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VOLUME 132 : ARTICLE 5 NEW YORK : 1966

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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

**Volume 132, article 5, pages 277–328,
figures 1–6, tables 1–12**

Issued August 19, 1966

Price: \$2.00 a copy

INTRODUCTION

RECENTLY I HAD THE OPPORTUNITY to examine seven small lizards from southern Costa Rica. In their general appearance, these delicate, attractive lizards reminded me of the genus *Echinosaura*. Closer study showed that they were a species of *Neusticurus*, members of a genus not otherwise known from Costa Rica or Panamá. The nearest locality is some 1200 kilometers to the southeast, in southern Colombia. The isolated Costa Rican population is separated from the main range of the genus *Neusticurus* by the range of the closely related genus *Echinosaura*. As background for discussing the new Costa Rican form, I have examined most of the specimens of *Neusticurus* available in North and South American collections.

ACKNOWLEDGMENTS

Many people have aided me in this study, and it is a pleasure to acknowledge their help. Mr. Charles M. Bogert, Dr. William E. Duellman, Dr. Jean Guibé, the late Dr. Norman Hartweg, Dr. Robert F. Inger, Dr. Fred Medem, Dr. Gustavo Orcés-V., Dr. James A. Peters, Dr. Janis Roze, Dr. Paulo Vanzolini, Dr. David Wake, Dr. Charles F. Walker, Dr. E. E. Williams, and Dr. Richard G. Zweifel provided me access to material in their charge or in their private collections. Mr. Bogert, Dr. James E. Böhlke, Dr. Dirk Hillenius, Dr. Å. Holm, and Mr. Edmund V. Malnate made it possible for me to examine type material of eight of the named forms. I wish particularly to thank Dr. Holm, Dr. Sven O. Hörstadius, and Dr. L. Hedström for their consideration and efforts in enabling me to study the holotype of *Lacerta bicarinata*. Mr. Malnate and Dr. Walter Hellmich answered questions about type material previously in the Academy of Natural Sciences in Philadelphia and the Zoologische Sammlung

des Bayerischen Staates. Dr. W. E. Duellman, Dr. Richard Etheridge, Hno. Nicéforo María, Dr. Juan A. Rivero, Dr. Rodolfo Ruibal, Dr. Jay M. Savage, and Dr. Wake provided important observations on the habits of these lizards, or data on specimens critical for zoogeographic interpretations. Mr. Bogert, Dr. Böhlke, Miss Margaret R. Bullitt, Dr. Hartweg, Dr. Inger, Mr. Hymen Marx, Mr. Malnate, Mr. Benjamin Shreve, and Dr. Walker extended courtesy and hospitality to me during visits to their institutions. The excellent figures of the new Costa Rican species are the work of Miss Suzanne Runyan. Dr. George B. Rabb kindly read the manuscript and offered many suggestions.

Abbreviations used in referring to specimens examined are:

A.M.N.H., the American Museum of Natural History
A.N.S.P., Academy of Natural Sciences of Philadelphia
B.M.(N.H.), British Museum (Natural History)
C.N.H.M., Chicago Natural History Museum (now Field Museum of Natural History)
D.Z.S.P., Departamento de Zoologia, São Paulo
E.P.N., Escuela Politécnica Nacional, Quito
L.A.C.M., Los Angeles County Museum
M.B.U.C.V., Museo de Biología, Universidad Central de Venezuela
M.C.N., Museo de Ciencias Naturales, Caracas
M.C.Z., Museum of Comparative Zoology at Harvard College
M.N.H.N., Museum National d'Histoire Naturelle, Paris
O.V., private collection of Gustavo Orcés-V.
U.K.M.N.H., University of Kansas Museum of Natural History
U.M.M.Z., University of Michigan Museum of Zoology
U.S.N.M., United States National Museum, Smithsonian Institution, Washington, D. C.
U.U.L., Uppsala Universitet Linnésamling
Z.M.A., Zoologisch Museum, Amsterdam

SYSTEMATIC SECTION

NEUSTICURUS DUMÉRIL AND BIBRON

Neusticurus DUMÉRIL AND BIBRON, 1839, p. 61.

DEFINITION: Tongue with imbricate, scale-like papillae. Nostril pierced in a single nasal; nasals separated usually by paired or single frontonasals, occasionally by irregular scales; prefrontals paired or irregular; interparietal usually bordered by a pair of parietals laterally, by a series of three to nine, usually six or seven, smaller scales posteriorly; temporal and occipital scales small, irregular; rostral large; mental and postmental single, followed by several paired chin shields, usually first pair in contact on midline. Gular and pregular scales flattened, convex, or spinose, generally in longitudinal rows radiating from between chin shields; median postgulars often larger than others; gular crease feeble or absent. Collar fold well developed. Lower eyelid developed, with an undivided, divided, or divided and pigmented disc. Tympanum at surface of head, slightly recessed, or deeply recessed and overhung by surrounding scales of surface of head. Dorsal scales uniformly small, or heterogeneous, with large, keeled tubercles intermixed with small flat or convex scales. Ventral scales usually flat, rectangular or rounded posteriorly, imbricate, in transverse and longitudinal rows; lateral rows keeled in some species. Limbs pentadactyl, digits clawed; forefoot with enlarged, plate-like scales along inner margin between thumb and wrist; under side of third and fourth toes with paired scales proximally, inner scale a rounded tubercle. Tail slightly to strongly compressed; a double caudal crest, feebly to strongly developed. Total femoral and preanal pores: 22 to 72 in males; one to 47 in females. Males with or without conspicuous, white-centered, black-bordered ocelli in pattern. Hemipenis without basal hooks; flounces with or without minute calcareous spinules.

REMARKS: Fourteen names are available for lizards of the genus *Neusticurus*, including two proposed here. I have examined the type material for eight of the 12 previously proposed names; one holotype was destroyed during World War II, and another is lost.

While preparing the following account, I

have examined 310 specimens and have recognized seven species, one of which is divisible into two subspecies. Several species show much geographic variation that has not been recognized nomenclatorially. All the taxa that I recognize are included in the following key. Lizards of this genus vary so extensively that identifications made by means of the key alone and not confirmed by comparison with the data presented for each taxon will often be incorrect. Some of the individual variation that I observed has been tabulated, both as an aid to solving certain taxonomic problems and as a caution to workers who are studying these animals.

KEY TO THE SPECIES AND SUBSPECIES OF *Neusticurus*

1. Tympanum deeply recessed within an external auditory meatus¹; tail strongly compressed² (Venezuela, the Guianas, Brazil) 2
Tympanum not or but slightly recessed; tail slightly or moderately compressed. 3
2. Body with several longitudinal rows of tuberculate scales; temporal scales keeled, keels parallel and longitudinal; frontonasal-frontal area usually with regular scales; two scales along side of tail for each two median ventral caudal scales (Brazil, the Guianas, Venezuela) *N. bicarinatus*
Body with at most a posterior dorsolateral series of enlarged scales; temporal scales conical; frontonasal-frontal area usually with irregular scales; three to five scales along side of tail for each two median ventral caudal scales (Venezuela) *N. tatei*
3. Tympanum slightly recessed; body with irregular rows of dorsal tubercles; disc in lower eyelid divided into sections by vertical grooves; three to five scales along side of tail for each two median ventral caudal scales (Venezuela, the Guianas) *N. rudis*
Tympanum slightly or not recessed; body with regular or irregular rows of tubercles, or no tubercles present; disc in lower eyelid divided or not; two or three scales along side of tail for each two median ventral caudal scales (Costa Rica; Amazonian Andes) 4
4. Tympanum slightly recessed; enlarged dorsal scales on body in four regular rows; lateral

¹ The holotype of *Neusticurus tatei* does not have the tympanum recessed.

² The tail is less strongly compressed in younger specimens.

- scales uniform, small; no tubercles on head or sides; tail short, 1.1 to 1.5 times body length; nostril surrounded by brown or black spot (Ecuador) *N. cochranæ*
- Tympanum not recessed; tubercles, if present, in regular or irregular rows; if tubercles present, lateral scales heterogeneous; tail 1.4 to 2.1 times body length 5
5. Upper lateral nuchal scales small, uniform, not forming longitudinal rows; two large posterior preanals; no conspicuous light areas on upper forelimbs. 6
- Upper lateral nuchal scales conical, forming one or more longitudinal rows of tubercles; two to five posterior preanals. 7
6. Tubercles absent (Ecuador, northern Peru). *N. s. strangulatus*
- Tubercles present (central Peru) *N. s. trachodus*
7. Frontonasal-frontal area with irregular scales; two series of supraoculars; three scales along side of tail for each two median ventral caudal scales; translucent disc in lower eyelid divided into sections by vertical grooves (Costa Rica). *N. apodemus*
- Frontonasal-frontal area with regular scales; one series of supraoculars; usually two scales along side of tail for each two median ventral caudal scales; translucent disc in lower eyelid rarely divided (Amazonian Andes) *N. ecpleopus*

Neusticurus bicarinatus (Linnaeus)

Lacerta bicarinata LINNAEUS, 1758, p. 201.

TYPE LOCALITY: "Indiis" (Linnaeus, 1758).

HOLOTYPE: Through the extraordinary kindness of Dr. Å. Holm, curator of the museum of the Zoological Institute, University of Uppsala, I have examined the single specimen of *Neusticurus* in that collection (U.U.L. No. 70). According to Dr. Holm, this specimen is noted in Thunberg's handwritten catalogue of 1828 as received from the Museum Adolphi Friederici. Although my counts of ventral scales differ from those given by Linnaeus, I do not question the authenticity of this specimen as the holotype of *Lacerta bicarinata*.

DESCRIPTION OF HOLOTYPE: The specimen is an immature male, about 38 mm. from snout to vent, about 124 mm. in total length. The canthus rostralis forms a sharp angle. The frontonasal is longitudinally divided, and there is a relatively large median azygous scale between the frontonasals and prefrontals; the median azygous scale may be di-

vided. There are 3-3 large supraoculars; anterior to these is a triangular space filled on the left by four, and on the right by five, granules. The disc in the lower eyelid is divided into three or four sections by vertical grooves. The tympanum is deeply recessed. There are five posterior preanals, the paramedian pair larger, the median and the lateral pair smaller. Anterior to these is a large median scale. The ventrals are in 28 transverse and 10 longitudinal rows; the scales of the outer two longitudinal rows on each side are apparently angulate, although this angularity may be a result of dessication. There are 16-16 lamellae under the fourth fingers, 24-25 under the fourth toes. The tail is compressed, with a continuous double crest dorsally. The crests are separated, near the base of the tail, by two or three rows of small scales. There is one caudal whorl per ventral caudal scale, except that the scales of the row just lateral to the crest scales are divided transversely. Approximately 24 femoral pores are present on each side.

The holotype of *Lacerta bicarinata* and the specimen on which Duméril and Bibron (1839) based the genus *Neusticurus* (M.N.H.N. No. 4181, probably from French Guiana) are conspecific. The description and figure given by Duméril and Bibron are excellent. Later workers have applied the name *bicarinata* correctly.

DEFINITION: The tympanum is deeply recessed, and there is thus a conspicuous external auditory meatus. The tympanum is overhung by the scales of the surface of the head, and the external opening of the auditory meatus is smaller than the tympanum.

The dorsal caudal crests are continuous. Shortly behind the base of the tail, they are separated by as many as six small flat scales; distally, the crests are in contact. There are no intercalated vertical rows of scales on the sides of the tail. The scales of the row just lateral to each dorsal crest, however, are divided transversely into two scales. Except for the small scales separating the crests, and the scales of the row just lateral to the crests, the whorls of caudal scales go completely around the tail.

The tail is strongly compressed.

The canthus rostralis is strongly angulate.

The translucent disc in the lower eyelid is

divided by vertical grooves into three to six, usually four or five, segments.

The sides of the neck and body are covered by intermixed tubercles and smaller convex scales. The large tubercles on the dorsum tend to form six longitudinal series. The median pair of series are the most regular and are separated from each other and from the two outer pairs by longitudinal series of small flat scales. The outer two pairs are less regular, and the two longitudinal series on each side are in contact with one another.

The temporal scales are keeled, with the keels parallel to each other and roughly longitudinal.

The posterior preanal scales number four to six, usually five; when five, the paramechanical pair is large, the lateral pair and median, small. There is a large median scale in the row of preanals anterior to these in all specimens examined.

All the specimens have the frontonasal divided, and all have a median azygous scale between the frontonasals and prefrontals, although the median azygous scale may be minute as in A.M.N.H. No. 61363. All the specimens have a series of minute scales separating part of the loreal, the freno-ocular, or the nasal from the supralabials.

There is no conspicuous pattern in *N. bicarinatus*. There are lighter and darker areas along the sides, but these do not form light-centered, dark-bordered ocelli in the single mature male (M.N.H.N. No. 4181) examined. The dorsum from the head to the tail is usually uniform tan. Both sexes are light beneath.

GEOGRAPHIC VARIATION: I have examined 17 specimens of *N. bicarinatus* from British Guiana, one probably from French Guiana, one from Venezuela, three from localities in Pará, Brazil, and two from Rondonia, Brazil (fig. 1). The specimens show little geographic variation.

Most specimens have 4-4 supraoculars; the specimens from Rondonia have 4-4 and 5-5, and the specimens from Pará have four on two sides and five on four sides. Usually the third supraocular, and in some cases the second and fourth, are separated from the superciliaries by a row of granules.

In the sample from British Guiana, seven

supralabials occur on 27 sides; four sides have six, and one side has five. In the Brazilian sample, the specimens from Pará have 6-6 supralabials, and the single specimen from Rondonia on which counts can be made has 5-5. The Venezuelan specimen has 7-7. The infralabials are usually 4-4, except for D.Z.S.P. No. 6311 (Pará), which has 4-5, and M.B.U.C.V. No. 8011 (Venezuela), which has 5-5.

A posterior median groove in the frontal occurs in three of the specimens from British Guiana; in addition, five specimens have an asymmetrical or irregular groove, and, in one, there are two small scales divided off from the posterior end of the frontal. The other eight specimens from British Guiana, and the other specimens examined, have no groove at the posterior end of the frontal.

The most frequent number of longitudinal ventral scale rows is eight. Only four specimens, all from British Guiana, differ; these have 10 rows.

Most of the specimens have a single pair of chin shields in contact on the midline. Eight specimens from British Guiana, however, and one from Pará, have two pairs of chin shields touching medially. One specimen from British Guiana has two chin shields on the left in contact with three chin shields on the right, and another has three pairs of chin shields in contact medially.

Too few males were examined for me to determine sexual dimorphism except in the femoral-preanal pore counts (table 1).

The largest male examined is 109 mm. from snout to vent; the largest female, 91 mm. Eight females with tails intact have tail over snout-vent length ratios of 1.69-2.21, mean 1.95.

One female examined has a single leathery egg in each oviduct. Another female has a single leathery egg in one oviduct; the other oviduct is empty.

RANGE: *Neusticurus bicarinatus* is a widespread species (fig. 1). Specimens have been examined from British Guiana, Venezuela, the Brazilian states of Pará and Rondonia, and probably French Guiana. The altitudes range from near sea level to 1000 meters above sea level. In the Guianas, this species is sympatric with *Neusticurus rudis*.

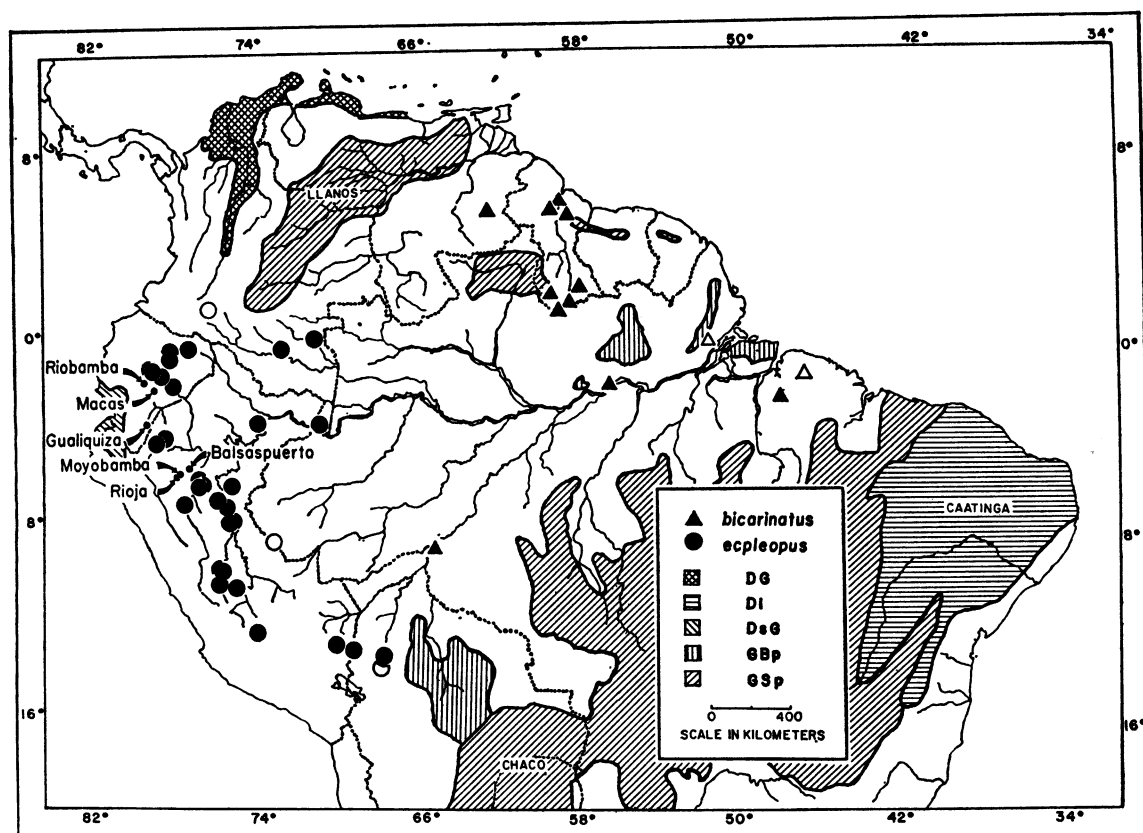


FIG. 1. Northern South America, showing savanna and grassland formations, and localities for *Neusticurus bicarinatus* and *Neusticurus ecpleopus*. Open symbols are literature records.

