Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE Vol. 125, No. 4

ON THE SPECIES OF PSEUDIDAE (AMPHIBIA, ANURA)

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WITH ONE PLATE

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
AUGUST, 1961



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INTRODUCTION

A very substantial contribution towards an understanding of the systematics of the frogs of the genera *Pseudis* and *Lysapsus* was achieved by Savage and Carvalho (1953). A few points, however, appear to require modification, among them the status of *Pseudis mantidactylus* Cope (thought by Savage and Carvalho to be a synonym of *P. paradoxus*).

A preliminary examination of specimens of Pseudis mantidactylus in the collection of the Sección Herpetología del Museo Argentino de Ciencias Naturales, of the Facultad de Ciencias Exactas y Naturales de la Universidad de Buenos Aires and of the Colegio Nacional de Buenos Aires (Argentina), as well as of others collected by myself in Argentina, Provincia de Buenos Aires (Paso de la Noria, San Miguel, Bella Vista, Santo Domingo), impressed upon me the constancy of the shape and position of the dark and light bands of the ventral aspect of the thighs. In contrast, specimens of Pseudis paradoxus from Rosario, Santa Fé and Corrientes, showed a quite different thigh pattern. The specimens of P. paradoxus from other areas in the Museum of Comparative Zoology (MCZ), United States National Museum (USNM), the American Museum of Natural History (AMNH), Chicago Natural History Museum (CNHM), and Carnegie Museum (CM) collections, which I was able to examine in 1959-60, showed still other patterns of thigh coloration. Such facts as these led me to regard P. mantidactylus as a distinct species and to recognize several subspecies within P. paradoxus as well. A study of Lysapsus limellus showed the existence of races in this form also.

My previous studies on *Bufo granulosus* and its subspecies have convinced me that there has been recognition of too many species and subspecies without proper reference to the ecological and physiographical features of the environment. I have attempted to study the present species in relation to natural geographical units, such as the hydrographical systems of South America. Such a procedure is particularly useful for the Pseudidae, which are exceedingly aquatic. The species I know best is *P. mantidactylus*. I am familiar with it in the wild and I have never seen it come out of the water voluntarily; instead, it stays always in pools and slow creeks, covered with floating vegetation (*Lemna* sp. and *Jussiaea* sp.). Fernández and Fernández (1921:

139) also report that *P. mantidactylus* in captivity does not leave the water, remaining in small muddy puddles. Possibly individuals move from pool to pool following heavy rains; ordinarily, however, the several populations very definitely tend to remain each within a given hydrographical basin. This is very apparent in the distributional patterns; of the six subspecies of *Pseudis paradoxus* which I describe below, one is restricted to the Guianas, another to the Orinoco system, others to the São Francisco, Arassuahy and Beni rivers and a last one to the Río de la Plata basin. It is not improbable that further subspecies may be recognized in the intervening regions.

PSEUDIS PARADOXUS (LINNAEUS)

Description of the species as a whole. Snout more or less sharp, canthus rostralis indistinct. Loreal region oblique. Tympanum distinct. Vomerine teeth between the choanae large, forming two straight bars, little separated. Tongue rounded, with a small notch. Male with a single internal vocal sac. Small granulations on the dorsum, extending on to the hind limbs. In the pectoral region two sharp angular marks, corresponding to the scars produced in metamorphosis by the eruption of the fore limbs (a character persistent in the adult). Fore limbs relatively weak; fingers long, the pollex opposable; all fingers with cutaneous fringes, and with basal interdigital membranes between the second, third and fourth fingers; a long internal palmar tubercle and a small external one; simple subarticular tubercles. Proximal part of the arm wholly included in skin of body. Hind limbs strong, thigh and leg broad. Tarsal fold present; internal metatarsal tubercle more or less developed (varying according to subspecies); no external metatarsal tubercle, cutaneous fringe on the outermost and innermost toes; interdigital membrane well developed, inserting between the metatarsals and extending to the terminal half of the dilatations; subarticular tubercles simple. Dorsal coloration intermediate between greenish and brown, with darker spots. Venter with more or less abundant brown spotting. Four longitudinal dark lines and alternate light spaces in the ventral aspect of the thigh (the shape and disposition of these dark lines vary in the different subspecies; in the descriptions I shall number them from 1 to 4, starting from the external edge). A long light spot over the cloaca and one or two below it, prolonged by a row of light spots.

Skeletal characters. Skull with swollen otic region; occipital condyles widely separated. Correlated with this, the atlas with two anterolateral prominences to receive the condyles which are far apart, the space between the prominences concave (i.e. "odontoid process" absent). [A similar atlas exists in some Leptodactylidae (Leptodactylus, Eleutherodactylus), Hylidae (Hyla), some Ranidae (Arthroleptides, Oeidozyga) and Phrynomeridae

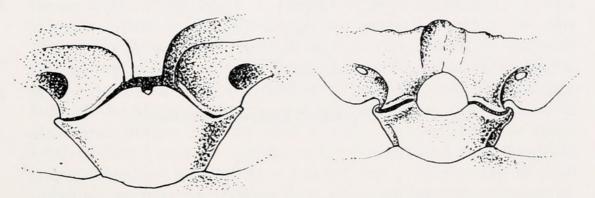


Fig. 1. Atlas and occiput of Bufo spinulosus (left) compared with atlas and occiput of Pseudis paradoxus (right).

