, distinctly pyramidal scales flank the posterolateral corners of the interparietal.

4. All scales of body and limbs more sharply keeled and distinctly mucronate.

5. Scales larger (Table I).

**umbra**

1. Vertebral scale row prominent on neck and anterior body, becoming indistinguishable from adjacent scales on posterior back, and forming only a slight denticulation on the neck.

2. Dorsal head scales smooth or nearly so.

3. Scales flanking posterolateral corners of interparietal smaller, and flat or nearly so.

4. Scales of body and limbs less sharply keeled, less distinctly mucronate, those of the belly only feebly keeled.

5. Scales smaller (Table I).
Synonyms of *Plica umbra ochrocollaris* are *Hyperanodon peltigerus* Cope, *Tropidurus holotropis* Boulenger, and *Plica tuberculatum* Andersson. A synonym of *Plica umbra umbra* is *Tropidurus uncinatus* Werner. These synonyms are further discussed in the following section.

**Remarks.** Boulenger (1885:179–180) adequately dealt with the synonomies of names proposed for *Plica umbra* prior to the appearance of his Catalogue. Subsequently two species of *Tropidurus* have been proposed that are in fact also synonyms of *Plica umbra: Tropidurus uncinatus* (Werner, 1899:480), and *Tropidurus holotropis* (Boulenger, 1912:420). In their type descriptions both species were compared only with other forms of *Tropidurus*, with no mention of the genus *Plica*. The reasons for their generic allocations were unspecified; however, the authors apparently based their decision to place these species in *Tropidurus* upon the presence of a very large interparietal scale. In my studies at a large number of American and European museums I was unable to find any specimens, other than the syntypes, catalogued as *Tropidurus uncinatus*. However, many Ecuadorian and Peruvian specimens of *Plica umbra* are catalogued as *Tropidurus holotropis*, and that name has appeared in such recent faunal lists as Mertens (1956:120), and Peters (1967:35).

*Tropidurus uncinatus* was based upon a subadult female and a male (N.M.V. 18728–9) from Surinam. Both syntypes are in good condition, and are identical in all details of scation, colour pattern, and proportions with specimens of *Plica umbra* of comparable size from northeastern South America. The number of scales in the vertebral crest from occiput to the anterior margin of the thigh (53, 56), the number of paravertebral scales in the same length (74, 78) and the number of scales around the middle of the body (59, 59) are within the limits of variation for specimens from this region (Table 1).

<table>
<thead>
<tr>
<th>Subspecies</th>
<th>Sex</th>
<th>N</th>
<th>Vertebral</th>
<th>Paravertebral</th>
<th>Midbody</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>umbra</em></td>
<td>M</td>
<td>19</td>
<td>49–(54'6)–61</td>
<td>70–(78'9)–90</td>
<td>49–(57'1)–71</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>23</td>
<td>46–(54'7)–63</td>
<td>66–(74'8)–91</td>
<td>48–(56'3)–65</td>
</tr>
<tr>
<td><em>ochrocollaris</em></td>
<td>M</td>
<td>26</td>
<td>32–(35'8)–46</td>
<td>47–(58'5)–69</td>
<td>43–(49'6)–57</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>17</td>
<td>36–(40'6)–47</td>
<td>48–(57'2)–67</td>
<td>41–(59'3)–55</td>
</tr>
</tbody>
</table>

Scale counts of the subspecies of *Plica umbra*. N = number of specimens examined for these counts. Vertebral scales are counted along the midline from occiput to a line even with the anterior margin of the thighs held at right angles to the body axis; paravertebral scales are counted for the same distance; midbody scales are counted around the body midway between the limb insertions. Mean figures are in parentheses.

*Tropidurus holotropis* was based upon a subadult individual from Alpayaca, Rio Pastaza, Ecuador (B.M.N.H. 1912.11.1.29 [RR 1946.8.29.64]). It is identical in all details of colour pattern, scation, and proportions with specimens of *Plica umbra* of comparable size from eastern Ecuador. The number of scales in the vertebral crest (35), the paravertebral scale row (55), and around the middle of the body (45) are within the range of variation for specimens from this region (Table 2).
Table 2

<table>
<thead>
<tr>
<th>Subspecies</th>
<th>Sex</th>
<th>N</th>
<th>Snout-vent Length</th>
<th>Tail/Snout-vent Length</th>
<th>Range in mm.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>umbra</em></td>
<td>M</td>
<td>15</td>
<td>72–100</td>
<td>2'02–(2.24)–2'44</td>
<td>2'02–(2.18)–2'42</td>
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<td></td>
<td>F</td>
<td>14</td>
<td>61–94</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>ochrocollaris</em></td>
<td>M</td>
<td>23</td>
<td>67–90</td>
<td>2'00–(2.16)–2'51</td>
<td>1'90–(2.06)–2'33</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>18</td>
<td>42–90</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Snout-vent lengths and tail/snout-vent length ratios for *Plica umbra*. N = number of specimens examined. Mean figures are in parentheses.