Abbreviations: DG, broadleaf deciduous trees and grass; DI, broadleaf deciduous trees, plants sufficiently far apart so that they frequently do not touch; DsG, broadleaf deciduous shrub forms, minimum height 3 feet, with grass; GBp, grass with broadleaf evergreen trees growing singly or in groups or patches; GSp, grass with semideciduous trees growing singly or in groups or patches.

***Neusticurus tatei* (Burt and Burt),
new combination**

Arthrosaura tatei BURT AND BURT, 1931, p. 313.
Neusticurus racenisi ROZE, 1958, p. 252.

HOLOTYPE: An immature male (A.M.N.H. No. 36649) from Vegas Falls, 15 miles north of Esmeraldas, about 1400 meters above sea level, Territorio Federal de Amazonas, Venezuela.

DEFINITION: The tympanum of all specimens except the holotype is recessed in an external auditory meatus; in some larger specimens, the scales at the anterior margin of the tympanum overhang the tympanum, and the opening of the external auditory

meatus therefore is smaller than the tympanum.

Each dorsal caudal crest of *N. tatei* consists of cycles of a large keeled scale followed by two or, anteriorly in some cases three, smaller keeled scales. Shortly behind the base of the tail, the large keeled scales are separated from each other by one longitudinal row of small scales. Distally, the crests are in contact, although there often is a small scale between the anterior ends of each pair of crest scales. A cycle of crest scales from large keeled scale to large keeled scale is subtended by two median ventral caudals. The whorl containing the large keeled scale goes completely around the tail except for the small scales

TABLE 1
VARIATION IN SPECIMENS OF *Neusticurus bicarinatus*
(Figures are means and, in parentheses, extremes.)

	Femoral-Preanal Pores	Subdigital Fourth Finger	Lamellae Fourth Toe	Transverse Rows of Ventrals
Venezuela				
One female	10	15.5 (15-16)	21	27
British and French Guiana				
One male	56	18.5 (18-19)	29.0 (28-30)	28
Fifteen females ^a	8.4 (4-10)	16.2 (15-19)	24.3 (22-26)	26.8 (26-28)
Pará				
Three females	7.7 (6-11)	15.2 (15-16)	24.2 (23-25)	27.3 (26-28)
Rondonia				
Two females	5.0 (5)	17.5 (17-18)	25.0 (24-27)	28.5 (28-29)

^a Two other females were examined, but complete data were not taken.

separating the crests. Extra vertical rows of scales are intercalated along the sides, and there are two to four, usually three or four, scales along the sides of the tail corresponding to the two or three smaller crest scales.

The tail is strongly compressed.

The canthus rostralis is angulate.

The translucent disc in the lower eyelid is divided by vertical grooves into five to seven, usually six, sections.

Neusticurus tatei is one of the less tuberculate members of the genus. In most specimens, the only definite tuberculation is dorsolaterally on the posterior part of the body, and on the tail. M.C.Z. No. 62208 is a dried immature male; its dorsal body scales are much distorted, and I cannot be sure that any of them are especially large. The holotype has definite tuberculation only on the tail.

The preanal scales usually number five, rarely six, in the posterior row, with the lateral pair and the median smaller than the paramedian pair. There are usually five scales in the row anterior to these, but occasionally, rather than a single large median scale, there are two smaller ones.

All the specimens examined have eight longitudinal rows of ventral scales.

There is little pattern evident in the specimens of *N. tatei*. There are irregular lighter and darker areas on the sides. Two specimens, both mature males, had bluish venters and eyes that were red in the posterior part when alive. In preservation, mature males are gray below; mature females are paler.

GEOGRAPHIC VARIATION: There is considerable geographic variation in this species. The specimens come from three different areas (fig. 2), three from Auyantepui (type locality of *N. racenisi*), five from the area of Cerro Duida (type locality of *N. tatei*), and two from Ugueto.

Of the specimens from Auyantepui, two have four scales bordering the frontonasal or frontonasals posteriorly, and one has five. Of the five specimens from Cerro Duida, three have five; one has four; and the fifth, the holotype of *N. tatei*, has three. Both of the specimens from Ugueto have four.

All three specimens from Auyantepui and both specimens from Ugueto have a single frontonasal. In two of the specimens from Cerro Duida, including the holotype of *N. tatei*, the frontonasal is single; in three, it is divided.

In the two specimens from Ugueto, the caudal whorls bearing the large keeled crest scales are separated shortly distal to the vent by three intercalated vertical rows of smaller scales. Of the five specimens from near Cerro Duida, three have three vertical rows of scales separating the whorls with strongly keeled crest scales; another has a few scales of a fourth vertical row intercalated just behind the whorl with the large crest scale; the holotype of *N. tatei*, the fifth specimen, has only two vertical rows separating the whorls that have large crest scales. Two of the specimens from Auyantepui have the whorl with the large keeled crest scale separated by four

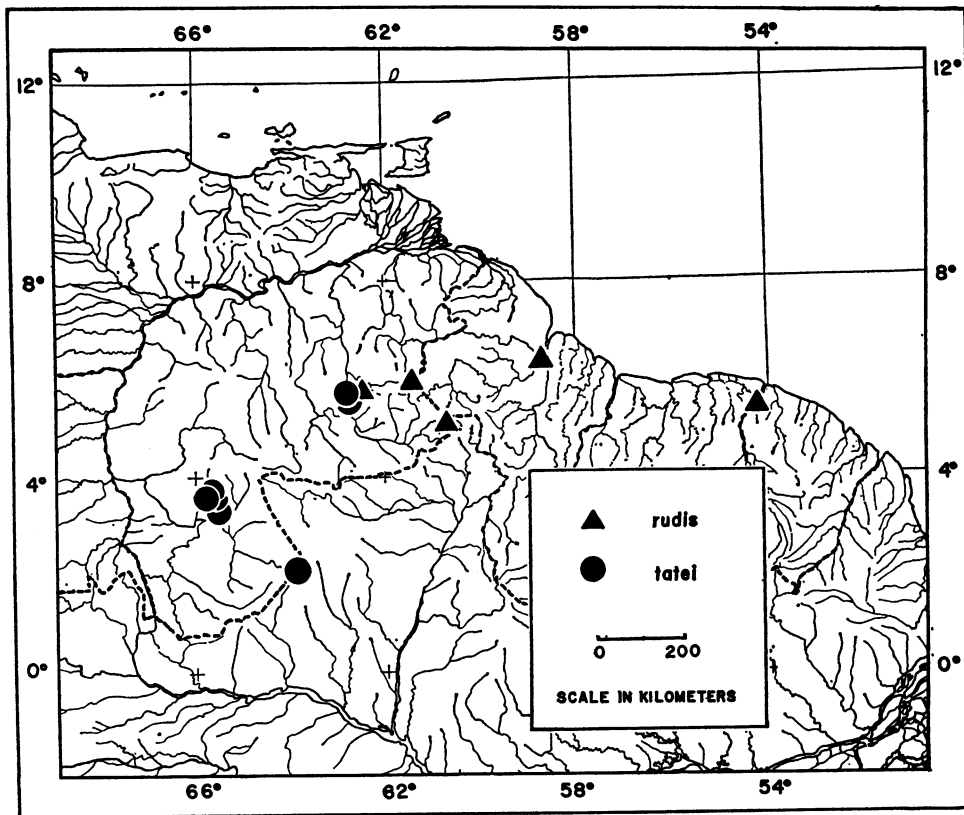


FIG. 2. Eastern Venezuela, the Guianas, and northern Brazil, showing localities for *Neusticurus tatei* and *Neusticurus rudis*.

vertical rows, but in M.B.U.C.V. No. 3541 only a few scales intercalated behind the whorl with the large crest scale represent the fourth row of small lateral scales.

REMARKS: Brongersma (1932) noted that *Arthrosaura tatei* differs from the other species of that genus in many ways. Examination of the holotype reveals that *tatei* is actually a member of the genus *Neusticurus*. The holotype is the least tuberculate specimen examined of a species that has far more restricted tuberculation than the better-known species, such as *N. ecpleopus* and *N. rudis*. The holotype of *tatei* fits my definition of the genus *Neusticurus*, and the species to which the type belongs should be known as *Neusticurus tatei* (Burt and Burt), new combination.

The holotype of *N. tatei* differs from the other specimens here referred to that species as follows: the tympanum is not recessed; no tubercles on the body; fewer (three) small

scales behind the frontonasal; a definite frontal, instead of irregular scales anteriorly and irregular pairs of scales posteriorly in the frontal region; two rows of small scales separating the whorls with the enlarged crest scales on the sides of the tail; and the lowest average number of small scales across the back and sides of the body (table 2).

In general, the holotype differs from other specimens in having a smaller number of more regular scales. It thus falls at one extreme of the variation in the specimens I have examined. The difference in the arrangement of the tympanum is surprising, but it seems possible that this is a preservational phenomenon, and that the enlarged scales that overhang the tympanum in most of the specimen have worn off in the holotype.

Within the genus *Neusticurus*, the holotype of *N. tatei* is most closely related to the other specimens here assigned to that species. Although I cannot demonstrate conclusively

TABLE 2
VARIATION IN *Neusticurus tatei*
(Figures are means and, in parentheses, extremes.)

	Femoral-Preanal Pores	Subdigital Fourth Finger	Lamellae Fourth Toe	Average Small Scales across Back and Sides*	Transverse Rows of Ventrals
Ugueto					
Two males	64.0 (64)	21.5 (21-22)	33.3 (32-34)	58.0 (57.3-58.7)	29.0 (28-30)
Male, holotype	61	20.0 (20)	29.5 (29-30)	36.3	27
Cerro Duida					
Two males	59.5 (58-61)	19.7 (19-21)	30.2 (28-32)	41.5 (41.3-41.7)	30.0 (30)
Two females	10.0 (10)	19.7 (19-21)	32.0 (30-34)	49.1 (47.0-51.3)	28.5 (28-29)
Auyantepui					
Two males	70.5 (69-72)	24.2 (22-26)	38.2 (37-39)	55.3 (53.7-57.0)	30.0 (30)
One female	13	25.5 (25-26)	33.5 (33-34)	61.7	30

* Average for each animal based on three counts.

that these other specimens are conspecific with the holotype of *N. tatei*, I feel that the similarities are more important than the differences. Most of the differences merely place the holotype of *N. tatei* at one extreme of the variation observed, rather than beyond the range of expected variation, and I suggest that *N. racenisi* is a junior synonym of *N. tatei*. Additional collections of this species may reveal that the characters in which the holotype of *N. tatei* differs from the other material referred to that form distinguish a population rather than a specimen. If so, the name *racenisi* is available to denote a closely related species or to denote a geographic segregate within the species *Neusticurus tatei*.

Sexual dimorphism in *N. tatei* is most conspicuous in the femoral-preanal pore series (table 2). The small sample from Cerro Duida suggests that males have fewer small scales on the sides and dorsum near midbody than females. Mature males are dark bluish black beneath in preservative; mature females are clear cream white beneath.

The largest male examined is 104 mm. from snout to vent; the largest female, 93 mm. Four males having intact tails have tail over snout-vent length ratios of 1.90 to 2.20, mean 2.09. The single female with intact tail has a ratio of 2.00.

Two of the females of *N. tatei* each have one leathery egg in each oviduct.

RANGE: *Neusticurus tatei* is restricted to the Guiana highlands of Venezuela, 400 to

1400 meters above sea level, in Territorio Federal de Amazonas and Bolívar (fig. 2). At Cerro Auyantepui, *N. tatei* is sympatric with *N. rudis*.

Neusticurus rudis Boulenger

Neusticurus rudis BOULENGER, 1900, p. 53.

Neusticurus surinamensis MÜLLER, 1924, p. 295.

Neusticurus dejongi BRONGERSMA, 1927, p. 543.

HOLOTYPE: *Neusticurus rudis* was described from a single male [B.M.(N.H.) No. 99.3.25.3, re-registered as 1946.8.31.64] taken near the foot of Mt. Roraima, British Guiana, about 1050 meters above sea level.

DEFINITION: The tympanum is at the bottom of a shallow pit; the scales of the surface of the head do not overhang the tympanum, and there is only a shallow external auditory meatus.

On the tail, the double crest is continuous on some individuals. It is composed of two or three sizes of scales in cycles: a large, keeled scale followed by a small, often flat scale and an intermediate-sized keeled scale, or a large keeled scale followed by a smaller keeled one. These cycles, from one large keeled scale to the next, may involve as many as three to five scales along the side of the tail, because of intercalated vertical rows. They are invariably subtended by only two of the median ventral caudal scales.

The tail is moderately compressed.

The canthus rostralis is moderately angular.

The translucent disc in the lower eyelid is divided by vertical grooves into three to seven, usually five or six, sections.

The sides of the body and neck are covered by a mixture of large tubercles intermixed with smaller, convex scales. The large tubercles of the dorsum tend to be irregularly arranged. In general, however, the middorsal region is free of tubercles, so that there is a longitudinal series of small scales, two to six, usually three or four, scales wide, along the center of the back.

There are five to eight, usually five or seven, preanal scales in the posterior row. When five or seven, the median is small and the parameian pair is relatively large.

All the specimens have eight longitudinal rows of ventral scales and 4-4 supraoculars.

The pattern of *N. rudis* is not conspicuous. Males and females are light underneath. The back and sides are brown, and on the back there is usually a series of dark brown spots alternating on one side and then the other. I have seen no specimen, among 14 mature males examined, with conspicuous ocelli. Occasionally, specimens show light and dark areas along the sides, but white-centered, black-bordered ocelli are unknown.

GEOGRAPHIC VARIATION: I have examined specimens of *Neusticurus rudis* from Arabopó, Auyantepui, Guayaraca, and La Laja in the uplands of Venezuela, from the lowlands of British Guiana, and from Surinam (fig. 2). There is considerable geographic variation in the species.

In the 18 Venezuelan specimens, the frontonasal is single. Of the three specimens from British Guiana, two have the frontonasal longitudinally divided. The third (A.M.N.H. No. 29926) has the frontonasal-prefrontal area covered by irregular scales; the frontonasal is not single. The specimen from Surinam has the frontonasal divided.

The Venezuelan specimens generally do not have a median azygous scale between the frontonasal and the prefrontals, although U.M.M.Z. No. 85246, from Arabopó, has a median scale completely separating the prefrontals from each other. There is a median azygous scale present in one of the specimens from British Guiana. A.M.N.H. No. 29925 has a median azygous, in contact on the left with another small intercalated scale; a similar small scale is present on the right, but separated from the median azygous. The third specimen from British Guiana has ir-

TABLE 3
VARIATION IN *Neusticurus rudis*
(Figures are means and, in parentheses, extremes.)

	Femoral-Preanal Pores	Subdigital Fourth Finger	Lamellae Fourth Toe	Transverse Rows of Ventrals
Venezuela				
Auyantepui				
Seven males	47.0 (42-51)	20.3 (18-23)	30.9 (28-34)	28.6 (28-30)
Three females	43.7 (42-47)	20.5 (19-21)	31.0 (30-33)	29.3 (27-32)
Arabopó				
Six males	47.7 (42-52)	18.2 (17-22)	27.5 (26-30)	29.5 (27-32)
One female	15 ^a	17.5 (17-18)	28.5 (28-29)	29
La Laja				
One male	46	16.0 (16)	27.5 (27-28)	28
British Guiana				
Three males	55.7 (52-60)	18.5 (18-20)	27.4 (26-30)	31.0 (30-32)
Surinam				
Male, holotype of <i>N. dejongi</i>	34	14.5 (14-15)	23.0 (23)	24
Female, holotype of <i>N. surinamensis</i> ^b	34	—	—	22

^a See text.