(Phrynomerus). In other Leptodactylidae (Batrachophrynus, Telmatobius, Ceratophrys, Calyptocephala), Pelobatidae (Scaphiopus), Pelodytidae (Pelodytes), some Ranidae (Astylosternus, Rana) and Bufonidae (Bufo), there are no lateral prominences; instead the median portion of the articular surface is convex (i.e. "odontoid process" present) and the occipital condyles are closer to each other. This characteristic of the Pseudis atlas makes it inadvisable to group Batrachophrynus, Telmatobius, Ceratophrys and Calyptocephala with Pseudis in a subfamily Pseudinae as Noble suggested. In addition, however, the presence of an accessory phalanx in all digits excludes from the Pseudinae not only the genera just mentioned but also other genera such as Eleutherodactylus which Noble also wished to place in the subfamily, and which do show the Pseudis type of atlas.] Transverse processes of the vertebrae, including the second and sacral, approximately cylindrical; at the proximal end of the urostyle there is a neural arch as in a 10th vertebra (cf. some skeletons of Batrachophrynus macrosternum); close to this there is a 10th pair of the calcarean sacs. Pectoral girdle arciferal, omosternum plus a xiphisternum as a short, notched, cartilaginous plate. Terminal phalanges long, reaching the tips of the digits, i.e. discs not present.

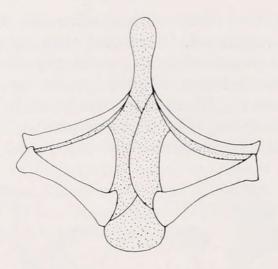


Fig. 2. Pectoral girdle of Lysapsus mantidactylus.

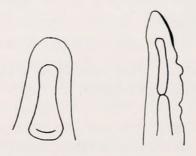


Fig. 3. Outline of tip of toe in relation to terminal phalanx. Lysapsus mantidactylus, left, dorsal view; right, lateral view.

SUBSPECIES OF PSEUDIS PARADOXUS

To differentiate the subspecies of *Pseudis paradoxus*, I use the following morphological characteristics: size of vomerine teeth, size of tympanum, whether the supratympanic fold is more or less visible, the shape of the internal metatarsal tubercle; and the following color characters: number of dark bands on the back, ventral spots on throat, breast and abdomen, dark lines and light spaces on the ventral thigh, one or two light spots below cloaca, and coloration of the ventral tibia.

PSEUDIS PARADOXUS PARADOXUS (L.)

1758 Rana paradoxa Linnaeus, p. 212.

1830 *Pseudis paradoxa* Wagler, p. 203; Günther, 1858, p. 5; Boulenger, 1882, p. 186.

Description. Adult male MCZ 12136, Demerara, British Guiana. The longitudinal diameter of the tympanum is equal to

eye diameter and also to the distance from eye to nostril. Supratympanic fold not distinct. Vomerine teeth large, with little separation. Metatarsal tubercle conical, oblique, not hooked. Back with four longitudinal dark lines, more or less interrupted. Dark spots on the dorsal aspect of limbs — longitudinal on the anterior limbs and transverse or oblique on the posterior limbs; external edge of the tibia with a dark longitudinal line; internal edge of tarsus dark. Dark spots on the interdigital membrane. Brown irregular spots on the throat and the ventral aspect of the fore limbs. On the pectoral region a dark comma-shaped line on each side at the pectoral angular scars; another pair of more lateral spots. Abdomen with scattered small round spots. Ventral surface of the thigh with longitudinal dark lines not very wide, sometimes broken up and with angular projections; the space between line 1 and the external edge is light and with irregular long spots; space between lines 1 and 2, light, immaculate, without invading angular projections from the bounding lines; space between 2 and 3 with such angular projections; lines 3 and 4 frequently joined towards the middle of the femur; space between line 4 and internal edge with angular projections that form light rectangles. Two light long spots below the cloaca. Ventral aspect of tibia with abundant short irregular lines.

Dimensions: Head and body 56 mm. Head length 18 mm. Head width 19 mm. Head height 8 mm. Eye 6 mm. Interorbital space 6 mm. Elbow to third finger 30 mm. Femur length 30 mm. Tibia length 32 mm. Tibia width 11 mm. Heel to fourth toe 45 mm. Foot length 32 mm. Adult female, same origin, MCZ 12135, head and body 54 mm.

Distribution: This subspecies is restricted to the British and Dutch Guianas.

Material studied: MCZ 12135-6 (2 specimens) British Guiana, Demerara, coast lands, E. Smith; MCZ 2775 (1 specimen) British Guiana, Demerara, C. W. Beebe, 1909; AMNH 13566-8 (3 specimens) British Guiana, Demerara River, Alayma, J. Rodway; MCZ 3901-2 (2 specimens) British Guiana, trenches near Georgetown, J. Rodway, 1914; AMNH 1305 (1 specimen) British Guiana, J. Rodway, 1912; AMNH 21423, 39588, 39638-40 (5 specimens) British Guiana, Georgetown; AMNH 49259 (1 specimen) British Guiana, Essequibo River, R. Snediger, V-31-1937; AMNH 5103 (1 specimen) Dutch Guiana, Paramaribo, J. A. Samuels; AMNH 24013 (1 specimen) Guiana.

PSEUDIS PARADOXUS CARIBENSIS SUBSP. nov.

1933 *Pseudis paradoxa* Parker, p. 10; 1934, p. 123; Gans, 1956, p. 2 (part); Kenny, 1956, p. 23.

1942 Pseudis paradoxis Ditmars, p. 51.

For diagnostic features see Table 1.

Description. Type, adult female MCZ 19890, Mayaro Bay, Trinidad, B. W. I. Tympanum rather smaller than the eye and smaller than the distance between eye and nostril. Oblique fold above the tympanum indistinct, but marked by a dark line. Vomerine teeth large, with little separation. Metatarsal tubercle with narrow base, forming a small hook. Back with six longitudinal dark lines more or less discontinuous. Dorsal surface of limbs and interdigital membrane as in the preceding subspecies. Throat, pectoral and abdominal regions with dark rounded spots (more abundant on the throat and breast). Ventral surface of thigh with thinner lines than in P. p. paradoxus; space between line 1 and external edge, with elongated punctations and spots; space between lines 1 and 2 light; space between lines 2 and 3 with abundant elongate spots; space between 3 and 4 light (the fourth line wider); between line 4 and internal edge abundant, elongate, irregular spots. One light, long, spot below the cloaca. Tibia ventrally with abundant short, irregular, lines. (The ventral coloration of the hind limbs is also perfectly visible in four-legged tadpoles.)