Andersson (1918 : 2) described *Uraniscodon tuberculatum* from San Fermin, northwestern Bolivia, and subsequently Burt and Burt (1930 : 19) referred to the species as *Plica tuberculatum*. Andersson compared *tuberculatum* with *umbra*, from which it was said to differ in the lepidosis of the head, especially the wider interparietal scale, the absence of a feeble, longitudinal fold on the chin, a more strongly raised supraciliatory ridge, and a different colour, especially on the head. The holotype (N.R.M. 3256) is a juvenile, 55 mm in snout–vent length, in fair condition except that the skin of the lateral neck region is badly lacerated. Andersson apparently compared the holotype of *tuberculatum* with adult specimens of *Plica umbra* from the northeastern portion of its range, for the differences he noted are clearly due to ontogenetic differences between juveniles and adults, and to geographic variation within the species. The feeble longitudinal fold on the throat of adults is not apparent in juveniles, and the vivid head pattern of juveniles becomes obscure in adults. Although not specifically mentioned by Andersson as a diagnostic character, the large interparietal scale, "much broader than half the breadth of the head," was used by Burt and Burt (1930 : 19) to distinguish *tuberculatum* from *umbra*, "... about half as wide as the head." The head width of the holotype is 11.0 mm, the interparietal width 6.4 mm; thus the interparietal is only slightly more than half (±58) as wide as the head, and within the range of variation of *umbra*. The strongly projecting supraciliatory ridge is characteristic of specimens of *umbra* from the western portion of its range. In these, and in all other details of scalation, colour pattern, and body proportions the holotype of *Uraniscodon tuberculatum* is typical of juvenile specimens of *Plica umbra* from the western portion of its range.

Range. (Text-fig. 4.) Most of northern South America east of the Andes, including British Guiana, Surinam, Cayenne, southern Venezuela, eastern Colombia, eastern Ecuador, eastern Peru, extreme northern Bolivia, and northern Brazil. The race *P. u. umbra* is confined to the Guianas; the remainder of the range of the species is occupied by *P. u. ochrocollaris*.


**Fig. 4.** Map of northern South America showing localities for *Plica umbra umbra* (triangles), and *Plica umbra ochrocollaris* (circles).

**No Specific Locality:** N.R.M. 1900 (2 exs) (syntypes, *Lacerta umbra*). Additional records from Surinam have been provided to me (*in litt.*) by Mr. Marinus S. Hoogmoed: Wilhelminagebergte, Fallawatra-Copename, Matta, Cultuurtuin, Coeromenieland, Sipaliwini, Surinamerivier Powakka, Maguire, Moengo Tapoe, Wanekreek.
Djaikreek, Calibi, Tibiti, Kaborkreek, Marowýne Nassaugebergte, Kaiserberg airdrip, Bigiston dist. Marowýne, Boven Nicherie.


Species Erroeneously Referred to *Plica*

Burt and Burt (1930: 19) described *Plica stejnegeri*, based upon a specimen (U.S.N.M. 73505) from "Argentina." Their reasons for referring this species to *Plica* were not specified; however, they were probably led to this allocation because the skin of the neck is strongly plicate and pouched, and on the sides provided with many tufts of small, erect, spinose scales, a condition that closely resembles that of *Plica plica.*
I have compared the holotype of *Plica stejnegeri*, an adult male, with series of *Tropidurus spinulosus* from Brazil, Bolivia, and Argentina, and find that it is identical in all important details of scutation, colour pattern, and proportions. In this species the scales of the middorsal crest become elongate, two to four times higher than long, in large adults, and the spininess of the body scales, especially those of the lateral neck region and the posterior tibial, becomes more pronounced. *Plica stejnegeri* is thus clearly a synonym of *Tropidurus spinulosus*.

In a recent check list of the lizards of Venezuela Donoso-Barros (1968: 114) placed *Tropidurus bogerti* Roze (1958 : 247) in the genus *Plica* without comment. Roze discussed in detail the superficial resemblance of *bogerti* to *Plica plica* and correctly concluded that the species should be placed in *Tropidurus*. To this I can only add that in every respect *bogerti* shows the characteristics of *Tropidurus* that I have used to distinguish that genus from *Plica*.

**REFERENCES**


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