^b Data from Müller (1924).

regular scales in this area. The specimen from Surinam does not have a median azygous scale.

Most specimens have 4-4 infralabials, but M.B.U.C.V. No. 8008 from Auyantepui has 4-3.

The Venezuelan specimens all have a single pair of chin shields in contact along the midline, although in U.M.M.Z. No. 85248, from Arabopó, they are just barely so. Two of the specimens from British Guiana have a single pair of chin shields in contact, but the third (A.M.N.H. No. 29925) and the specimen from Surinam have two pairs of large scales in contact along the midline; the anterior pair is a divided postmental.

The specimen from Surinam has two small scales between the lower part of the loreal and the supralabials. One of the Venezuelan specimens (M.C.Z. No. 54722, Guayaraca) has a single scale between the loreal and the supralabials on the right side. Another (M.B.U.C.V. No. 3067, Auyantepui) has this extra scale on both sides.

All the males from Auyantepui have enlarged median scales in the anterior row of preanals. The females vary; one has an irregular large scale, another has two small scales, and a third has two irregular small scales. The male from La Laja has a single large median scale. The series from Arabopó, except for U.M.M.Z. No. 85244, has two small scales. A.M.N.H. No. 29926 from British Guiana and the specimen from Surinam have single enlarged scales; two of the specimens from British Guiana have two small scales.

The Venezuelan material generally does not have a median groove in the posterior end of the frontal; an irregular groove is present in U.M.M.Z. No. 85244 from Arabopó, and M.B.U.C.V. No. 3067 from Auyantepui has a posterior groove. All three specimens from British Guiana have some irregularity at the posterior end of the frontal. In A.M.N.H. No. 29927, there is a short median groove. In A.M.N.H. No. 29925, there is a single small scale split off on the right-hand end of the frontal. In A.M.N.H. No. 29926, there is a pair of unequal scales at the posterior end of the frontal. The specimen from Surinam does not have a posterior groove in the frontal; the posterior end of the frontal is quite regular.

Of the 10 specimens from Auyantepui, one

has 5-5, one 5-6, four 6-6, and four 6-7, supralabials. The seven specimens from Arabopó have six supralabials on 12 sides; one individual has 7-5. The specimens from British Guiana have six supralabials on three sides, seven supralabials on the other three, with one asymmetrical individual.

Femoral-preanal pore variation is striking. The females from Auyantepui have almost as many pores as the males (table 3). The single female from Arabopó has 11 preanal pores; at the distal end of each thigh there are two additional pores. On the right there are 13 intervening scales; on the left, 12. If each of the intervening scales surrounded a pore, this female would have 40 pores, rather than 15. The Venezuelan males have fewer pores than the males from British Guiana. The male from Surinam has only 34, the same as the number given for the female holotype of *N. surinamensis* (Müller, 1924).

REMARKS: *Neusticurus dejongi* was described from an immature male from an unknown locality in Surinam (Brongersma, 1927). Through the kindness of Dr. Dirk Hillenius, I have examined the holotype (Z.M.A. No. 10241).

Neusticurus dejongi was considered to differ from *N. rudis* because the holotype of *N. dejongi* has a smaller ear opening, the transparent disc in the lower eyelid divided by vertical grooves into three sections, the interparietal enclosed by the parietals rather than by a series of five small scales, the occipitals regular, two pair of chin shields in contact along the midline, and eight collar shields (Brongersma, 1927). Many of these characters, however, are individually variable within the species *N. rudis*, or are based on literature reports from different authors.

Certain characters, not emphasized by Brongersma, also distinguish the holotype of *N. dejongi* from other specimens of *N. rudis* examined. Thus, the holotype of *N. dejongi* has fewer femoral pores (34) than other males examined, and the outermost pair of the five posterior preanal scales is smaller than in other specimens of either sex examined.

On the other hand, the holotype of *N. dejongi* shares many features with other specimens of *N. rudis*. In particular, the arrangement of the dorsal scales, the pattern, the fact that the slightly depressed tym-

panum is not overhung by scales of the surface of the head, and the arrangement of the caudal scales all resemble the conditions found in *N. rudis*.

Although the holotype of *N. dejongi* differs from other specimens of *N. rudis* in certain characters, the similarity in characters distinctive of *N. rudis*, together with the fact that many of the characters of *N. dejongi* are within the range of variation of *N. rudis*, indicates that *N. dejongi* is conspecific with *N. rudis*.

Neusticurus surinamensis was described from a single specimen from Albina, Surinam, near sea level (Müller, 1924). Dr. Walter Hellmich has informed me that the holotype, formerly in the Zoologische Sammlung des Bayerischen Staates, was destroyed during World War II.

I have examined specimens of two species of *Neusticurus* from the lowlands of the Guianas: *N. rudis* and *N. bicarinatus*. Some of the characters of *N. surinamensis* suggest one, some the other, of these two species.

In the description, the holotype of *N. surinamensis* was compared only with *N. ecpleopus*. The ear of *N. surinamensis* was large compared to the eye; no external auditory meatus was mentioned. Since *N. ecpleopus* has no external auditory meatus, it seems likely that the holotype of *N. surinamensis* also did not.

Neusticurus bicarinatus has a conspicuous external auditory meatus. The external opening of the ear of *N. bicarinatus* is relatively small because the scales of the side of the head overhang the tympanum. In *N. rudis*, the tympanum is only slightly depressed below the surface of the head and is not overhung by scales of the side of the head. The ear opening of *N. rudis* is thus relatively large. The type of *N. surinamensis* probably resembled specimens of *N. rudis* rather than *N. bicarinatus*.

The holotype of *N. surinamensis* was reportedly an adult female, with a total of 34 well-developed femoral pores. This number is much larger than that observed in females of any species of *Neusticurus* except *N. rudis*. Even if the holotype was a male, however, the femoral pore count is matched within *N. rudis* by the holotype of *N. dejongi*, whereas the single count for a male of *N. bicarinatus*

(M.N.H.N. No. 4181, probably from French Guiana) is much higher (56).

The holotype of *N. surinamensis* had 22 rows of ventral scales. The specimen of *N. rudis* from Surinam has 24, and other counts for *N. rudis* vary from 24 to 32. The counts for *N. bicarinatus* vary from 26 to 29. The range of variation for *N. rudis* includes the holotype of *N. surinamensis*, but the known range for *N. bicarinatus* does not.

The enlarged keeled scales on the tail of the holotype of *N. surinamensis* did not lie close behind one another, but at the end of "Segmente"; they were separated by a smaller keeled scale and usually by a very small smooth one. In *N. bicarinatus*, the large keeled scales follow one behind another without separation. In *N. rudis*, the large keeled scales are often separated by smaller keeled scales or by a small scale followed by a keeled scale of intermediate size. The holotype of *N. surinamensis* thus approached a condition seen in many individuals of *N. rudis* but not observed in *N. bicarinatus*.

On the other hand, the arrangement of the dorsal tubercles on the body reported for *N. surinamensis* suggests *N. bicarinatus* rather than *N. rudis*, because the tubercles formed four unbroken longitudinal rows, of which the middle two were particularly regular and ran exactly parallel to one another. Although neither species has such straight rows of tubercles in the material examined, the description of *N. surinamensis* seems closer to the condition in *N. bicarinatus* than that in *N. rudis*, in which the dorsal tubercles only vaguely suggest linear series.

Many of the characters given in the description of *N. surinamensis* are variable in both *N. rudis* and *N. bicarinatus*. When the description is compared to the two species, and especially to the specimens from Surinam and French Guiana, the characters of *N. surinamensis* seem much closer to those of *N. rudis*. The present synonymy is tentative, however, and additional material from Surinam is needed for the situation to be clarified.

The largest male examined is 88 mm. from snout to vent; the largest female, 89 mm. Four males with tails intact have tail over snout-vent length ratios of 1.75 to 2.19, mean 2.04; three females, 2.02 to 2.30, mean 2.15.

I have not seen oviducal eggs in any female of this species. Roze (1958) reported that in captivity one female deposited two eggs.

RANGE: The known range of *Neusticurus rudis* is the uplands of Venezuela in Bolívar and the lowlands of British Guiana and Surinam, in an altitudinal range from near sea level to 1800 meters above sea level (fig. 2). In Venezuela, *N. rudis* is sympatric with *N. tatei*; in the Guianas, with *N. bicarinatus*.

***Neusticurus ecpleopus* Cope**

Neusticurus ecpleopus COPE, 1875, p. 161.

Neusticurus ocellatus SINITSIN, 1930, p. 1.

Neusticurus tuberculatus SHREVE, 1935, p. 209.

HOLOTYPE: This species was described from a specimen obtained by James Orton somewhere along the Amazonas, Maraón, or Huallaga rivers. The present known range indicates that the holotype almost certainly came from Peru. When the localities at which most of Orton's material was collected are considered, it seems likely that the holotype of *N. ecpleopus* came from the drainage of the Río Huallaga, somewhere between Rioja, Moyobamba, Balsaspuerto (fig. 1), and the place where the Huallaga flows out onto the lowlands of the Amazon basin. As far as I know, the holotype is no longer in existence.

DEFINITION: The tympanum is at the surface of the head; no scales overhang the tympanum, and there is no external auditory meatus.

The dorsal caudal crests consist of a slightly larger keeled scale followed by a slightly smaller one. The crests are separated near the base of the tail by two small scales lying one behind the other; distally, they are in contact. Proximally the scales of the row just lateral to the crest scales are half as long as the crest scales, and there are two scales per crest scale in this row on the anterior part of the tail. Distally, these scales are relatively longer, and there is one per crest scale in the posterior half of the tail. In most of the specimens, the caudal whorls go completely around the tail except near the base, where they are interrupted by the small scales separating the crests and the small scales of the row just lateral to the crest scales. An occasional specimen has a vertical row of small scales intercalated on the sides of the tail just posterior to the whorl with the larger crest scale.

The tail is only moderately compressed.

The canthus of this species is moderately angular.

The oval disc in the lower eyelid is not divided into sections by vertical grooves, although two specimens from Chontilla and six specimens from Ecuador have the disc irregularly divided on one side, and one from near Leticia has it irregularly divided on both sides.

Neusticurus ecpleopus is one of the more tuberculate species of the genus. Tubercles are present on the posterior part of the head, on the throat, and on the sides and dorsum of the neck, body, and tail. The upper surface of the limbs is also tuberculate. The presence of longitudinal rows of enlarged tubercles on the neck of *N. ecpleopus* distinguishes this species from tuberculate specimens of *N. strangulatus*.

The posterior preanal scales in *N. ecpleopus* are usually three: two large paramedian scales, and a variably sized median scale. Counts ranged from two to five. From north to south, the following variation was observed: In Ecuador, one male and one female among 22 specimens from the lowlands have two posterior preanals. Two males among 23 specimens from above 700 meters in Ecuador have two scales each. One male has four, another five, in the lowland Ecuadorian series. One female and one male from the foothills of Ecuador each have five scales. In a sample of 13 from between Macas and Gualaquiza, three females have five posterior preanal scales. In a sample of 18 from the Huallaga Valley, four males and two females have only two posterior preanals; one female has five. Among 10 from the Ucayali Valley, one male has two, another four, and a female has five, posterior preanal scales. In a sample of four from Junín, two males each have only two posterior preanals, while among eight from Puno, one male has four, and the single female has five, posterior preanal scales.

Most of the specimens have eight longitudinal rows of ventral scales. Three counts of six and one of seven were recorded from males from the Ecuadorian lowlands, and a count of six was recorded for a male from Junín. Most of the specimens also have 4-4 supraoculars. From north to south, the following variation was observed: One female from the Perené Valley has 4-5; another,

3-3. Three males from the Perené Valley have 3-3, and one has 4-5; three females have 3-3; two, 3-4; and two, 4-5. In the sample from Junín, one male has 3-3, and in the sample from Puno, one male has 5-5, while the female has 3-4.

GEOGRAPHIC VARIATION: The 177 specimens (97 males, 80 females) examined have been divided into 11 geographic groups (fig. 1). From north to south, these are:

1. "Colombia" includes three specimens from altitudes of 100 to 200 meters above sea level in Vaupés and Comisaria de Amazonas.

2. "Ecuadorian foothills" includes 15 males and eight females from altitudes of 700 to 1300 meters above sea level.

3. "Ecuadorian lowlands" includes 16 males and six females from altitudes between 100 and 600 meters above sea level in eastern Ecuador and the drainage of Río Marañón in Peru and Colombia. Four males from localities that were not found but that are in this vicinity and one female from Iquitos are listed as "not otherwise included" in table 5.

4. "Between Macas and Gualiquiza" includes six males and seven females from an uncertain locality in eastern Ecuador, with no altitude assignable.

5. "Huallaga Valley" includes 10 males and eight females from altitudes between 100 and 300 meters above sea level in the drainage of the Río Huallaga in Peru.

6. "Ucayali Valley" includes five males and five females from altitudes between 100 and 300 meters above sea level in the drainage of the Río Ucayali in Peru.

7. "Chontilla" includes three males and six females from about 780 meters above sea level, taken in the valley of the Río Iscozazin, 39 kilometers north-northeast of Oxapampa, Peru.

8. "Pan de Azucar" includes four males and six females from 380 meters above sea level, taken in the valley of the Río Iscozazin, 33 kilometers north-northeast of Oxapampa, Peru.

9. "Perené Valley" includes 22 males and 29 females from altitudes between 1000 and 1500 meters above sea level in the drainage of the Río Perené in Peru.

10. "Junín" includes three males and one female from near Satipo, Junín, Peru.¹

¹ An additional male was examined.

11. "Puno; Bolivia" includes seven males and one female; the specimens from Puno were taken at two localities probably between 1000 and 1300 meters above sea level; the Bolivian specimen is from Rurrenabque at 227 meters, but does not seem to differ from the Puno sample. A single male from Ayacucho, well to the west (fig. 1), is included.

FRONTONASAL: Divided or single frontonasals occur in many populations (table 4). In Ecuador, the sample from above 700 meters has a high percentage of divided frontonasals; specimens from 600 meters or lower have a high percentage of undivided frontonasals. This relationship holds for many of the samples. Thus, the lowland samples from the Huallaga Valley and from Pan de Azucar have high percentages of undivided frontonasals, and the sample from the Perené Valley has a high percentage of divided ones. The sample from Chontilla (780 meters) has a lower percentage of entire frontonasals than the sample from Pan de Azucar (380 meters). On the other hand, the sample from the Ucayali Valley (100-300 meters) has too few undivided frontonasals to fit the Ecuadorian picture. The "Colombia" animals (100-200 meters) all have divided frontonasals. Similarly, the extreme southern populations do not fit the Ecuadorian picture. The Bolivian specimen, probably from about 250 meters, has a divided frontonasal, while the specimens from Puno (1000 to 1300 meters) have the frontonasal undivided. These animals thus reverse the Ecuadorian situation.

In specimens that have a median azygous following the divided frontonasal, the suture between the two halves of the frontonasal is usually symmetrical; in cases in which the median azygous is absent, this suture frequently is slightly asymmetrical and does not form a straight line with the suture between the prefrontals.

MEDIAN AZYGUS: This scale is usually absent unless the frontonasal is divided (table 4). I have seen only one exception in this species, and, in that animal, other scales were irregular on this part of the head. Although the data on presence or absence of this scale add little to the geographic picture, they do reflect the variability of the head scales seen in many species of this genus.

TABLE 4

VARIATION IN FRONTAL NASAL, MEDIAN AZYGOS, AND MAXIMUM BODY SIZE OF MALES AND FEMALES IN ELEVEN POPULATIONS OF *Neusticurus epleopus*

	Number		Entire	Frontonasal		Median Azygous Present	Maximum Body Size (Mm.)	
	Males	Females		Median Groove	Divided		Male	Female
Colombia	1	2	0	0	3	0	36	56
Ecuador								
Foothills	18	8	0	2	20	6	69	67
Lowlands	17	7	14	1	8	6	66	60
Macas to Gualiquiza	6	7	13	0	0	0	67	63
Peru								
Huallaga Valley	10	8	11	3	4	2	64	60
Ucayali Valley	5	5	3	0	7	3	58	56
Chontilla	3	6	4	3	2	1	54	62
Pan de Azucar	4	6	7	0	3	0	63	61
Perené Valley	22	29	1	3	47	40	64	66
Junín	3	1	0	0	4	1	71 ^a	55
Puno; Bolivia	7	1	6	1	1	0	83	61

^a Estimated; skull removed.

BODY SIZE: It is difficult to assess differences in body size based on small samples, but there is some suggestion of a geographic pattern in the maximum sizes of the specimens examined. The body length of the largest male and female examined from each population is given in table 4.

Among the males, the largest specimens come from Bolivia and southern Peru. Of 10 males measured, six are more than 70 mm. from snout to vent. The only other area with males approaching this size range is the foothills of Ecuador, where five of the 15 males are between 60 and 69 mm. from snout to vent. The lowland Ecuadorian sample, by contrast, contains only two males out of 15 that are larger than 60 mm. from snout to vent. It does not seem likely that this phenomenon is purely altitudinal. Among the 22 males from the Perené Valley, probably taken at altitudes between 1000 and 1500 meters above sea level, only two are more than 60 mm. from snout to vent.