Dimensions: Head and body 64 mm. Head length 22 mm. Head width 25 mm. Head height 11 mm. Eye 6 mm. Snout height 4 mm. Interorbital space 7 mm. Elbow to third finger 33 mm. Femur length 39 mm. Tibia length 33 mm. Tibia width 11 mm. Heel to fourth toe 50 mm. Foot 36 mm. Paratype, adult male, CM 33787, head and body 60 mm.

Distribution: Nearly all the material that has been studied by me comes from the same locality, Mayaro, S.E. Trinidad Island. (This locality has recently been described, and photographs of it published by Gans, 1956.) Additional Trinidad localities have been reported by Kenny (1956): Plum Mitan ricefields near Biche (tadpoles); Icacos swamp near Cedros (adults); Apex oilfields at Fyzabad (males singing). This subspecies, however, seems to exist also in Venezuela. At least the specimen of Pseudis paradoxus figured by Lutz (1927, Plate II, figs. 18-19), from Maracay, Venezuela, has a ventral pattern similar to the Trinidad specimens. I have seen also one specimen from Hato Gabinero, Venezuela, that in general has the characteristics of this subspecies. In

this specimen the ventral coloration of the thighs is nearly the same as typical $P.\ p.\ caribensis$, with spots in the space between line 1 and external edge; some spots (but few and small) in the distal portion of the space between 2 and 3; short and irregular lines between the knee and the union of 3 and 4; moreover the commashaped spots on the pectoral region are lacking and the metatarsal tubercle is hook shaped. Other characteristics are close to those of $P.\ p.\ paradoxus$, as is the presence of four interrupted longitudinal dark dorsal bands; it is, however, different from both subspecies by having the ventral surface of the tibia without spots.

Material studied: MCZ 19890-1; 19893 (3 specimens) Trinidad, Mayaro Bay, N. A. Weber, XII-1934; MCZ 19892 (1 skeleton) Trinidad, Mayaro Bay; MCZ 26157 (1 specimen) Trinidad, St. Bernard Estate, Mayaro, M. G. Kugler, 1945; CNHM 49705-6 (2 specimens) Trinidad, Plaisance Mayaro, Stander, 1947; CM 33787 (1 specimen) Trinidad, Pond at Mayaro, C. Gans, IX-22-1953; USNM 137347 (1 specimen) Venezuela, Cojedes, Hato Gabinero near San Carlos, Pérez, IV-8-1955.

Pseudis paradoxus bolbodactylus A. Lutz

1925 Pseudis bolbodactyla A. Lutz, p. 138; Cochran, 1955, p. 312, fig. 20, Pl. 32, figs. G, H.

Description. Female, MCZ 25729, Lagoa do Curralinho, Lassance, Minas Gerais, Brasil. Tympanum rather smaller than the eve and smaller than the distance from eye to nostril. Supratympanic fold not very evident. Vomerine teeth more reduced than in the two preceding subspecies and separated on the mid line. Metatarsal tubercle more or less conical, not forming a hook. An interocular spot produced posteriorly on the two sides in two broad arms with an indentation between, thence continued on the back by two longitudinal irregular lines. Dorsal aspect of limbs with spots, internal edge of the femur with large light-edged ocelli. Interdigital membrane of the foot with spots barely evident. Throat, pectoral and abdominal regions with dark rounded spots, more abundant on the breast. Ventral region of thigh with relatively thick lines, but several of them interrupted, space between line 1 (which is rather curved) and the external edge light; proximally between lines 1 and 2 an elongate spot (line 2 starts with two spots); space between lines 2 and 3 light (line 3 composed of elongate spots); space between 3 and 4 light (line 4 is formed by round spots); space between 4 and internal edge light. One light long spot below the cloaca. Ventral aspect of tibia with a few dark spots.

Dimensions: Head and body 45 mm. Head length 16 mm. Head width 17 mm. Head height 8 mm. Eye 4 mm. Interorbital space 3 mm. Elbow to third finger 22 mm. Femur length 25 mm. Tibia length 24 mm. Tibia width 9 mm. Heel to fourth toe 35 mm. Foot 27 mm.

Variation: In general the lines on the thigh are not so much interrupted as in the specimen described, especially lines 3 and 4, which are usually continuous or have one spot at the beginning or at the end. More constant is the short line in the space between 1 and 2 (sometimes united to line 2 and forming an angle) and the spot at the beginning of line 2. This subspecies has many similarities with P. p. platensis, but it is different in having line 1 thinner, no angular projections from any of the lines and no fusion of lines 3 and 4.

Distribution: Confined to the São Francisco River in the State of Minas Gerais, Brasil. Cochran (1955: 215) cites material from various localities in this state and from Itá in the state of Espirito Santo, though it would be interesting to check whether the present subspecies or another one exists in the latter locality.

Material studied: MCZ 25729 (1 specimen) Brasil, Minas Gerais, Lassance, Lagoa do Curralinho, Cochran and Venancio; USNM 98534 (1 specimen) Brasil, Piraporá, III-23-1935; USNM 98173, 175-79, 181-88, 190-95, 197-99, 200, 202 (25 specimens) Brasil, Lassance, Lagoa do Curralinho, Cochran and Venancio, III-22-1935; USNM 97022 (1 cotype) Brasil, Minas Gerais, Lassance, Lagoa de Genipapo.

Pseudis paradoxus fuscus Garman

1883 *Pseudis fusca* Garman, p. 47; Cochran, 1955, p. 216, Pl. 32, figs. I-K.

Description. Cotype MCZ 1872, Rio Arassuahy, Minas Gerais, Brasil. Tympanum approximately the same size as the eye and as the distance from eye to nostril. Supratympanic fold present. Snout relatively short (a variable character in P. p. paradoxus). Vomerine teeth relatively reduced and separated in the middle. The metatarsal tubercle not forming a hook. Dorsal color pattern rather indistinct; ground color of cotype brown, perhaps due to poor preservation; ventral parts light, rather spotted towards the throat. In the cotype it is practically impossible to see the coloration of the ventral aspect of the femur, though it would seem that the space between line 1 and the external edge has abundant dark

spots. Space between line 4 and the internal edge, with large irregular light spots. A light line above the cloaca; another light line below it, nearly divided into two spots and continued by other light spots. Ventral aspect of tibia with abundant irregular dark spots.



Fig. 4: Ventral aspects of thighs in *Pseudis* and *Lysapsus*. Upper row: left, *P. p. paradoxus* MCZ 12135; center, *P. p. caribensis* MCZ 19890; right, *P. p. bolbodactylus* MCZ 25729. Lower row: left, *P. p. platensis* MCZ 24808; center, *P. p. occidentalis* MCZ 29961; right, *Lysapsus mantidactylus* MCZ 28730.

Dimensions: Head and body 51 mm. Head length 16 mm. Head width 19 mm. Head height 8 mm. Eye 6 mm. Interorbital space 4 mm. Elbow to third finger 26 mm. Femur 29 mm. Tibia length 28 mm. Tibia width 9 mm. Heel to fourth toe 36 mm. Foot 26 mm. Another cotype, head and body 41 mm.

Distribution: No specimens have been reported since Garman's, and the only known locality is the Arassuahy River in the State of Minas Gerais. This locality is very close to that of P. p. bolbodactylus, but separated by the Serra do Espinhaço which divides the São Francisco basin from that of the Jequitinhonha

basin, to which the Arassuahy River belongs. Partly on the basis of this geographical separation (cf. Cochran 1955: 217) and in spite of the absence of new material, I am disposed to retain this form as distinct from $P.\ p.\ bolbodactylus$.

Material studied: MCZ 1872 (2 specimens) cotypes, Brasil, Minas Gerais, Rio Arassuahy, Hartt and Copeland, Thayer Expedition, 1864-7.

Pseudis paradoxus platensis subsp. nov.

1894 Pseudis paradoxa Boulenger, p. 347; Miranda Ribeiro, 1926, pl. II, figs. 1-1a; Müller and Hellmich, 1936, p. 27, fig. 9; Freiberg, 1942, p. 228 (part); Travassos and Freitas, 1942, p. 284; Vellard, 1948, p. 173; Cei, 1956, pl. V, figs. 36-37; Gans, 1960, p. 303 (part).

For diagnostic features see Table 1.

Description. Type, adult male, MCZ 24808, Colonia Nueva Italia, Dept. Villeta, Paraguay. Tympanum approximately the same size as the eye and as the distance from eye to nostril. Practically no supratympanic fold. Vomerine teeth large, with little separation. Metatarsal tubercle rather prominent, but without hook. On the back two large dark spots shaped like commas, extending from the interorbital space to the scapular region; two interrupted dorsal dark lines. Dorsal aspect of the limbs and interdigital membrane of the foot with dark spots. Throat, pectoral and abdominal regions with more or fewer round dark spots. Ventral aspect of the thigh with dark thick lines; space between line 1 and external edge without spots; space between line 1 and line 2 with an extensive proximal spot; light space between line 2 and line 3 with the projections from the lines only slightly indicated; space between line 3 and line 4 light; between line 4 and the internal edge, light rectangles. Two light long spots below the cloaca. Ventral aspect of tibia with extended dark spots interrupted and irregular.

Dimensions: Head and body 50 mm. Head length 15 mm. Head width 16 mm. Head height 7 mm. Eye 5 mm. Interorbital space 3 mm. Elbow to third finger 24 mm. Femur length 28 mm. Tibia length 25 mm. Tibia width 8 mm. Heel to fourth toe 36 mm. Foot 25 mm. Paratype MCZ 24809, from the same locality, head and body 42 mm.

Distribution: This subspecies is found from the Upper Paraguay River to Rosario (Santa Fé) on the banks of the Paraná

Table 1: The diagnostic features of the subspecies of Pseudis paradoxus	occidentalis	Large	Smaller	Covers part of tympanic mem- brane	Not hooked	Dark lines very blurred, sometimes 1 and 2 mIssing. Spaces without spots	Four	Without spots	Without spots	One
	platensis	Large	Same size	Not distinct	Not hooked	Dark lines wide. Space 1-2 a long spot, 4-int. light rectangles; others without spots	Two	Some long dark spots	Round spots	Тwo
	fuscus	Medium size	Same size	Present	Not hooked	Spots 1-ex- ternal edge	1	Abundant long dark spots	Throat spotted	1
	bolbodactylus	Medium size	Smaller	Not distinct	Not hooked	Dark lines wide. Spaces without spots, except 1-2 which has a long basal spot	Two	Some long dark spots	More abundant on throat	One
	caribensis	Large	Smaller	Not distinct, but with dark line	Hooked	Dark lines thinner. Space 1-ext., 2-3, 4-int. long spots; 1-2, 3-4 without spots	Six	Short dark lines	Round spots. More abundant in throat and breast	One
	paradoxus	Large	Same size	Not distinct	Not hooked	Dark lines not very wide. Space 1-ext. long spots; 2-3, 4-int. angular projections; 1-2, 3-4 without spots	Four	Abundant short dark lines	Spots: throat, breast (comma- shaped), abdomen (scarce)	Тмо
		Vomerine teeth	Tympanum - eye/ eye - nostril	Supratympanic fold	Metatarsal tubercie	Ventral coloration of thigh	Longitudinal dorsal lines	Ventral tibia	Ventral body	Light spots below cloaca