Two males out of nine from the Huallaga Valley are 60 mm. or longer from snout to vent. Two out of the four males from Pan de Azucar and two out of the six from between Macas and Gualiquiza are greater than 60 mm. from snout to vent.

The distribution of sizes among the males

suggests that large specimens are characteristic of the extreme southern populations and of those found in the foothills of Ecuador. The situation among the females is not inconsistent with this picture. The largest females come from the Ecuadorian foothills; two of the eight females are 60 to 67 mm. from snout to vent. The samples that contain the largest males, those from Puno, Junín, and Bolivia, are represented by only two females; one of these is 61 mm. from snout to vent. The areas other than the foothills of Ecuador that have large females are the Ecuadorian lowlands where two of the six females are 60 mm. from snout to vent; the Perené Valley, where four of 29 are between 60 and 66 mm.; Chontilla, where two of six are 62 mm.; Pan de Azucar, where one of six females is 66 mm. from snout to vent; and the Huallaga Valley, where one of eight females is 60 mm. from snout to vent.

COLOR: There is much variation in this species, associated with sex, size, and geography.

The largest male from southern Peru is spectacularly colored. The anterior part of the head, including the parietals and interparietal, postocular scales, labials, and chin shields, is black except for the area of the eye. There is a bright white band nearly

surrounding the eye and encompassing most of the palpebrals. This band runs from the posterior corner, between the last superciliary and the upper postocular, down and beneath the eye, around the anterior corner. It is interrupted above the middle of the eye. The disc in the lower eyelid is largely covered by a black spot. The posterior part of the head is gray. The belly and throat are generally cream-white, but the sides of the belly are darker. The dorsum is generally dark brown. There is one conspicuous, black-bordered, white-centered ocellus on each side, near the forelimb insertions; posterior to this are three fainter ocelli on each side.

The Bolivian specimen, 73 mm. from snout to vent, is similar, but there is less contrast in the head pattern. The venter is cream-white, with a few scattered melanophores; the dorsum is uniformly dark cream-brown. There are three conspicuous, black-bordered, white-centered ocelli on the right, four on the left. The head is generally the same color as the dorsum, but there are black marks on the posteriormost superciliary, the postoculars, and on the anterior suboculars. There are light areas at both corners of the eye: between the posterior superciliary and postocular, and on the upper part of the freno-ocular.

The smaller males and the female from southern Peru are similar to the Bolivian specimen, but even less conspicuously marked.

Patterns similar to that seen in Bolivia and southern Peru occur also in the foothills of Ecuador. Two males, 63 and 67 mm. from snout to vent, have dark brown-black heads except around the eye; the palpebrals, suboculars, and upper part of the supralabials are whitish, producing a white triangle in the eye region. These two specimens have the chin and throat almost uniformly black. The belly is almost uniformly dark brown anteriorly, mottled brown and cream-white posteriorly; the under side of the tail is heavily mottled. The dorsum is dark brown-black, and there is a conspicuous ocellus near each forelimb insertion.

The long series of specimens from the Perené Valley show no such coloration. Nine males between 44 and 64 mm. from snout to vent (the largest in the series) are generally

cream-white below on chin and belly; dark flecks are scarce or absent. The under side of the tail is darker. The dorsum is generally uniform and of a darker brown than the belly. There are usually from two to five conspicuous ocelli along the sides. The anterior ocelli are the brightest, particularly the one nearest the forelimb insertions; posteriorly, they become irregular. There is no conspicuous coloration on the head.

Eight females between 55 and 66 mm. from snout to vent from the Perené Valley differ somewhat from the males. The ground color of the venter is cream-white, but there are more numerous dark flecks, especially along the sides; the chin is also more mottled than in the males. The under side of the tail is blotched with dark and cream areas. Ocelli are present along the sides, but they are irregular. The dorsum is less uniform than in the males. On both sides, beginning at the posterior corner of the eye, a light brown line extends across the temporal region onto the neck. On the body, the line becomes broken up, forming a series of light spots on the tubercles. Especially on the head and neck, lines of brown, darker than the ground color, border the light dorsolateral lines. The supraoculars and the anterior part of the head of the females are often mottled. There are light lines from the posterior corner of the eye and center of the eye across the supralabials and infralabials.

The many young animals from the Perené Valley all have lighter tails than bodies, especially dorsally.

Specimens generally similar to the series from the Perené Valley are found in the Huallaga and Ucayali valleys of Peru and in the lowlands of Ecuador and Colombia. In these, however, the males tend to be more heavily mottled underneath than the males from the Perené Valley. The male from these areas with the darkest ventral coloration, 58 mm. from snout to vent, is not so dark beneath as males from the foothills of Ecuador. Usually males in these regions have at least one bright ocellus near the forelimb insertions; other fainter ocelli may also be present.

A brightly colored specimen from near Leticia, Colombia (M.C.Z. No. 61150), a male 62 mm. from snout to vent, is creamy

white on chin, throat, and belly; the under side of the tail is dark brown. The dorsum is generally light brown. On the body, there are four longitudinal rows of lighter spots; these light spots also form diagonal lines across the back. There is one bright, black-bordered, white-centered ocellus on each side near the forelimb insertions. From the posterior corner of the eye, a light line extends across both the supralabials and infralabials.

The females from northern Peru and the lowlands of Ecuador and Colombia have dark flecks scattered on the cream-white venter. The chin and throat are heavily mottled with dark, black-brown areas. These tend to form lines crossing the infralabials and chin shields at right angles to the jaw margins, and to form longitudinal bars on the throat. The ocelli in these females are irregular, and the light dorsolateral lines on the head and neck are less distinct than in females from the Perené Valley.

The animals from Pan de Azucar and Chontilla were preserved more recently than most of the specimens of *N. ecpleopus* examined. The two largest males from Pan de Azucar (62 and 63 mm.) are cream-white below, with a few dark flecks. Both show a reddish tint on the venter and on the under side of the basal part of the tail. These two males are black-brown above and have one or two well-defined ocelli near the forelimb insertions.

Three of the four largest females from Pan de Azucar (53 to 61 mm. from snout to vent) resemble the males, but have weak dorsolateral stripes and ill-defined ocelli. Another large female, 57 mm., is heavily spotted below.

The only large male from Chontilla, 54 mm., is heavily spotted below, and has a single, ill-defined ocellus on each side. The four largest females from Chontilla, 56 to 62 mm. from snout to vent, are dark above and light below.

The smallest animal from these two localities, 25 mm. from snout to vent, has the tail lighter than the body.

Color notes from life are available for three of the specimens from Pan de Azucar. L.A.C.M. No. 8522, a male 63 mm. from snout to vent, was olive brown above, with

black-bordered white lateral ocelli; some of the temporal and lateral body scales had a reddish cast. The upper and lower lips and throat were bright yellow. The belly was greenish, with black spots, and the basal half of the tail was red underneath. L.A.C.M. No. 8523, a male 43 mm. from snout to vent, was similar, but the dorsum was reddish. In L.A.C.M. No. 8524, a female 42 mm. from snout to vent, the dorsum of body and tail was olive brown.

In summary, the extreme southern specimens and those from the foothills of Ecuador resemble one another in coloration. The males in these two areas have the greatest amount of dark pigment on the head, and, in extremely dark males, a white triangle in the eye region is conspicuous. The males from these two areas differ in that the specimens from the foothills of Ecuador become darker underneath, whereas the extreme southern males tend to be light below.

Specimens from the lowlands of Ecuador and northern Peru and from the Perené Valley of Peru are relatively similar to one another in coloration. They differ from the southern populations and from the specimens from the Ecuadorian foothills in being a lighter brown. The males do not develop the conspicuous black heads seen in the southern populations and in the sample from the Ecuadorian foothills, and often the males have as many as three to five conspicuous ocelli along each side. The females are often more heavily flecked below than the males, and often have light dorsolateral lines on the head and neck.

The specimens from Pan de Azucar and Chontilla in general are similar to the specimens from the Huallaga, Ucayali, and Perené valleys, but tend to be darker, to have fewer bright ocelli in the males, and to be more uniform above, especially the females.

There are thus in *N. ecpleopus* two groups based on color and pattern. In one group the males are black-headed with few ocelli, and the females have poorly developed dorsolateral light lines; in the other, the males generally have brown heads and more ocelli and the females have well-developed dorsolateral light lines. To what extent the color and pattern of these two groups depend on the size of the specimen is unknown. Whether

TABLE 5
VARIATION IN *Neusticurus ecpleopus*
(Figures are means and, in parentheses, extremes.)

	Femoral-Preanal Pores	Subdigital Lamellae Fourth Finger	Fourth Toe	Transverse Rows of Ventrals
Colombia				
One male	?—?	12.5 (12–13)	22.0 (21–23)	22
Two females	1.5 (1–2)	14.7 (13–15)	23.7 (22–24)	20.0 (19–21)
Ecuador				
Foothills				
Fifteen males	38.3 (33–43) ^a	13.7 (11–16)	22.6 (20–26)	21.6 (19–24) ^a
Eight females	7.0 (5–10)	13.1 (12–15)	22.0 (21–24)	21.2 (20–22)
Lowlands				
Sixteen males	32.3 (25–42)	13.3 (10–16)	21.9 (18–26)	21.3 (20–22)
Six females	5.2 (4–7)	12.9 (12–15)	21.2 (18–25)	20.8 (20–21)
Macas and Gualiquiza				
Six males	34.3 (29–38)	12.5 (11–16)	21.4 (19–23)	21.3 (20–22)
Seven females	6.7 (4–15)	11.9 (11–13)	20.4 (18–22)	21.1 (20–22)
Peru				
Huallaga Valley				
Ten males	31.5 (29–36)	13.5 (12–15) ^b	23.4 (21–26) ^b	20.5 (19–21) ^b
Eight females	7.5 (2–13)	13.7 (12–15)	22.8 (21–24)	21.2 (20–22)
Ucayali Valley				
Five males	32.4 (29–36)	14.4 (13–15)	23.9 (22–26)	20.2 (19–22)
Five females	9.0 (4–13)	13.3 (11–16)	21.4 (18–25)	21.2 (19–24)
Chontilla				
Three males	33.3 (32–36)	13.7 (13–15)	22.5 (21–25)	23.3 (23–24)
Six females	4.7 (3–7)	13.6 (12–15)	23.0 (20–24)	22.2 (20–24)
Pan de Azucar				
Four males	34.0 (31–35)	13.4 (13–14)	22.5 (22–23)	22.0 (21–23)
Six females	7.3 (4–13)	13.3 (13–14)	21.7 (21–23)	22.3 (21–23)
Perené Valley				
Twenty-two males	41.0 (35–44)	13.1 (12–15)	20.5 (18–23)	23.0 (20–24)
Twenty-nine females	4.8 (2–8)	13.2 (11–15)	20.7 (17–23)	23.5 (22–25)
Junín				
Three males	40.7 (30–48)	13.3 (13–14)	21.8 (21–23)	22.0 (22)
One female	8	13.5 (13–14)	21.0 (20–22)	21
Puno; Bolivia				
Seven males	40.3 (38–43)	14.1 (13–16)	24.1 (21–28)	23.1 (21–25)
One female	4	14.5 (14–15)	23.5 (23–24)	23
Not otherwise included				
Four males	36.7 (34–42)	13.5 (13–15)	23.5 (23–25)	21.5 (20–22)
One female	6	12.5 (12–13)	21.5 (21–22)	21

^a Fourteen males.

^b Nine males.

the groupings based on body size and color reflect similar adaptations or closeness of relationship is also not known.

TOTAL FEMORAL PORE NUMBER: From table 5, it can be seen that the specimens from Bolivia and southern Peru (Junín, Puno, Perené Valley) all have high numbers

of femoral-preanal pores in the males. The sample from the Ecuadorian foothills also has a relatively high number of pores in the males. The remaining samples have low numbers. Possibly this variation is altitudinal.

There is striking sexual dimorphism in total femoral-preanal pore counts in this

species as in most other species of *Neusticurus*. The total pore counts for the females do not seem to form any clear pattern.

TRANSVERSE ROWS OF VENTRAL SCALES: Although there is little variation in this character, the populations from Bolivia and southern Peru (Puno, Junín, Perené Valley) have more transverse rows of ventral scales than the remaining populations (table 5). The population from the Ecuadorian foothills resembles the lowland Ecuadorian population. This character shows no conspicuous sexual dimorphism.

Color, size, and the arrangement and number of scales distinguish several populations of *N. ecpleopus*. Thus, the Bolivian and southern Peruvian specimens (Puno, Junín) have numerous femoral pores in the males, large body size, high numbers of transverse rows of ventral scales, and conspicuous blackening of the head in large males. Perhaps these characters reflect the large body size of these populations. In addition, these populations generally have an undivided frontonasal, a light venter, and often only a single conspicuous ocellus.

The sample from the Perené Valley has numerous femoral-preanal pores in the males and numerous transverse rows of ventral scales. The body is short, and the males generally have uniformly brown heads, light venters, and more numerous ocelli. The females have light dorsolateral stripes on the head and neck. Almost all the specimens from the Perené Valley have a divided frontonasal.

The animals from Chontilla and Pan de Azucar have fewer femoral-preanal pores in the males and perhaps fewer transverse rows of ventral scales than animals from the geographically close Perené Valley. The samples from Chontilla and Pan de Azucar usually have short bodies, and many have the frontonasal undivided. Both sexes are generally dark above; ventrally they are often light, with varying amounts of dark flecking. The males have one or two bright ocelli; the females, some indication of dorsolateral light lines.

The specimens from the Huallaga and Ucayali drainages and from the lowlands of Ecuador and Colombia share many characters. They are short-bodied and have few

transverse rows of ventral scales, and few femoral pores in the males. The samples from the Ucayali Valley and from the lowlands of Colombia frequently have the frontonasal divided, but most of the specimens from the lowlands of northern Peru, Ecuador, and Colombia have the frontonasal undivided. The individuals from the Ucayali Valley tend to be lighter underneath than the others in this lowland area. In all these samples, the males often have as many as three to five bright ocelli along the sides, and the females tend to have light dorsolateral lines on the head and neck.

The specimens from the foothills of Ecuador are long-bodied; the males have numerous femoral-preanal pores. Frequently, the larger males tend to become black-headed, and generally the males have only one or two bright ocelli along the sides. The specimens from the Ecuadorian foothills usually have the frontonasal divided, a low number of transverse rows of ventral scales; the belly is often heavily mottled with black in the larger males.

REMARKS: The description of *Neusticurus ecpleopus* (Cope, 1875) is very brief, but it mentions the undivided disc in the lower eyelid, the longitudinal rows of tubercles on the sides of the neck, and the tubercles on the sides of the body. These characters are sufficient to assure that the species name *ecpleopus* is correctly applied.

The holotype had a total of 30 femoral pores, and was 66 mm. from snout to vent. It was chocolate brown above, showing darker spots in proper lights; below, it was yellow, speckled with brown except for the throat, lips, and chin, which were black. These characteristics suggest that the holotype was a mature male. Ocelli were not mentioned in the description.

Cope compared his species with *N. bicarinatus*. The arrangement of the scales in the frontonasal area was not included by Cope in his list of differences between these two species. It therefore seems likely that the arrangement of the scales in this region was similar in the two forms, and that the holotype of *N. ecpleopus* had a divided frontonasal followed by a median azygous scale.

Of these characters, most can be matched in several populations from northern Peru

and Ecuador. The femoral pore number suggests one of the lowland populations (table 5).

The exact locality from which the holotype of *N. ecpleopus* came is unknown. If the localities given by Cope for most specimens in his 1875 report are considered, the type probably came from somewhere along the Río Marañón or the Río Huallaga, and quite possibly from near Moyobamba, Rioja, or Balsaspuerto on the Río Huallaga (fig. 1).

The holotype of *N. ecpleopus* was probably at one time in the collection of the Academy of Natural Sciences of Philadelphia. Mr. Edmund V. Malnate has looked for this specimen for me on several occasions but has been unable to find it. The holotype does not appear to be in the collection of other American museums that have types of Cope's forms.

Neusticurus tuberculatus was described (Shreve, 1935) from four specimens (M.C.Z. Nos. 37711, 37264–37266) from the lowlands of Ecuador and of Peru north of the Río Marañón between 100 and 500 meters above sea level. Shreve noted their similarity to *N. ecpleopus*. Through the kindness of Dr. E. E. Williams, I have been able to examine the holotype and three paratypes. These specimens have no characters that cannot be matched in specimens of *N. ecpleopus* from adjacent parts of Ecuador and Peru.

The type localities of *N. tuberculatus* are not far distant from the probable type locality of *N. ecpleopus*. *Neusticurus tuberculatus* certainly belongs to the lowland group of populations found in the area. If the total femoral-preanal pore count of the holotype of *N. ecpleopus* is a reliable guide, *N. tuberculatus* probably is a member of the same population from which the type of *N. ecpleopus* came. I consider the two synonymous. If it can be shown that the name *ecpleopus* does not belong to the population that occurs in the lowlands of the Río Huallaga, the name *tuberculatus* is available for this lowland population.