River. In Brasil it has been collected in Mato Grosso: S. Luiz de Cáceres (the northernmost locality known at present) and near Bodoquena; in Bolivia, San Fermín at 100 km NW of Puerto Suárez and in nearby El Carmen; in Paraguay, near Asunción, Fortín Esteros and Nueva Italia; in Argentina in the Provinces of Misiones, Corrientes (Ituzaingó, Isla Apipé) and Santa Fé (La Geraldina, Santa Fé, Rosario).

Material studied: MCZ 24808-9 (2 specimens) Paraguay, Dept. Villeta, Colonia Nueva Italia, P. Willim, XII-6-1943; CNHM 42313-4 (2 specimens) Paraguay, Colonia Nueva Italia, P. Willim; AMNH 50657 (1 specimen) Paraguay, Villeta, Colonia Nueva Italia, P. Willim; MCZ 29958 (1 specimen) Bolivia, El Carmen, C. Gans, II-26-1954.

PSEUDIS PARADOXUS OCCIDENTALIS subsp. nov.

1956 - Pseudis paradoxa Gans, p. 2 (part); Gans, 1960, p. 303 (part).

For diagnostic features see Table 1.

Description. Type, adult male, MCZ 29961, El Pailón, Bolivia. Tympanum slightly smaller than the eye and smaller than the distance from eye to nostril. The skin of the supratympanic fold covers part of the tympanic membrane. Loreal region slightly concave. Vomerine teeth large, very slightly separated. Metatarsal tubercle rather prominent, but without hook. Back brown with four black longitudinal lines which are very irregular and have lateral projections, forming dark edged circles towards the rear. Dorsal aspect of the extremities with dark spots. Internal edge of the tarsus dark. Interdigital membrane of the foot with large dark spots. Sides of trunk with light spots. Ventral aspect of thigh with the four dark lines very blurred (sometimes lines 1 and 2 are missing); lines 3 and 4 are more distinct and thicker; the spaces among the lines are light. One light long spot below the cloaca. The fourth ventral line of thigh follows the internal edge. Tibia ventrally light. Throat, pectoral and abdominal regions light and unspotted (in the male the throat slightly darker).

Dimensions: Head and body 51 mm. Head length 18 mm. Head width 20 mm. Head height 9 mm. Eye 5 mm. Interorbital space 6 mm. Elbow to third finger 23 mm. Femur 25 mm. Tibia length 26 mm. Tibia width 9 mm. Heel to fourth toe 35 mm. Foot 27 mm. Paratype MCZ 29959, adult female, the same locality, head and body 72 mm.

Distribution: Though the material studied, with good locality, comes from only one place in Bolivia, El Pailón, it is possible that this susbspecies occupies the valleys of the Beni and its tributaries. Recently, Shreve (1959) has described a new species of Phyllomedusa (P. pailona) from the same locality, remarking that Phyllomedusa sauvagii, its closest relative, was collected by Gans in El Carmen; this distribution parallels that of Pseudis paradoxus occidentalis and P. p. platensis.

Material studied: MCZ 29959, 61 (2 specimens) Bolivia, El Pailón, C. Gans, III-5-1954; USNM 94390 (1 specimen) South America, J. H. Lunn, 1932.

INTERRELATIONSHIPS OF THE SUBSPECIES

P. p. paradoxus, P. p. caribensis and P. p. occidentalis of northern and western South America seem to me more closely related, while P. p. fuscus and P. p. bolbodactylus of southeast Brasil form another group. P. p. platensis provides the connecting link.

THE STATUS AND ALLOCATION OF PSEUDIS MANTIDACTYLA COPE

This species must be considered distinct from Pseudis paradoxus and more closely related to Lysapsus limellus. In general it fits the definition of the genus Lysapsus given by Savage and Carvalho (1953: 194). Thus it has terminal discs on the digits, the interdigital webbing of the toes reaching to the base of the discs; the vomerine teeth arranged obliquely, slightly towards the rear of the choanae; the pectoral girdle with a long and cartilaginous omosternum, of the same length as the epicoracoids. It differs specifically from L. limellus in having the terminal phalanx of the toes relatively not so short, although they do not reach the extreme end of the digits on account of the presence of discs and in the male with two vocal sacs. (The latter character also separates mantidactylus from paradoxus.)

I propose therefore that Cope's species be called *Lysapsus mantidactylus* (Cope). Parentheses are used since the generic name employed by Cope (1862b: 352) in the original description was *Pseudis* and not *Lysapsus*, as wrongly stated by Boulenger (1882: 187), Freiberg (1942: 228), Savage and Carvalho (1953: 193) and Cei (1956: 57).

Lysapsus mantidactylus (Cope)

1862b Pseudis mantidactyla Cope, p. 352; Boulenger, 1882, p. 187, 1883, p. 17; Boettger, 1892, p. 26; Berg, 1896, p. 162; Fernández and Fernández, 1921, p. 134; pl. III, figs. 14-15; Nieden, 1923, p. 367; Miranda Ribeiro, 1926, p. 25; Freiberg, 1942, p. 228; Gallardo, 1957, p. 354, 1958, pp. 291-298.

1953 Pseudis paradoxus Savage and Carvalho, p. 193 (part); Cei, 1956, p. 57 (part).

Description. Adult female, MCZ 25730, Uruguay, Montevideo. Tympanum equal to eye diameter and slightly larger than the distance from eye to nostril. Head relatively shorter than in P. paradoxus; practically no canthus rostralis. Vomerine teeth short and separated, placed slightly to the rear of the choanae. Small granulations on dorsum and hind limbs, forming lines on the tibia. Leg (tibial region) thinner than in P. paradoxus. The interdigital membrane only at the base of the fingers prolonged onto the toes by digital fringes which reach the base of the terminal discs. The metatarsal tubercle sharp and oblique, not forming a hook. Tarsal fold not very prominent. One light oblique band from the eye to the corner of the mouth. Back with some dark spots. Sides of the trunk with a light longitudinal band. A longitudinal dark band on the side of the fore limb. Throat with some scattered spots, pectoral and abdominal regions light. Ventral design of the femur: dark longitudinal lines, better defined, in increasing order 1, 2, 3, 4; line 1 very blurred, formed of long irregular spots; spaces among the lines light. One light band over the cloaca and a fifth dark band at the level of the cloaca; space between dark lines 4 and 5, light. Tibia ventrally with infrequent spotting, more abundant on the edges.

Skeletal characters: Skeleton bluish green (in live animals and freshly preserved specimens); Boulenger (1883: 17) makes reference to this coloration. A green skeleton is also found in other species of the genus, as in L. limellus (Miranda Ribeiro, 1926: pl. II, fig. 2a), and according to Parker (1935: 510) in P. laevis. Pectoral girdle arciferal; coracoid and precoracoid ossified and well developed; omosternum long and cartilaginous (same length as the epicoracoids); sternum and xiphisternum as a short cartilaginous plate. The terminal phalanges are long, not reaching the tips of the digits.

Dimensions: Head and body 35 mm. Head length 12 mm. Head width 12 mm. Head height 4 mm. Eye 4 mm. Interorbital space 2 mm. Elbow to third finger 18 mm. Femur length 20 mm. Tibia length 19 mm. Tibia width 5 mm. Heel to fourth toe 27 mm. Foot 19 mm.

Distribution: This species, first described by Cope from Buenos Aires, was later reported by Boulenger and also by Boettger from Rio Grande do Sul (Brasil) and Montevideo (Uruguay); by Berg again from Buenos Aires, and Misiones (Argentina); and by Vellard from Salta (Hickman) and Formosa (Puerto Dalmacia) in Argentina. From the material I studied in Argentinian collections and from my own collecting, I can say it is common in the neighborhood of the city of Buenos Aires, extending to the N.E. of the Buenos Aires Province and the lagunas of the Partido de General Lavalle; it can also be recorded for Santa Fé Province, where also exist Pseudis paradoxus and Lysapsus limellus. Cei (1949: 539) citer it for Corrientes.

Material studied: MCZ 25730 (1 specimen) Uruguay, Montevideo; USNM 71124-6 (3 specimens) Uruguay, Puerto La Paloma, W. L. Smith; USNM 70633-4 (2 specimens) Uruguay, Montevideo; USNM 65617-8 (2 specimens) Uruguay, Montevideo, near Playa Ramirez, H. M. Smith, IX-30-1922; AMNH 11953 (1 specimen) Argentina, Prov. Buenos Aires, Punta Lara, Pedro Serie, VI-15-1920; CNHM 9698 (1 specimen) Argentina, Prov. Buenos Aires, La Plata, K. P. Schmidt, X-28-1926; USNM 22751-2 (2 specimens) Argentina, Prov. Buenos Aires, La Platá; USNM 63506 (1 specimen) Argentina, Prov. Buenos Aires, Dolores, A. Wetmore, X-1920; CNHM 83291 (1 specimen) Brasil, Rio Grande do Sul; CNHM 80554, 60, 90 (3 specimens) Brasil, Rio Grande do Sul, Millstead; MCZ 22996-23000 (10 specimens) Brasil, Rio Grande do Sul, Santa María, L. I. Price and T. E. White, 1936; USNM 118180-1 (2 specimens) Brasil, Rio Grande do Sul, Santa María, L. I. Price and T. E. White, 1936; USNM 121328 (1 Brasil, Rio Grande do Sul, Santa María, Inst. specimen) Butantan.

LYSAPSUS LIMELLUS COPE

Savage and Carvalho (1953: 193) erroneously state that the original description was based on Uruguayan material, when in reality Cope (1862a: 156) says: "Habitat-Paraguay. Taken on _____river" (leaving blank the name of the river). Though it was first described for Paraguay, Cope later himself (1862b:

351) cites it for Corumbá, Steindachner (1864: 262) for Caicara, and Miranda Ribeiro, (1926:27) for Cáceres, all three localities in Mato Grosso (Brasil). The latter author reports it also from Rio Grande do Sul (Brasil), Uruguay, and Buenos Aires Province (Argentina). Previously, Boulenger (1889; 246) had reported the species from Resistencia, Chaco, Argentina and (1894: 347) from Asunción, Paraguay; Peracca (1895: 24) added Río Apa, Upper Paraguay, and Berg (1896: 161) Corrientes, Argentina. Müller and Hellmich (1936: 25) and Vellard (1948: 169) had specimens from the Province of Formosa; Santa Fé can be added to the Argentine localities (specimens in the Museo Argentino de Ciencias Naturales). Outside of this general area of the basin of the Paraguay, Paraná, Plata and south of Brasil, Boulenger (1898: 4) lists it for Beni, Bolivia; Baumann (1912: 122, 124, 161) for the Upper Amazon; Müller and Hellmich (1936: 26) for the Marajó Island; Parker (1939:87) for Grão Pará; Savage and Carvalho (1953: 195) for the Pará and Amazonas states. Moreover, Parker (1935: 510) describes a closely related species, Pseudis laevis, based on nine specimens from British Guiana and one specimen from the Beni region (Bolivia); Savage and Carvalho (1953: 196) place this species in the genus Lysapsus.