The characterization of *Neusticurus ocellatus* given by Sinitsin (1930) is extremely vague. The holotype (A.M.N.H. No. 22512) is from Rurrenabaque, in central Bolivia, at about 250 meters above sea level. The paratypes came from the Perené Valley of central Peru at about 1000 to 1500 meters above sea

level. This form was redescribed by Burt and Burt (1931) as a subspecies of *N. ecpleopus*.

Through the kindness of Mr. C. M. Bogert, I have examined the holotype and paratypes of *N. ocellatus*. The holotype is quite different from the paratypes. Regardless of the status of the name *N. e. ocellatus*, the paratypes are much more like specimens from northern Peru, to which another name is applicable.

I have not recognized a southern subspecies of *Neusticurus ecpleopus* because it seems to me that the present picture of geographic variation makes such a course unwise. Several populations can be distinguished with the use of the data presented here, but recognition of these would require additional names, the status of which will be uncertain until the name *ecpleopus* is safely and firmly applied to the lowland or foothills populations of northern Peru and Ecuador. Furthermore, collection of additional material is likely to add to the geographic non-concordance of characters already apparent within this species.

RATIO OF TAIL LENGTH TO SNOUT-VENT LENGTH: Given populations reaching different maximum sizes, any allometric growth in body and tail would result in different mean values in the ratio of the tail length over the snout-vent length. Too few of the specimens examined have intact tails for interpopulational differences to be detected. The data available were grouped by sex for the entire species. Twenty-one males with tails intact have ratios of 1.37 to 1.79, mean 1.64; 15 females have ratios of 1.45 to 1.81, mean 1.64. There seems to be little sexual dimorphism in this character.

Twelve females examined each have a single leathery egg in each oviduct.

RANGE: *Neusticurus ecpleopus* occurs from central Bolivia north along the eastern slopes of the eastern Andes to southern Colombia (fig. 1); elevations range from 100 to 1500 meters above sea level. This species has been reported from the Río Beni and Río Suapi in Bolivia (Werner, 1910); from Seringal Oriente, Territorio do Acre, Brazil (da Cunha, 1961); and from La Morelia, Colombia (Dunn, 1944). (See fig. 1.)

The range of *Neusticurus ecpleopus* encompasses the ranges of *Neusticurus cochranae* and *Neusticurus strangulatus*

***Neusticurus apodemus*¹ new species**

Figures 3, 4

TYPE MATERIAL: Holotype, male (U.K.-M.N.H. No. 67375), apparently mature, from 15 kilometers southwest of San Isidro del General, San José, Costa Rica; 865 meters above sea level; collected June 2, 1961, by William E. Duellman; original number, W.E.D. No. 20692. Paratypes: U.K.M.N.H. Nos. 67377-67380; U.M.M.Z. No. 124688; same locality and date as holotype; U.K.M.N.H. No. 67381; same locality as holotype; July 11, 1961.

DIAGNOSIS: A species of *Neusticurus* characterized by (1) irregular scales in fronto-nasal-prefrontal region; (2) small size; (3)

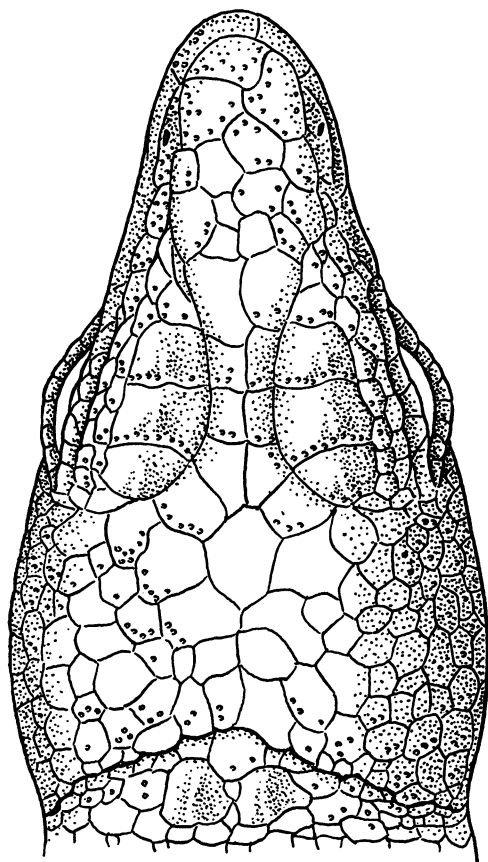


FIG. 3. Dorsal head scales of the holotype (U.K.M.N.H. No. 67375) of *Neusticurus apodemus*, new species.

¹ The name *apodemus* is from the Greek ἀπόδημος, "away from home."

generally a double row of supraoculars; (4) tympanum at surface of head; no external auditory meatus; (5) caudal crests discontinuous; whorls carrying large keeled crest scales separated, on sides of tail, by two vertical rows of scales; (6) tail weakly compressed; (7) canthus rostralis rounded; (8) division of translucent disc in lower eyelid into sections by vertical grooves; (9) tubercles on sides of neck in longitudinal rows; (10) conspicuous light areas on upper forelimbs; and (11) minute calcareous spinules in flouces of hemipenes.

DESCRIPTION OF HOLOTYPE: Body long, thin, depressed; neck elongate; head slightly wider than neck. Tail long, slightly compressed, 1.7 times as long as body. Limbs delicate.

Head scales: Irregular (fig. 3); rostral in contact with first supralabial and narrowly with nasals; nasals separated by irregular scales; supraoculars in two complete rows, inner four large, anteriormost smallest; all weakly keeled; outer row all smaller than anterior inner superciliaries. Scales of snout flat, irregular, not granular; scales between supraocular series irregular, weakly keeled; interparietal large, surrounded by a symmetrical series of eight scales. Temporal area covered by small polygonal scales. Five supralabials. A lower series of medium-sized scales and an upper series of small scales separating lower palpebrals from supralabials. Clear area in lower eyelid divided by vertical grooves into three parts. Tympanum heavily pigmented, its greatest diameter 1.6 times length of eye opening, at surface of head; no reflexed ridge of scales at anterior margin of tympanum. Five infralabials; one unpaired, and two pairs of chin shields in contact, paired chin shields with azygous scale between them. Posterior to these, two pairs of smaller scales that might be considered chin shields, separated from opposite member of pair and from infralabials. Gular fold absent. Gular scales polygonal, flat, juxtaposed, not in transverse rows, but anterior scales in linear series, paralleling jaw rami. Posterior gulars somewhat larger, flat or slightly convex, slightly imbricate, median rows scarcely wider than long. Eight scales in collar.

Scales of sides of neck heterogeneous, low

conical scales interspaced with smaller, more granular scales, cones of upper sides of neck in longitudinal rows.

Body scales (fig. 4): Four rows of larger keeled scales beginning near midpoint of neck, running onto back, forming four weak keels on body to just posterior to base of tail. Lateral rows of keeled scales less regular than median ones. Four rows tending to be separated by at least two granules, where enlarged scales juxtaposed, and may be separated by as many as four or five at level of contact between successive larger scales. Two median rows separated usually by two or three rows of smaller scales. Ventral scales mainly flat, quadrangular in outline, slightly rounded posteriorly, and slightly imbricate. Arrangement on type irregular in that, at midline, several rows alternate. Outer two ventral scale rows keeled. Lateral body scales near ventrals and near lower row of dorsal keeled scales convex and enlarged or small and flat; scales midway between mainly small and flat. Two large scales in posterior row, and two larger median and four very small lateral scales in anterior row, of preanals.

Dorsal caudals, near base of tail, irregular; for most of length of tail, however, larger, weakly keeled scales forming whorls separated by two vertical rows of smaller flat scales, two rows of smaller scales occupying as much tail length as one row of larger scales. Two median rows of ventral caudal scales are flat, rounded posteriorly, generally quadrangular.

Dorsal scales of upper arm leaf-shaped, keeled, imbricate; of lower arm, subquadrangular, weakly keeled, slightly imbricate. Scales of under side of arm rounded, slightly convex. Scales of dorsal surface of palm flat, dorsal finger lamellae simple. Scales of palm small, thenars slightly enlarged, not forming ridge. Subdigital lamellae undivided.

Scales of upper surface of thigh and shank and of outer surface of shank keeled; scales of ventral surface of thigh flattened. Femoral pores 14 on right, 13 on left, femoral pore series separated by two small scales anterior to vent. A single enlarged scale on either side of vent. Scales of dorsal surface of foot keeled, of palm of foot rounded, convex. Supradigital lamellae simple. Subdigital lamellae divided basally, undivided distally,

inner section of divided subdigital lamellae forming weak ridge on fourth toe.

Color: Top of head light olive brown, with some mottling of darker brown; snout unmottled. Sides of snout much more heavily mottled with dark brown, outlining lighter area of snout. Two light bars crossing labials from center and posterior corner of eye. Labials dark brown, infralabials with white posterior border. Mentals and chin shields white. Gulars dark brown, white, or brown with a white spot, giving throat mottled appearance. Tympanum dark brown. Dorsal ground color light brown, finely mottled with

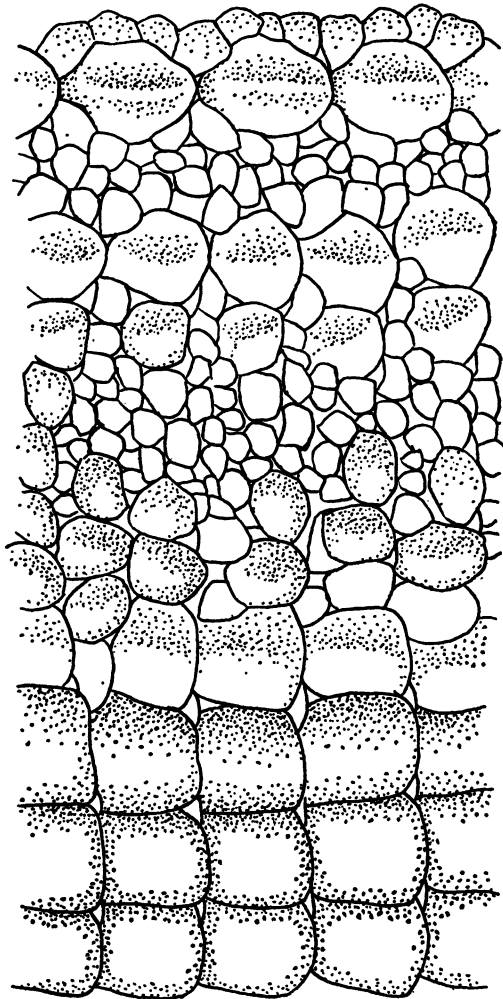


FIG. 4. Scales from middorsal to midventral lines near midbody on the holotype of *Neusticurus apodemus*, new species (U.K.M.N.H. No. 67375). Anterior is to the left.

dark. Outer row of large keeled dorsal scales generally marked with yellowish white, forming two irregular light bands on body; these more nearly continuous on neck and disappearing as lines above base of tail. Sides generally darker, with six (left) and seven (right) indistinct, light-centered, dark-bordered ocelli between limb insertions. Bright white patch posteroventral to tympanum. Median ventral scales mostly light, lateral and anterior ones with light centers and dark borders. Tail with light ventral scales anteriorly, generally dark laterally. Dorsally ground color light brown, but heavily marked with dark brown. Dorsolateral enlarged keeled scales of tail lighter, forming two longitudinal rows of light dots.

Forelimbs blotched with dark brown and yellowish white: most of upper arm, except at insertion and near elbow, light; light spot on elbow; most of inner side of lower arm and of hand light; dark areas essentially confined to outer margin. Hind limbs mainly dark brown above, light mottled with dark brown below. One large and one small light spot on outer surface of thigh.

VARIATION: The paratypes are generally similar to the holotype. All the specimens have eight longitudinal rows of ventral scales. The posterior preanals include two large scales, except in U.K.M.N.H. Nos. 67377 and 67378, the two females, which have four large posterior preanals. The supraocular series includes four large inner scales in all but U.K.M.N.H. No. 67377, which has five scales on the right. The outer supraocular series includes six to eight scales, usually seven; in U.K.M.N.H. No. 67378, the outer series of supraoculars is broken on the left.

The color of the paratypes generally resembles that of the type. The tympanum is

dark, and there is usually a light spot posteroventral to it. The forelimbs are boldly marked with dark brown and yellowish white; the upper arms especially have large light areas. The lateral ventral scales are usually dark brown, with a narrow, midventral, light area.

DISTINCTIVE CHARACTERS: The tympanum of *Neusticurus apodemus* is joined to the surface of the head in a relatively smooth curve; it is not recessed nor overhung by a fold or ridge of scales; there is no external auditory meatus.

The dorsal caudal crests are very weak; each consists of cycles of a large keeled scale followed by two small flat ones. The large keeled scales are in contact with one another from near the base of the tail to the tip; occasionally, near the base of the tail, they are separated at the posterior ends by a small median scale. The whorls containing the large keeled scales are separated from one another by two whorls of smaller scales. A cycle from one large keeled dorsal caudal to the next is subtended by two pairs of median ventral caudals.

The tail is only slightly compressed.

The canthus rostralis in the specimens examined is rounded.

The translucent disc in the lower eyelid is divided by vertical grooves into two or three, usually three, sections.

The sides of the body and neck, and the dorsum from the posterior part of the head onto the tail, are tuberculate; tubercles are present on both forelimbs and hind limbs. The dorsal body tubercles are arranged in linear series.

The posterior preanals number two or four, usually two; the variation may be sexual dimorphism. The anterior row of preanals has four scales: a larger median pair and a very small lateral pair.

TABLE 6

VARIATION IN *Neusticurus apodemus*

(Figures are means and, in parentheses, extremes)

	Femoral-Preanal Pores	Subdigital Lamellae Fourth Finger	Fourth Toe	Transverse Rows of Ventrals
Five males	28.4 (26-30)	12.7 (11-14)	20.2 (19-22)	23.0 (22-24)
Two females	4.0 (4)	12.7 (12-14)	19.5 (18-21)	23.5 (23-24)

The most distinctive features in the pattern are the light blotches on the upper forelimbs, the light spot posteroventral to the tympanum, the dark sides of the head, and the dark lateral and light medial ventral areas. Ocelli are poorly developed in the largest male examined.

Jay M. Savage (personal communication) has informed me that, in life, a large male had an orange-red chin; a large female was pale orange below.

REMARKS: *Neusticurus apodemus* is closely related to *N. ecpleopus* (table 12). The hiatus between the known ranges of the two species is extensive (fig. 5) and probably real. *Neusticurus ecpleopus* is a diurnal form; it is abundantly represented in collections from its known range. If it occurred in the Pacific or Caribbean drainages of South America, its size and activity period would almost surely

have resulted in its being observed. *Neusticurus apodemus* probably is more secretive than *N. ecpleopus*. This secretiveness perhaps is the reason that it is unknown from the hiatus, although other secretive lizards, *Echinosauro horrida*, for example (Uzzell, 1965), have been collected there in fair numbers.

Sexual dimorphism is apparent in the femoral pore number and probably in the preanal scale number (table 6).

The largest male examined is 47 mm. from snout to vent; the largest female, 38 mm. The five males have intact tails; the ratio of the tail length to the length from snout to vent varies from 1.55 to 1.69, mean 1.63; one of the females has a ratio of 1.53.

RANGE: *Neusticurus apodemus* is known only from the type locality. No other species of *Neusticurus* occurs in this area.

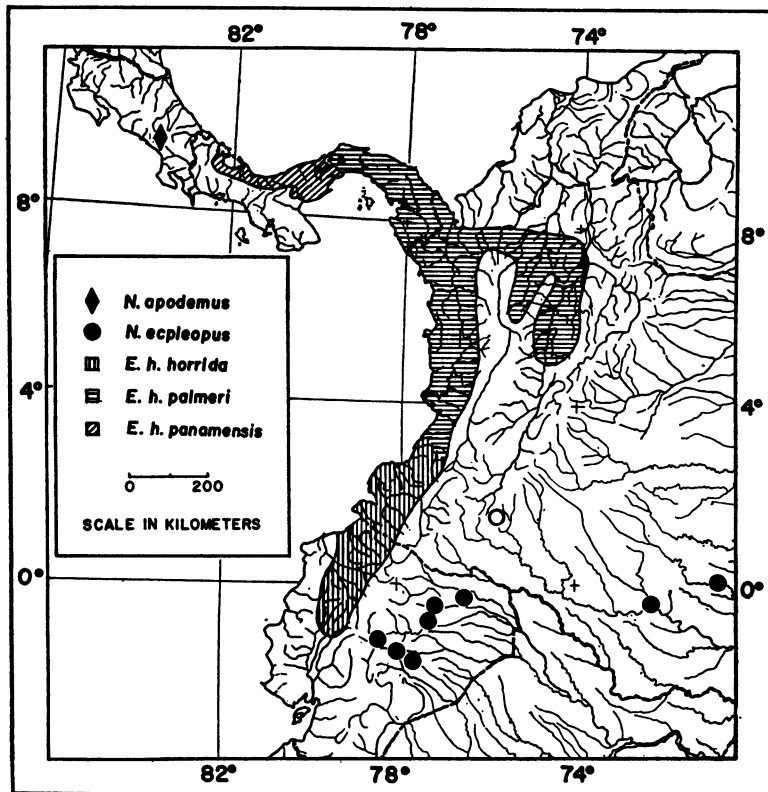


FIG. 5. Northwestern South America and eastern Central America, showing locality for *Neusticurus apodemus*, new species, selected Ecuadorian and Colombian records of *Neusticurus ecpleopus*, and the ranges of three subspecies of *Echinosauro horrida*.

***Neusticurus strangulatus strangulatus*,**
new combination

Euspondylus strangulatus COPE, 1868, p. 99.

Euspondilus festae PERACCA, 1897, p. 10.

TYPE LOCALITY: Probably between Papalacta and Napo, or along the Río Napo before it joins the Río Marañón, in Ecuador or Peru (Uzzell, 1961).

HOLOTYPE: Thanks to the efforts of Mr. Edmund V. Malnate, the holotype (A.N.S.P. No. 7538, original number 6636) has recently been rediscovered. The specimen is an adult male, 60 mm. from snout to vent, 176 mm. in total length. The ventrals are in eight longitudinal, and 25 transverse, rows. There are 46 scales around the midbody region, and 68 dorsal scales between the interparietal and the posterior surface of the hind limbs. The femoral pores number 28 on the right side, 27 on the left. The frontonasal is single, and the loreal is separated from the supralabials by contact between the nasal and the frenocular. There are seven small scales around the posterior margin of the interparietal. The lamellae under the fourth fingers number 17 and 18; under the fourth toes, 28 and 29. The disc in the lower eyelid is divided into sections by vertical grooves. The ratio of the length of the tail to the snout-to-vent length is 1.93. There is one distinct, black-bordered, light-centered ocellus on each side near the forelimb insertions. The holotype of *N. strangulatus* falls within the variation observed in other material referred to this form (Uzzell, 1961).

DEFINITION: The tympanum of *Neusticurus strangulatus* is joined to the surface of the head in a smooth curve; no ridge or fold of scales overhangs the tympanum, and there is no external auditory meatus.

The caudal crests of *N. s. strangulatus* are obsolete. A southern race has them more strongly developed. The median dorsal pair of caudals are in contact with one another from shortly behind the base of the tail to the tip, although in the basal half there is often a small median scale separating the two scales of a pair at their anterior ends. There are no intercalated rows of scales on the side of the tail, and the caudals form whorls going completely around the tail. The dorsal and lateral caudals of *N. s. strangulatus* are faintly keeled.

The tail of *N. strangulatus* is moderately compressed.

In this species, the canthus rostralis is only moderately angular.

The oval disc in the lower eyelid is entire or divided by vertical grooves into two or three sections; in specimens of *N. s. strangulatus*, it is usually divided into two sections.

Neusticurus strangulatus strangulatus is the least tuberculate member of the genus. The dorsal scales are more or less regular quadrangles in transverse rows; these rows in some individuals alternate along the midline. A southern race has tubercles on many parts of the body.

The posterior preanal series in this species invariably includes two large scales; occasional specimens have minute scales at the

TABLE 7

ALTITUDINAL VARIATION IN SPECIMENS OF *Neusticurus s. strangulatus*
FROM THE DRAINAGE OF THE RÍO PASTAZA

(Figures are means and, in parentheses, extremes.)

	Males		Females	
	600 Meters or Less Three Males	700 Meters or More Six Males	600 Meters or Less Two Females	700 Meters or More Three Females
Dorsal scale rows	76.6 (67-85)	64.3 (55-70)	89.0 (88-90)	70.0 (66-74)
Transverse rows of ventrals	23.3 (23-24)	24.2 (21-26)	23.0 (23)	23.0 (23)
Scales around midbody	47.3 (45-49)	42.5 (40-46)	47.5 (47-48)	44.0 (44)
Femoral-preanal pores	54.3 (54-55)	46.0 (45-47)	7.5 (6-9)	8.0 (6-10)
Scales, posterior margin of interparietal	8.0 (7-9)	6.0 (5-7)	8.0 (7-9)	7.3 (7-8)

anterolateral corners of these in the posterior row. The anterior row of preanals consists of several scales, with a larger median pair.

All specimens examined have eight longitudinal rows of ventral scales.

Certain additional data on 20 of a series of Ecuadorian specimens previously discussed should be recorded. The largest male of 16 was 87 mm. from snout to vent; the largest female of four, 76 mm. The ratio of the length of the tail to that from snout to vent for six males with tails intact varies from 1.65 to 2.10, mean 1.82; comparable data are not available for the four females. The number of lamellae under the fourth toe varies from 23 to 29, mean 25.7, for the males; from 24 to 26, mean 25.6, for the females. The number of lamellae under the fourth finger varies from 14 to 17, mean 15.8, for the males; from 14 to 17, mean 15.5, for the females.

All the specimens previously examined from Ecuador had a single frontonasal; none had a median azygous between the frontonasal and the prefrontals.

Altitudinal variation in nine males and six females from the Río Pastaza drainage of Ecuador was examined previously (Uzzell, 1961). Specimens from 700 meters or more above sea level have more dorsal scales between the interparietal and the base of the tail, more scales around the midbody region, more scales around the posterior end of the interparietal, and more femoral-preanal pores in males (table 7) than specimens from below 700 meters.

A series of six males and 10 females from an unknown altitude in southern Ecuador (C.N.H.M. Nos. 42485-42500) extend the

known range of variation in several of these characters (table 8).

Data in tables 7 and 8 encompass most of the variation observed in 43 Ecuadorian specimens, but one excluded female has 13 femoral-preanal pores, and another only four small scales bordering the posterior margin of the interparietal.

REMARKS: *Euspondylus festae* was described on the basis of three Ecuadorian specimens taken in the valleys of the Río Santiago and Río Zamora; these localities are probably in Moruna-Santiago (Peters, 1955; Uzzell, 1961); they are the southernmost previous records.

Specimens of *Neusticurus strangulatus* from Ecuador differ from the description of *Euspondylus festae* in having 40 to 49 rather than 35 to 38 scales around the midbody region (Uzzell, 1961). I have recently examined three Peruvian specimens of *N. strangulatus* (A.M.N.H. Nos. 56490 and 56492 from Melendez, A.M.N.H. No. 56491 from Pongo de Manseriche) collected near the confluence of the Río Santiago and the Río Marañón (fig. 6); these localities are south of the localities for *Euspondylus festae*. The three specimens differ from Ecuadorian specimens examined only in that the females have more femoral pores (table 9). They have regular quadrangular dorsal scales, no evidence of tuberculation, and 44 to 49 scales around the midbody region, including the ventrals. In the shape and arrangement of the dorsal and lateral body scales, these specimens agree not only with Ecuadorian material examined, but also with the figure of *N. festae* (Peracca, 1897).

TABLE 8
VARIATION IN A SERIES (C.N.H.M. Nos. 42485-42500)
OF *Neusticurus s. strangulatus*
(Figures are means and, in parentheses, extremes.)

	Dorsal Scale Rows	Transverse Rows of Ventrals	Scales Around Midbody	Femoral-Preanal Pores	Scales, Posterior Margin of Interparietal
Six males	63.0 (61-67)	22.8 (22-24)	44.8 (42-48) ^a	53.8 (50-57)	8.0 (6-10)
Nine females	65.7 (63-70)	22.9 (22-24)	45.3 (43-47)	8.3 (6-12) ^b	7.4 (5-9) ^b

^a Five males.

^b Ten females.

TABLE 9

VARIATION IN FIVE SPECIMENS OF *Neusticurus strangulatus*
FROM NORTHERN PERU

A.M.N.H. Number	Sex	Body Length (Mm.)	Total Femoral Pores	Scales, Posterior Margin of Interparietal	Transverse Rows of Ventrals	Total Subdigital Fourth Finger	Lamellae Fourth Toe
56307	Female	54	33	8	24	28	48
56382	Male	27	— ^a	6	?24	28	50
56490	Female	59	21	8	24	29	52
56491	Female	65	6	5	23	31	53
56492	Male	63	49	7	22	30	52

^a Twenty-four or 25 on right; left not counted.

I have examined two other specimens of *N. strangulatus* from northern Peru. A.M.N.H. No. 56382, a small male (27 mm. from snout to vent) from the front range of the Andes between Moyobamba and Cahuapanas, has heterogeneous dorsal body scales. There is a median longitudinal series of small flat scales, two to three scales wide. The larger dorsal scales are oval- to diamond-shaped. Instead of being in broad contact with each other laterally, the anterior and posterior ends are separated by small intercalated scales. If only the large dorsal scales are included, there are about 35 or 36 scales around the midbody region. If the count is made to include the smaller scales, there are 42 to 44 scales around the midbody region.

The fifth specimen of *N. strangulatus* from northern Peru (A.M.N.H. No. 56307; Lamas, San Martín) came from slightly to the southeast of Moyobamba (fig. 6). The dorsal scales are not regular quadrangles, but are rounded in outline and weakly keeled, or small and irregular. If the scales around the body are counted so as to include the larger oval keeled scales, the counts average about 38; if counted to include only the smaller scales, they average about 46. These two specimens are intermediate between Ecuadorian and northern Peruvian specimens of *N. s. strangulatus* and the tuberculate population from central Peru described below. There remains a possibility that in the Río Santiago Valley of Ecuador and northern Peru there may be a population of *Neusticurus* closely related to *N. strangulatus* but differing in having 35 to 38 scales around the

midbody region. I suspect that the data provided for the syntypes of *E. festae* excluded rather than included the ventral scales, despite Peracca's statement to the contrary. I consider *Euspondylus festae* a junior synonym of *Neusticurus strangulatus*.

All five of these northern Peruvian specimens have eight longitudinal rows of ventral scales, the loreal separated from the supralabials by contact between the nasal and freno-ocular, a single frontonasal, and 4-4 supraoculars. In A.M.N.H. No. 56491 there is a median azygous scale posterior to the frontonasal and between the anterior angles of the prefrontals. The disc in the lower eyelid is entire in A.M.N.H. No. 56491 and possibly in A.M.N.H. No. 56382; it is irregularly divided on one side in A.M.N.H. No. 56490; the other discs in this series are divided into sections by vertical grooves. Certain other data on these specimens are given in table 9.

Males of *N. s. strangulatus* average fewer dorsal scales between the interparietal and the base of the tail than females. The males have strikingly more femoral-preanal pores than the females.

Each of two females has a single leathery egg in each oviduct.

RANGE: The range of *N. s. strangulatus* is the Amazonian slopes in Ecuador and northern Peru, at altitudes of 200 to 1300 meters above sea level. In this area, *N. s. strangulatus* is sympatric with *N. ecpleopus* and *N. cochranæ*. Intermediates between *N. s. strangulatus* and a southern subspecies are known from two localities in Loreto and San

Martín in northeastern Peru, at altitudes of about 500 to 1000 meters above sea level.

Neusticurus strangulatus trachodus,¹
new subspecies

TYPE MATERIAL: Holotype, an adult male (C.N.H.M. No. 55992) from "Divisoria" (=Cordillera Azul), Huánuco, Peru 1300–1600 meters above sea level; collected by José M. Schunke, September 8, 1947. Paratypes: C.N.H.M. Nos. 55989–55991, same data as holotype; C.N.H.M. No. 55993, same locality and collector, September 11, 1947; C.N.H.M. No. 56109, Fundo Cinchona, Huánuco, José M. Schunke, August, 1947; M.C.Z. No. 43764; Hacienda Pampayaco, Huánuco, Warren F. Walker, Sr., July 16, 1936.

DIAGNOSIS: A subspecies of *Neusticurus strangulatus* differing from *N. s. strangulatus* in having tubercles on the dorsal surface of the body, keeled dorsal and lateral caudal scales, a lower number (32 to 39) of scales around the middle of the body, and more (two to seven in males, one to two in females) conspicuous, black-bordered, white-centered ocelli along the sides of the body in adults.

DESCRIPTION OF HOLOTYPE: Head moderately enlarged, broader than neck; canthus rostralis moderately angular; body long, not compressed; hind limbs long; tail moderately compressed.

Rostral broadly in contact with first supralabial, nasal, and frontonasal; frontonasal single, slightly wider than long, in contact along its lateral border with nasal and narrowly with loreal, posteriorly with paired prefrontals; prefrontals slightly longer than wide, in contact with each other by a short seam, in contact with loreal, first superciliary, first supraocular, and frontal; no median azygous scale; frontal about two-thirds as wide as long, in contact laterally with first, second, and narrowly, third supraoculars; followed by paired frontoparietals; frontoparietals two-thirds as wide as long, in contact on a long seam, bordered laterally by third and fourth supraoculars; interparietal two-thirds as wide as long, laterally bordered by large parietals, posteriorly by eight small irregular scales radially arranged.

¹ The name *trachodus* is from the Greek *τραχύδης*, "of rough nature."

Loreal separated from supralabials by contact between nasal and freno-ocular; superciliary series of four elongate scales completely separating supraoculars from upper palpebrals; oval disc in lower eyelid not divided; upper temporal scales relatively large and convex, lower ones smaller, flatter, and irregular; a complete series of scales separating supralabials from lower palpebrals, two above fourth supralabial much smaller. Six supralabials, fourth extended toward orbit above line of supralabials 1 through 3; suture between fourth and fifth supralabials very narrow.

Tympanum superficial, not overhung by row or fold of scales, lightly pigmented.

Mental and unpaired first chin shield large; six infralabials, first five in contact with chin-shield series; four pairs of chin shields, first two in contact; gular and pre-gular scales small, moderately convex, posterior medial ones larger, flatter, quadrangular, and arranged in rows. Collar scales seven. Lateral nuchal scales small, rounded in outline, convex.

Dorsal scales heterogeneous: large oval scales with strong keels arranged in transverse and diagonal series; middorsally a series, two to four scales wide, of small, flat, polygonal scales; large keeled scales just lateral to this middorsal series forming a longitudinal series. Usually, larger keeled scales in contact both anteriorly and posteriorly with other large keeled scales; laterally, usually separated by small, flat irregular scales; a lateral area of intermediate-sized convex scales, eight to 10 scales wide. Ventral scales mainly quadrangular, in eight longitudinal rows at midbody, in 23 transverse rows, excluding two rows of pre-anals. Posterior preanal row with two very large scales, each bordered at anterolateral corner by very small scale, anterior row of six scales, middle pair largest, outermost pair minute. Twenty-four femoral-preanal pores on each side, one on left and two on right forming a double row.

Upper arm with quadrangular, keeled scales above, small, rounded, convex scales below. Anterior row of scales on lower arm large and flat; scales of other surfaces irregular, small to intermediate, frequently keeled. Scales of upper surface of hand flat,

medium-sized, of palm very small and convex; thenar scales moderate-sized; supradigital and subdigital lamellae simple, 17-17 under fourth fingers.

Sides and upper surface of thigh and shank with keeled scales; scales on anterior surface of thigh and ventral surface of shank large and flat; posterior surface of hind limb granular; supradigital lamellae simple; subdigital lamellae divided basally on digits 1-4; undivided distally; inner section on toes 3 and 4 forming weak ridge; 27-28 subdigital lamellae on fourth toes.

On much of tail, scales of upper half with longitudinal keel; two median dorsal rows of scales in contact from shortly behind vent to tip of tail; basally, anterior ends of two median dorsal caudals in some cases separated by a small median scale; except for this scale, caudals arranged in whorls going completely around tail.

Color of body not certain because of sloughing scales; dorsally probably dark brown in preservative, tail lighter; five to six black-bordered, light-centered ocelli along sides, grouped near forelimb insertions, black borders often confluent. Large, black-margined white bar, higher than wide, on supralabial 4 and subocular just above it; small white spot at posterior corner of eye. Chin lightly marked with dark brown; ventral surface generally suffused with brown pigment.

VARIATION: All the specimens of *N. s. trachodus* have eight longitudinal rows of ventral scales, 4-4 supraoculars, and two large posterior preanals. The loreal is separated from the supralabials by contact between the nasal and freno-ocular. The frontonasal is single in all specimens, although in

C.N.H.M. No. 55990 there are longitudinal median grooves in both the anterior and posterior thirds of the scale. None of the specimens has a median azygous scale between the frontonasal and prefrontals. Four specimens have the disc in the lower eyelid entire; in three it is divided by vertical grooves.