In the Museum of Comparative Zoology and in the Chicago Natural History Museum I have studied material from Paraguay and Bolivia, in which some differences are noticeable between specimens from the two localities. These differences permit the species Lysapsus limellus to be divided into two subspecies: L. l. limellus Cope, from the Paraguay and Paraná basin, and L. 1. bolivianus subsp. nov. from the Beni Province (Bolivia). I have not seen material from Uruguay nor from southern Brasil; any such specimens belong to the subspecies L. l. limellus, but I prefer not to assert this without having seen them. On the other hand. Lysapsus laevis can be considered as a third subspecies of L. limellus, except for the Beni specimen, which undoubtedly belongs to L. l. bolivianus. Finally, it is possible that the specimens from Pará and Amazonas states belong to L. l. bolivianus; but specimens from Rio Branco (Brasil) that I saw in the United States National Museum belong to L. l. laevis.

Lysapsus limellus limellus Cope

1862a Lysapsus limellum Cope, p. 155; 1862b, p. 351.

1882 Pseudis limellum Boulenger, p. 187; 1889, p. 246; 1894, p. 347; Boettger, 1885, p. 242; Peracca, 1895, p. 24; Berg, 1896, p. 161; Müller and Hellmich, 1936, p. 25

(part), fig. 8; Vellard, 1948, p. 169.

1953 Lysapsus limellus Savage and Carvalho, p. 194 (part).

Description. Adult female, MCZ 25834, Río Pilcomayo, 15 miles W. of Río Paraguay, Chaco, Paraguay. Snout rather sharp, nostrils 2 mm. from the tip of the snout. Back and ventral regions with granulations. Cutaneous fringe of fingers insignificant. Digital discs of the feet elliptic with rather sharp tips. Interdigital membrane not very large; when the toes are adpressed it does not form wide folds.

Coloration: A dark continuous line on the ventral internal edge of the femur; posterior part of the femur without pattern. Small black granulations on the ventral region of the femur.

Dimensions: Head and body 17 mm. Head length 6 mm. Head width 6 mm. Head height 3 mm. Eye 2 mm. Snout 2 mm. Interorbital space 2 mm. Elbow to third finger 10 mm. Femur length 12 mm. Tibia length 12 mm. Tibia width 2 mm. Heel to fourth toe 14 mm. Foot 10 mm.

Distribution: Paraguay and Paraná Rivers and their affluents. From Mato Grosso to Río Tigre (Buenos Aires Province, Argentina), as cited by Miranda Ribeiro (1926: 27). It has been reported in Argentina from Formosa, Chaco, Santa Fé, Corrientes and Buenos Aires. (The photo published by Cei, 1956: pl. V, fig. 38, as of Pseudis minutus from Corrientes seems to belong to L. l. limellus.)

Material studied: MCZ 25834 (1 specimen) Paraguay, Chaco, 15 miles W. of Río Paraguay, Río Pilcomayo, P. Willim, II-3 to III-3-1944; CNHM 42315-7 (3 specimens) Paraguay, Colonia Nueva Italia, P. Willim, 1944; USNM 139277 (1 specimen) Paraguay, San Bernardo, Lago Ypacaray (beach pools, C. J. D. Brown, VIII-16-1956; USNM 139278 (1 specimen) Paraguay, Asunción Bay, Río Paraguay nr. Asunción, C. J. D. Brown, I-2-1957; USNM 132739 (1 specimen) Brasil, Mato Grosso, Paraguay River above L. Gahiba-mirim, K. P. Schmidt, 1926; USNM 97146 (1 specimen) Brasil, Mato Grosso, Cáceres; USNM 115975 (1 specimen) Brasil, Mato Grosso, Sâo Luiz de Cáceres, old cut-off of Río Paraguay, V-24-1909; USNM 132992 (1 specimen) Brasil, Mato Grosso, Porto Esperança.

Lysapsus limellus bolivianus subsp. nov.

1898 Pseudis limellum Boulenger, p. 4.

1935 Pseudis laevis Parker, p. 510 (part).

For diagnostic features see Table 2.

Description. Type, adult male, MCZ 17493, Reyes, Bolivia. Snout shorter than in L. l. limellus; nostrils very close to the tip of the snout. Dorsal and ventral skin much granulated. Cutaneous fringe of fingers well devloped. Digital discs of the feet without sharp tips. Interdigital membrane very well developed, forms wide folds when toes adpressed.

Coloration: A continuous dark line on the internal edge of the ventral aspect of the femur, as in L. l. limellus, but also another line more external, irregular and interrupted. Hind side of thigh with a third dark line, interrupted, below the cloaca. Less abundant small dark granulations on the ventral aspect of the femur.

Dimensions: Head and body 18 mm. Head length 6 mm. Head width 7 mm. Head height 4 mm. Eye 2 mm. Snout 1.5 mm. Interorbital space 2 mm. Elbow to third finger 9.5 mm. Femur length 12 mm. Tibia length 12 mm. Tibia width 2 mm. Heel to the fourth toe 15 mm. Foot 10 mm. Paratype, adult female, MCZ 10076, from the same locality, head and body 21 mm.