In general, the males in the type series are colored like the holotype. A young male (C.N.H.M. No. 55991) has a much more heavily mottled throat. A young female (C.N.H.M. No. 55990) resembles the males in ventral color, but an adult female (C.N.H.M. No. 55993) is very different. Dorsally on the snout there are darker areas in the centers of the scales; beginning at the posterior corner of each eye, there is a light nuchal band that continues on the body as a dorsolateral series of light spots. The mid-dorsal area is tan, and there is an irregular brown-black band separating the tan area from the light dorsal spots; the dorsum appears blotchy. There are two distinct ocelli on the sides of the body. The dorsal half of the tail has a mottled pattern of dark brown and tan. Ventrally, the chin and throat and the anterior and lateral parts of the belly are marked with black on a clear ground color. The throat markings show some tendency toward linearity.

Except for the differences noted in the diagnosis, this subspecies conforms to the definition presented under *N. s. strangulatus*.

REMARKS: Because the dorsal scales are heterogeneous, counts of scales around the midbody region are very variable; the counts finally recorded range from 32 to 39.

The name *Euspondylus festae* was proposed for a population of *Neusticurus strangulatus*

TABLE 10

VARIATION IN *Neusticurus s. trachodus*
(Figures are means and, in parentheses, extremes.)

	Femoral- Preanal Pores	Scales at Posterior Margin of Interparietal	Transverse Rows of Ventrals	Subdigital Fourth Finger	Lamellae Fourth Toe	Average Scales Around Midbody*
Five males	44.4 (39-49)	7.8 (7-9)	23.8 (23-25)	16.5 (14-18)	26.3 (23-28)	36.3 (33-38)
Two females	11.0 (9-13)	7.5 (6-9)	23.0 (22-24)	16.3 (15-18)	24.5 (24-26)	34.5 (33-36)

* Average based on three counts for each individual.

with a low number of midbody scale rows. Although one of the ways that *N. s. trachodus* differs from *N. s. strangulatus* is exactly the way that *Euspondylus festae* is supposed to differ from *N. s. strangulatus*, there is no possibility of applying the name *festae* to this southern population. *Euspondylus festae* differs from *N. s. strangulatus* only in the number of scales around the midbody region; the difference may not be real but may depend on whether or not the ventral scales were included. Nevertheless, northern Peruvian specimens of *N. strangulatus* from south of the type localities of *E. festae* do not differ from Ecuadorian specimens sufficiently to justify the recognition of a distinct subspecies in southern Ecuador and northern Peru. On the other hand, the specimens of *N. strangulatus* from central Peru differ from the Ecuadorian specimens not only in the low scale counts around the midbody region, but also in having tubercles on the body, a common feature of lizards of the genus that the Ecuadorian specimens remarkably do not have.

The specimen of *N. strangulatus* from Lamas (A.M.N.H. No. 56307) and the specimen from the range between Moyobamba and Cahuapanas share characters of both *N. s. strangulatus* and *N. s. trachodus*. The dorsal scales are not uniform: there are large oval scales with weak keels that seem to be incipient tubercles as well as small irregular scales around and between them. The lateral body scales are not so convex as the small tubercular scales on the side of *N. s. trachodus*, but resemble more the scales on the sides of *N. s. strangulatus*. Similarly, the lateral nuchal scales are smaller and less convex than those of *N. s. trachodus* and are closer to those of *N. s. strangulatus*.

The tubercles of *N. s. trachodus* give the animal a marked similarity at first glance to *Neusticurus ecpleopus*, with which the typical material has been confused. The character of the lateral nuchal scales is the most clearcut difference, but the two large preanal scales in the posterior row and the arrangement of the caudal scales indicate the relationship with *N. strangulatus* rather than *N. ecpleopus*. Comparison of the data in table 10 with the data for the adjacent populations of *N. ecpleopus* (table 5) indicates other minor differences by which specimens may be assigned.

The localities for *N. s. trachodus* are not shown on most maps. Cordillera Azul is the watershed between the Huallaga and Ucayali rivers (Sanborn, 1949). The political boundary between Huánuco and Loreto runs along the crest. Schunke, who collected the Chicago Natural History Museum specimens, worked along the road from Pucalpa on the Río Ucayali to Tingo Maria on the Río Huallaga, from about 1300 meters above sea level to the crest at about 1600 meters (Traylor, 1958). His specimens came from between these elevations where the Tingo Maria-Pucalpa road crosses the divide; this locality is probably in Huánuco, but not certainly so. Fundo Cinchona is an experimental cinchona station (Sanborn, 1949, p. 285); it and Cordillera Azul are almost equivalent (Traylor, 1958).

Hacienda Pampayaco is in the Distrito Chinchao, Sección Chihaungala, of Huánuco, above 750 meters in the Río Huallaga Valley south of Tingo Maria.

The largest male of *N. s. trachodus* examined is 73 mm. from snout to vent; the largest female, 74 mm. Three males with tails intact have the ratio of the length of the tail to that from snout to vent of 1.67 to 1.92, mean 1.83; comparable data for females are not available.

Most of the Peruvian specimens of *N. strangulatus* apparently come from ridges; in contrast, collections from along the courses of the larger rivers contain mainly *Neusticurus ecpleopus*. These few data suggest some degree of ecological separation between the two species, at least in Peru.

RANGE: The known range of *N. s. trachodus* is the Amazonian slopes of the Andes, at altitudes of above 750 to 1600 meters above sea level, in the Departamento de Huánuco of central Peru. No other species of *Neusticurus* is known from this immediate area, although *N. ecpleopus* is represented by numerous collections from surrounding localities.

***Neusticurus cochranæ*, new combination**

Neusticurus ecpleopus cochranæ BURT AND BURT, 1931, p. 350.

TYPE MATERIAL: Holotype, an adult male (A.M.N.H. No. 28891) from San José de Sumaco (San José Viejo; *vide* Peters, 1955),

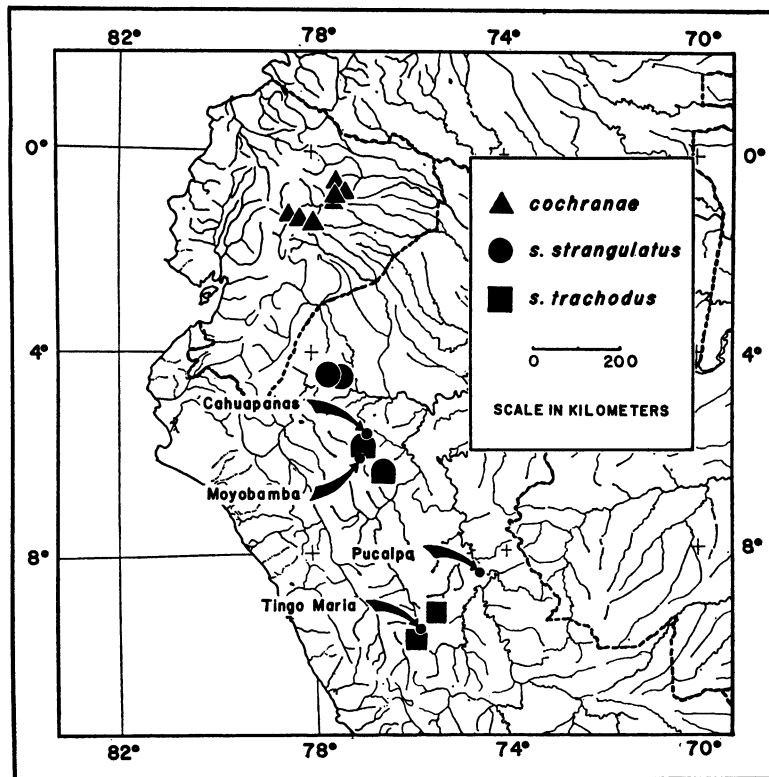


FIG. 6. Ecuador and parts of Peru and Brazil, showing Peruvian localities for *Neusticurus strangulatus* and localities for *Neusticurus cochranæ*. Symbols that are part circles, part squares, represent specimens intermediate between *Neusticurus s. strangulatus* and *N. s. trachodus*, new subspecies. Ecuadorian localities for *N. s. strangulatus* are figured in Uzzell (1961, fig. 1).

Napo-Pastaza, Ecuador. The altitude associated with this locality is probably between 700 and 1000 meters above sea level. Paratypes: A.M.N.H. No. 28868, same locality as holotype, and A.M.N.H. No. 38814, Mera, Napo-Pastaza, Ecuador.

DEFINITION: The tympanum of *N. cochranæ* is at the bottom of a shallow pit. The scales of the surface of the head do not overhang the tympanum, and there is a shallow external auditory meatus.

The dorsal caudal crests consist of larger, longer scales with keels that diverge posteriorly, and shorter scales with parallel keels. Shortly behind the base of the tail, the larger scales are separated by two small scales, one behind the other. The smaller crest scales are in contact for the length of the tail, and distally the larger scales are also in contact.

There are no intercalated scales along the sides of the tail, and, except for the small scales separating the larger crest scales, the caudal scales are arranged in whorls that go completely around the tail.

The tail is only moderately compressed.

The canthus is only moderately angulate.

The eye disc is divided by vertical grooves into three to six sections, usually four or five. The disc is lightly to heavily pigmented.

Neusticurus cochranæ has tubercles on the dorsal surface of the body and tail; the limbs are moderately tuberculate. There are no tubercles on the head, throat, or sides of the neck and body.

There are three to five scales in the posterior row of preanals. Frequently when five, the outermost pair is minute. The median is usually a little larger than the paramedian

TABLE 11
VARIATION IN *Neusticurus cochranæ*
(Figures are means and, in parentheses, extremes.)

	Femoral-Preanal Pores	Subdigital Lamellae Fourth Finger	Fourth Toe	Transverse Rows of Ventrals
Four males	24.0 (22-26)	13.1 (12-15)	18.9 (17-21)	18.9 (18-20)
Nine females	3.4 (1-4) ^a	13.1 (12-15)	17.4 (16-22) ^a	19.2 (19-20) ^a

^a Eight females.

pair. In the next anterior row, there are usually two median scales.

All the specimens examined have a single frontonasal. Eleven of the 12 specimens for which data are available have six longitudinal rows of ventral scales; one has eight. Eleven of the 13 examined have no median azygous scale between the prefrontals and frontonasal. The two specimens from San José de Sumaco, however, have a median scale between the prefrontals that is in contact with both the frontonasal and the frontal.

The pattern of *N. cochranæ* is striking. Males have a uniformly olive brown head, except that the nostril is often surrounded by a spot of black. The sides and the small scales of the dorsum are brown. The outer pair of rows of tubercles is light tan; the inner, brown. Some specimens have three or four small, black-bordered ocelli posteriorly along the sides. The under sides are light except near the vent and beneath the hind limbs; these areas are spotted with dark pigment. The lower labials and mental are tan; the chin and throat, clear yellow. Between the tan and the yellow, there is a dark line around the chin, along the sides of the throat, breaking up along the sides of the venter and posterior surface of the arms. The dorsal surface of the limbs have no light markings. Females are similar to the males, but with much more dark pigment below, and with the dark line around the chin and throat less dis-

tinct. Occasional females have small ocelli posteriorly along the sides.

In addition to the sexual dimorphism in color pattern, there is a large difference in total femoral pore counts between males and females (table 11).

REMARKS: *Neusticurus cochranæ* was described as a subspecies of *N. ecpleopus*, but the two are quite distinct, and *N. ecpleopus* occurs throughout the range of *N. cochranæ*. *Neusticurus ecpleopus*, in contrast to *N. cochranæ*, has conspicuous tubercles present on the posterior part of the head, on the throat, and on the sides of the neck, body, and tail. James A. Peters (personal communication) noted the distinctness and sympatric occurrence of the two species several years ago.

The largest male examined is 70 mm. from snout to vent; the largest female, 79 mm. Three males with tails intact have ratios of the length of the tail to that from snout to vent of 1.18 to 1.42, mean 1.31; three females have ratios of 1.11 to 1.51, mean 1.34.

One of the females of *N. cochranæ* has a single leathery egg in each oviduct.

RANGE: The known range of *Neusticurus cochranæ* is the eastern slopes of the Ecuadorian Andes, in the Napo and Pastaza drainages of Napo-Pastaza and Tungurahua, between 200 and 1300 meters above sea level (fig. 6). In this area, it is sympatric with *N. s. strangulatus* and *N. ecpleopus*.

HEMIPENIS OF *NEUSTICURUS*

EXAMINED *in situ*, the hemipenis of *Neusticurus ecpleopus* (U.S.N.M. No. 157106, left organ) has a short basal part about one-sixth of the length of the organ, a longer middle part about two-thirds of the length, and a short distal part. In the basal and middle parts there is a dorsal welt with free lateral edges opposite the ventral sulcus spermaticus.

The basal part of the organ is devoid of spines. In the middle part there are a lateral and a medial series of chevron-shaped flounces. The apex of the chevron is basal, and the free ends are on the dorsal welt and the sulcus lip. The flounces run from the sulcus lip basad to underneath the dorsal welt; here they reflex and run distad on the two sides of the free edge of the welt, ending in the center of the welt. Both laterally and medially, there are 19 flounces. The flounces contain numerous spinules that are X-ray opaque and that stain with alizarin red S; the spinules thus appear to be calcareous. They are parallel to one another, with the tip in the free edge of the flounce. The distal part of the hemipenis is bilobate, with the lobes subdivided by fleshy folds.

The everted hemipenis of *N. ecpleopus* (L.A.C.M. No. 8529, left organ) has no basal spines. In the middle part, there are a series of spinulate flounces, 17 on the lateral side, 19 on the medial side. On the anterior surface of the organ, the four basal flounces continue across the largely smooth area formed from the dorsal welt when the organ everts. The remaining flounces do not cross the anterior surface of the organ. The flounces on the lateral and medial sides are U-shaped and surround the two lobes of the clavate organ. The apexes of the U's are anterolateral and anteromedial; the free ends of the U's are anterior and posterior. The distal part of the organ consists of two lobes with intricate fleshy folds and a terminal filament.

The fully everted hemipenis of *N. apodemus* (U.K.M.N.H. No. 67375, left organ) is clavate and bilobed. The basal part is about two-thirds of the length of the organ and is devoid of ornamentation. Both the lateral and the medial lobes are surrounded by a series of concentric flounces, 12 medially and 11

laterally. These flounces are U- or V-shaped, with the apexes anterobasal; the axes of the U or V run obliquely around the sides of the organ, basal anteriorly and distal posteriorly. The flounces do not cross from one lobe to the other, but are interrupted posteriorly by the sulcus spermaticus and anteriorly by the smooth area formed from the dorsal welt. The flounces have numerous calcareous spinules. The lobes of the distal part have a series of fleshy folds and a terminal filament.

The inverted organ of *Neusticurus s. strangulatus* (U.M.M.Z. No. 90772, right organ) has a short basal part, about one-sixth of the length of the organ, a longer middle part about two-thirds of the length, and a short distal part. There is a dorsal welt with free lateral edges in the basal and middle parts, opposite the ventral sulcus spermaticus. The basal part has numerous longitudinal folds but is devoid of spines. The middle part has a medial and a lateral series of chevron-shaped flounces, the apexes basal, the free ends on the sulcus lips and the median welt. There are 20 flounces on the medial side, 18 on the lateral side. The flounces begin on the sulcus lips, run basally to underneath the free edges of the dorsal welt, reflex and run on the free edge of the dorsal welt to the end. The chevrons of the medial and lateral halves are separated from one another ventrally by the sulcus spermaticus and dorsally by a longitudinal smooth area on the dorsal welt. The flounces contain numerous calcareous spinules. The distal part of the organ is bilobed; the lobes are subdivided by fleshy folds. The presence of a terminal filament cannot be determined.

The inverted organ of a specimen of *N. s. trachodus* (C.N.H.M. No. 55992, right organ) is similar. There are 16 spinulate, chevron-shaped flounces on both the lateral and the medial sides of the middle part.

The inverted hemipenis of *N. cochranæ* (A.M.N.H. No. 28891, left organ) has a short basal part, less than one-sixth of the length of the organ, a middle part about two-thirds of the length, and a short distal part. The dorsal welt, in the basal and middle parts opposite the ventral sulcus spermaticus, has

free edges. The basal part is devoid of ornamentation. In the middle part, there appear to be 20 chevron-shaped flounces on the lateral side, the apexes basal and under the edge of the dorsal welt, the ends on the sulcus margin and the dorsal welt. There are 18 median flounces. The calcareous spines of the flounces are larger and heavier than those of *N. ecpleopus*, *N. apodemus*, or *N. strangulatus*, and they are diagonally arranged in the flounce, although the tips are at the free edge of the flounce. The distal part is bilobed, and the lobes are subdivided by fleshy folds. The presence of a terminal filament cannot be determined.

The hemipenes of these four species (*N. ecpleopus*, *N. apodemus*, *N. strangulatus*, and *N. cochranæ*) resemble one another in having chevron-shaped flounces with calcareous spinules or spines, and a dorsal welt with free edges in the inverted organ. They differ, however, from the hemipenes of the three other species of the genus.