Distribution: The specimens studied come from the NW of Bolivia, Beni Department, Amazonian drainage through the Beni River and the Madeira. Thus it is probable that the specimen which Parker (1935: 510) ascribes to Pseudis laevis, from Santa Ana de Movrinas, Beni River, Bolivia, actually belongs to L. l. bolivianus. (Boulenger, 1898: 4, reported L. limellus from the same locality in Bolivia.) Also very likely to be this subspecies are the specimens of Lower Madeira River in Amazonas State and of Municipio of Monte Alegre in Pará State, Brasil, mentioned by Savage and Carvalho (1953: 195) and considered by them to be L. limellus on account of the granulose skin (in contrast to Pseudis laevis which has smooth skin).

Material studied: MCZ 10076, 17493 (2 specimens) Bolivia, Reyes, N. E. Pearson; MCZ 10077 (1 specimen) Bolivia, Lake Rogagua, N. E. Pearson.

Lysapsus limellus laevis (Parker)

1935 Pseudis laevis Parker, p. 510 (part).

Description. Adult male, USNM 137745, Fraseo, Boa Vista, Rio Branco, Brasil. Snout short. Dorsal and ventral skin smooth. Cutaneous fringe insignificant. Digital discs of the feet nearly round. Interdigital membrane very well developed, forms wide folds when toes adpressed.

Coloration: A continuous dark line on the internal edge of the ventral aspect of the femur; more externally some dark spots in line. A third dark line below the cloaca.

Dimensions: Head and body 21 mm.

Distribution: British Guiana, Rupununi Savannah and Pacaraima foothills; in Brasil, Rio Branco near Boa Vista (this locality is very near the British Guiana boundary).

Material studied: USNM 137744-6 (3 specimens) Brasil, Río Branco, Boa Vista, Fraseo, J. D. Haseman, XII-5-1912.

L. l. limellus and L. l. laevis differ in the type of skin, the shape of the snout, the extent of the interdigital membrane and the coloration of the thigh; the two are related by way of L. l. bolivianus which has granular skin like L. l. limellus but in snout shape, extent of interdigital membrane and in coloration is near L. l. laevis, which differs from both by the extent of fringing on the fingers.

L. l. laevis is restricted to the British Guiana and Rio Branco, L. l. bolivianus to the Beni drainage and probably also the Amazon, L. l. limellus to the system of the Paraguay, Paraná and Plata rivers.

Table 2. Diagnostic features of the subspecies of Lysapsus limellus

	limellus	bolivianus	laevis
Snout	Rather sharp	Obtuse	Obtuse
Nostril from tip of snout	Not very near	Very near	Very near
Dorsal and ventral skin	Granulated	Granulated	Smooth
Cutaneous fringe of fingers	Insignificant	Well developed	Insignificant
Discs of feet	Elliptic with rather sharp tips	Elliptic without sharp tips	Nearly round
Interdigital membrane	Not very large, not forming wide folds	Very well developed, forming wide folds	Very well developed, forming wide folds
Black lines on ventral thigh	Internal edge with a continuous line	Internal edge with a continuous line and a discontinuous line externally	Internal edge with a continuous line and some external spots in line
Posterior side of femur	Without design	With a third line	With a third line

Two of the species of the genus *Pseudis* are difficult to allocate; these are *P. minutus* Günther, described on a specimen collected by Darwin from "South America" (later regarded as coming from South Brasil), and *P. meridionalis* Miranda Ribeiro, described from Rio Grande do Sul, Brasil.

Pseudis minutus in some characters approaches P. paradoxus; such features are the general shape of the head, the lack of terminal discs and the development of the interdigital membrane; however, it resembles L. mantidactylus in size (40 mm. according to Nieden) and in the presence of two vocal sacs (so specified by Günther in the original description, but Boulenger reports only one). If Boulenger was right about the single vocal sac, it is very probable that P. minutus is one of the southern races of P. paradoxus; we must remember that Cope (1885: 187) reported P. paradoxus from Rio Grande do Sul. Doubt was cast on this by Boulenger (1885b: 298) who said confidently that Cope had the species confused with L. mantidactylus. I think, however, that this last is not at all probable since L. mantidactylus is a species described by Cope.

Pseudis meridionalis, on the basis of its size (20 mm.) and the resemblances to L. limellus mentioned by Miranda Ribeiro, could very well be the representative in southern Brasil of the latter species; however, according to Miranda Ribeiro, the digital discs are absent. (It must be remarked that what has sometimes been identified as P. minutus or as P. meridionalis in many collections is in reality L. mantidactylus.) All this makes desirable a better study of the Pseudidae from southern Brasil, based on adequate material.

SUMMARY

1) On the basis of both external and internal characters (pectoral girdle, digital phalanges), *Pseudis mantidactyla* Cope is placed in the genus *Lysapsus*.

2) The color pattern of the ventral aspect of the thigh is sufficiently constant in the species and subspecies of *Pseudis* and *Lysapsus* to be taken as one of the useful characteristics in their classification.

3) The distribution of the subspecies seems to be correlated with the drainage system of the large South American rivers.

4) Six subspecies are defined for *Pseudis paradoxus*, three of them new, and three for *Lysapsus limellus*, one new.

ACKNOWLEDGMENTS

I must thank the Consejo Nacional de Investigaciones Científicas y Técnicas de la República Argentina for the fellowship given me for investigations on neotropical amphibians and for study of the collections of the North American museums. I am grateful also to Dr. A. S. Romer, Director of the Museum of Comparative Zoology at Harvard University and to Dr. E. E. Williams, Curator of Reptiles and Amphibians at this museum, for the facilities afforded me during 1959-60; to the Council of the American Museum of Natural History and the Karl P. Schmidt Fund of the Chicago Natural History Museum for support given me and to Mr. C. M. Bogert, Dr. R. Inger, Dr. D. Cochran, Dr. M. G. Netting, and Mr. N. Richmond for courtesies and assistance offered me during my work in their several museums; and to Dr. C. Gans of Buffalo University for supplying data on material collected by him in Bolivia.

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