The inverted hemipenis of *N. tatei* (M.C.Z. No. 62206, left organ) has a short basal part, a large middle part, and a short distal part. The dorsal welt in the basal and middle parts is reduced and does not have free edges. The walls of the basal part are folded, but there is otherwise no ornamentation. In the middle part there are two series of flounces, 12 laterally and 12 medially. On both sides, these flounces run from the lips of the sulcus spermaticus distally for a short leg, reflex and run basally to form a leg two to three times as long, reflex again and run distally for a leg of equal length, and reflex a third time to form a short leg ending on the dorsal welt.

The flounces of *N. tatei* do not contain calcareous spinules. Examined microscopically, the flounces have areas of greater and lesser density, but the dense areas are irregular, not invariably parallel, occasionally branched, and not always elongate. The dense areas do not stain with alizarin red S and are not X-ray opaque.

The distal part of the organ is bilobed, and the pockets of the inverted lobes are divided by fleshy folds. The presence of a terminal filament cannot be determined.

The inverted hemipenis of *Neusticurus rudis* (U.M.M.Z. No. 85244, left organ) is divided into short basal, long middle, and

short distal parts. The dorsal welt is much reduced and does not have free lateral edges. The basal part is devoid of ornamentation. There are a series of eight lateral and nine medial flounces in the middle part of the organ. These are zigzag structures, running basad for a long leg from the sulcus lips, reflexing and running distad for a long leg, and reflexing a second time to form a short leg ending on the dorsal welt. There are thus only two acute angles in the flounces. As in *N. tatei*, the flounces do not contain calcareous spinules, although they contain denser supporting areas. The distal part of the organ is bilobed, and the lobes are subdivided by fleshy folds. The presence of a terminal filament cannot be determined.

The inverted hemipenis of *N. bicarinatus* (M.N.H.N. No. 4181, right organ) has a short basal, a long middle, and a short distal part; these parts are about one-sixth, two-thirds, and one-sixth of the length of the organ, respectively. The dorsal welt is much reduced, without free lateral edges. The basal part is folded but spineless. In the middle part there are nine medial flounces and eight lateral ones. The lateral flounces run distad from the dorsal welt for a short leg, reflex and run basad for a leg about three times as long, reflex again to form another leg equally long, and end on the sulcus lip. The medial flounces run distally from the dorsal welt for a short leg, reflex to form a long leg, reflex to form another leg equally long, and then appear to run to the sulcus margin by a short leg at right angles to the sulcus. The flounces do not contain calcareous spines, but do contain relatively dense supporting structures. These are more regularly organized than are the similar structures in *N. tatei* and *N. rudis*, but they are still irregular compared to the spines of *N. ecpleopus*, *N. apodemus*, *N. strangulatus*, and *N. cochranæ*. The dense supporting structures of the flounces do not stain with alizarin red S. The distal part of the organ is bilobed, and the lobes are subdivided by fleshy folds. The presence of a terminal filament cannot be determined.

The hemipenis of *N. bicarinatus* differs from the others examined in that the basal part is black. Black pigment is also present on the basal side of many of the flounces, although the distal side is usually light. The

distal part is light, as it is in other specimens examined.

The hemipenes of *N. tatei*, *N. rudis*, and *N. bicarinatus* are similar to one another in that the dorsal welt is reduced, the flounces are reflexed at least twice, the flounces do not contain calcareous spines or spinules, and the number of flounces is low (eight to 12). They thus differ considerably from the hemipenes of *N. ecpleopus*, *N. apodemus*, *N. strangulatus*, and *N. cochranæ*. The number of flounces in *N. apodemus* (11–12) is similar to the range seen in *N. tatei*, *N. rudis*, and *N. bicarinatus*.

Compared to the hemipenis of *Echinosaura* (Uzzell, 1965), the hemipenis of *Neusticurus* differs in lacking basal spines, and in having acutely reflexed rather than U-shaped flounces when the inverted organ is examined.

Neusticurus tatei, *N. rudis*, and *N. bicarinatus* share with *Echinosaura* a low number of flounces (six to 11 in *Echinosaura*). They differ, however, in the complete absence of spines or spinules, and in having at least two reflexions in the flounces. *Neusticurus ecpleopus*, *N. strangulatus*, and *N. cochranæ*, like *Echinosaura*, have calcareous spines in the hemipenial flounces, but the spines are uniform in size within a species, the flounces are acutely reflexed when the organ is inverted, a well-developed dorsal welt with free lateral margins is present, and the flounces are more numerous (16–20) than in *Echinosaura*. *Neusticurus apodemus* has a low number of flounces, but otherwise it resembles *N. ecpleopus*, *N. strangulatus*, and *N. cochranæ*.

BIOLOGY OF *NEUSTICURUS*

REPRODUCTION

THE NORMAL NUMBER OF EGGS per clutch for lizards of this genus is two. Observations are available on all species except *N. apodemus*; in 19 of 20 cases, the clutch consisted of two eggs, either oviducal and ready to be deposited, or deposited in captivity. The only exception, a female of *N. bicarinatus*, contained but a single egg ready to be deposited. It seems plausible that, in this case, half of the clutch had been deposited at the time the lizard was captured.

David Wake and Richard Etheridge (personal communication) observed *Neusticurus ecpleopus* along the Río Iscozazin, about 40 kilometers north-northeast of Oxapampa, Pasco, Peru. On July 12, 1961, Wake found two nests of *Neusticurus* eggs in a large, well-rotted log. The log was at the edge of a small, clear pool, about 3 feet in diameter and surrounded by boulders, in a partly dry stream bed. One of the nests, at the water's edge in a saturated part of the log, contained four eggs, one of which had just hatched. The second, a little farther from the water, contained five eggs, four already hatched and one hatching. Since 12 females of *Neusticurus ecpleopus* contained clutches of two eggs, these nests contained eggs of more than one female.

HABITS

It is generally thought that lizards of the genus *Neusticurus* have aquatic tendencies; confirmatory observations are scant. Beebe (1945), discussing *N. rudis* at Kartabo, British Guiana, reported that it lives in holes in the banks of jungle streams and rivers, and that it is a swimming lizard. He listed fish, tadpoles, water beetles, and parts of fish and tadpoles as stomach contents of two specimens. Beebe's observation may apply to *N. bicarinatus*, however, since both species occur at Kartabo. Roze (1958) reported that *N. rudis* is semiaquatic, that it swims well, and, when pursued, always seeks refuge in the water. One of the specimens of *N. tatei* (M.C.Z. No. 62206) was collected in water by Juan A. Rivero, who has informed me (per-

sonal communication) that this species swims well.

The most extensive observations are those of Wake and Etheridge on *N. ecpleopus*. All of their 19 specimens were collected in deep forest, but in close proximity to water, usually a stream. When pursued, the lizards often retreated to the water. One specimen was found in a stream; another was swimming in a forest pool. Many were found on boulders at the edge of streams. When swimming, the lizard holds only the head above water; swimming is accomplished by sinuous movements of the body and tail. James A. Peters (personal communication) found a single specimen of *N. ecpleopus* (U.S.N.M. No. 157106) running across a marshy area.

The holotype and paratypes of *N. apodemus* were collected in leaf litter in a stream bed (U.K.M.N.H. Nos. 67375, 67377–67380; U.M.M.Z. No. 124688) and under a rock (U.K.M.N.H. No. 67381). Jay M. Savage (personal communication) has informed me that *N. apodemus* has been observed on two occasions in the water at night, wading in debris or swimming.

Observations on the habits of *N. bicarinatus*, *N. cochranæ*, and *N. strangulatus* are not available.

Most species of *Neusticurus* are diurnal. Roze (1958) reported that *N. rudis* is a diurnal species. The observations by Peters and by Wake and Etheridge on *N. ecpleopus* were made during the day. One of the specimens of *N. tatei* (M.C.Z. No. 66933) was collected at night on the branch of a tree; it seems likely that this diurnally semiaquatic species passes the night above ground in bushes and trees much as does *Anolis*. Specimens of *N. apodemus* were found in leaf litter during the day; some of them were active. They have also been observed on two occasions moving about at night (J. M. Savage, personal communication).

Comparative ecological data on all species of *Neusticurus* are not available; the morphological features of the various species probably reflect in some degree the ecological adaptations. A long flat tail with a continuous dorsal crest is probably an adaptation for

a semiaquatic existence. By this criterion, *N. bicarinatus* is the most aquatic species, followed by *N. tatei*. *Neusticurus rudis* and *N. strangulatus* probably are somewhat less aquatic; they have long tails, but not conspicuously flattened ones. *Neusticurus ecpleopus* and *N. apodemus* have relatively short tails, and, in *N. cochranæ*, the tail is very short. *Neusticurus cochranæ* may be the least aquatic member of the genus. The short legs (indicated by low femoral pore and subdigital lamellar counts), short tail, and large head give *Neusticurus cochranæ* an appearance not unlike that of the relatively terrestrial *Echinosaura horrida horrida*.

Although behavioral interpretations of color are extremely hazardous, it is possible that the well-developed ocelli in *N. ecpleopus* and some individuals of *N. strangulatus* reflect diurnal habits in these animals. The reduced size of ocelli in *N. cochranæ*, and their general faintness in *N. apodemus*, may reflect a behavioral difference in these two species. *Neusticurus apodemus* is active both by day and at night. Perhaps *N. cochranæ* is also partly nocturnal. The absence of ocelli in *N. bicarinatus*, *N. tatei*, and *N. rudis* is a character of that group; it does not reflect, in itself, ecological differences between those species and *N. ecpleopus* or *N. strangulatus*.

RELATIONSHIPS WITHIN THE GENUS *NEUSTICURUS*

THE LIZARDS OF THE GENUS *Neusticurus* occur in three geographical areas. *Neusticurus apodemus* is known only from southwestern Costa Rica. Three species (*N. strangulatus*, *N. ecpleopus*, and *N. cochranæ*) are found on the eastern slopes of the Andes. Three other species (*N. tatei*, *N. rudis*, and *N. bicarinatus*) are found in the Venezuelan and Guayana uplands and in the lowlands to the north and south of that ancient land mass.

Several characters that bear on the relationships among the species of the genus are listed in table 12. Of these, the characters that provide the most convincing subdivision of the genus are in the structure of the hemipenis. On this basis, *N. tatei*, *N. bicarinatus*, and *N. rudis* form one group, and *N. ecpleopus*, *N. apodemus*, *N. strangulatus*, and *N. cochranæ* form another group.

Characters not associated with the hemipenis can be adduced to support this grouping. *Neusticurus bicarinatus*, *N. rudis*, and *N. tatei* have generally a high number of transverse rows of ventral scales. They also have a high number of posterior preanal scales, usually five, of which the lateral pair and the median are small, and the paramedian pair is large. The canthus rostralis of these three is more angulate than that of the forms in the Andes and Costa Rica.

Several characters shared by two or three members of these groups lend a degree of internal consistency to the two groups. The tympanum in *N. tatei*¹ and *N. bicarinatus* is deeply recessed, and often overhung by scales of the surface of the head. This condition is not found elsewhere in the genus. These two species are also the largest and have the most compressed tails and most complex hemipenial flounces in the genus. They appear to be very closely related. On the other hand, *N. tatei* and *N. rudis* share the highest number of lateral caudal scales per median ventral caudal scale found in the genus. *Neusticurus rudis* and *N. bicarinatus* have the lowest number of hemipenial flounces found in the genus.

In the Andean and Costa Rican group, *N. ecpleopus* and *N. apodemus* share many characters. They have rows of tubercles on the

sides of the neck and well-developed tubercles on the limbs. Both have tubercles present on the sides of the body and the back of the head. The number of femoral pores and subdigital lamellae are similar, and both have the tympanum joined to the surface of the head in a smooth curve. These two share the highest number of lateral caudal scales per median ventral caudal scale found in this group of the genus; there are regularly three lateral caudal scales per median ventral caudal scale in *N. apodemus* and three as an individual variant in some *N. ecpleopus* populations. These two species appear to be very closely related.

Neusticurus ecpleopus and *N. strangulatus* are the only members of the genus known to have well-developed ocelli. In these two, the ocelli are often a bright white dot surrounded by a broad black band. These two species, with *N. apodemus*, have the tympanum joined smoothly to the surface of the head. Except for the holotype of *N. tatei*, this condition is not found elsewhere within the genus.

Within the group containing *N. ecpleopus*, *N. cochranæ*, *N. strangulatus*, and *N. apodemus*, *N. cochranæ* seems to be the distinctive member, especially in view of its short tail, slightly recessed tympanum, large hemipenial spines, small ocelli, and low number of femoral pores. Although *N. s. strangulatus* appears very different from *N. ecpleopus* because the former lacks tubercles, the similarity in more basic characters is strong; in addition, the southern population of *N. strangulatus* (*N. s. trachodus*) is tuberculate. There is no character found in *N. cochranæ* and *N. strangulatus* that is not found also in *N. ecpleopus*.

There is little to link the two groups of species separated on the basis of hemipenial characters. In several ways, however, *N. rudis* may be a clue to the relationships of the two groups. The zigzag hemipenial flounces of *N. rudis* are closest in its group to the chevron-shaped flounces found in *N. ecpleopus*, *N. strangulatus*, *N. cochranæ*, and *N. apodemus*. *Neusticurus rudis* is also close to those forms in its moderately recessed tympanum and moderately compressed tail. The absence of clearcut intermediates between the two groups indicates that they have had a long period of independent development.

¹ In the holotype of *N. tatei*, the tympanum is not recessed.

TABLE 12
COMPARISONS OF CHARACTERS IN THE SEVEN SPECIES OF THE GENUS *Neusticurus*
(Figures are observed ranges except for body length, of which maxima are listed.)

	<i>bicarinatus</i>	<i>tatei</i>	<i>rudis</i>	<i>ecpleopus</i>	<i>apodemus</i>	<i>strangulatus</i>	<i>cochranae</i>
Canthus rostralis	Angulate	Angulate	Angulate	Moderately angulate	Rounded	Moderately angulate	Moderately angulate
Ocelli	Absent	Absent	Absent	Conspicuous	Weak	Conspicuous	Weak
Transverse rows of ventrals	26-29	27-30	24-32	19-24	22-24	21-26	18-20
Tail shape	Strongly compressed	Strongly compressed	Moderately compressed	Moderately compressed	Weakly compressed	Moderately compressed	Moderately compressed
Tympanum location	Deeply recessed	Deeply recessed	Slightly recessed	Superficial	Superficial	Superficial	Slightly recessed
Lateral caudals per two ventrals	2	3-5	3-5	2-3	3	2	2
Femoral-preanal pores, males	56	58-72	34-60	25-48	26-30	39-57	22-26
Posterior preanals	4-6	5-6	5-7	2-5	2-4	2	3-5
Subdigital lamellae							
Fourth finger	15-19	19-26	14-23	10-16	11-14	14-18	12-15
Fourth toe	22-30	28-39	23-34	17-28	18-22	23-29	16-22
Largest male; largest female (body length, mm.)	109; 91	104; 93	88; 89	83; 67	47; 38	87; 76	70; 79
Tail length/snout-vent length	1.7-2.2	1.9-2.2	1.7-2.3	1.4-1.8	1.5-1.7	1.6-2.1	1.1-1.5

RELATIONSHIPS OF *NEUSTICURUS* AND *ECHINOSAURA*

Echinosaura AND *Neusticurus* BELONG to a section of the family Teiidae, Group II (Boulenger, 1885), that has the nasal plates separated by one or more frontonasal scales, and five clawed digits. Group II is very distinct from the rest of the family. It has a diversity of forms, and includes almost half of the genera of the family. Subdivisions within Group II are more or less well marked.

Echinosaura and *Neusticurus* share several characters. The extremely heterogeneous scalation of *Echinosaura* is found to some extent in all the species of *Neusticurus*. The irregularity of the scales on the posterior end and sides of the head of *Neusticurus* is developed to a greater degree in *Echinosaura*. The large tympanum of *Echinosaura* is not recessed; it has the same position as the tympanum in *N. ecleopus*, *N. apodemus*, and *N. strangulatus*. The gular crease in both genera is weak or absent, so that the gular and preular scales form an essentially continuous series, radiating out from between the chin shields.

Although these similarities suggest a close relationship between *Echinosaura* and *Neusticurus*, there are many differences between the two. *Echinosaura* differs from *Neusticurus* and from all other teiid genera, as far as I know, in having large basal hemipenial spines. Although the development of these from the spines of the flounces is not difficult to imagine, their presence gives the hemipenis of *Echinosaura* an appearance quite different from that of *Neusticurus*, in which the smooth basal area is broken only by the sulcus spermaticus.

Echinosaura has a very weak collar fold, so that the posterior gular scales and the anterior ventral scales almost merge. The collar is well developed in *Neusticurus*. The interparietal and parietal scales in *Neusticurus* are distinct; the interparietal extends well posterior to the parietals and is followed by a series of small scales that ring the interparietal posteriorly. The number of scales at the posterior end of the interparietal may be as few as three, but usually there are six or seven. The other posterior head scales of *Neusticurus* may be large or small, flat or tuberculate. In *Echinosaura*, the interparietal and parietal

areas are covered by small irregular scales.

The dorsal body tubercles of *Neusticurus* are unlike those of *Echinosaura*. In *Neusticurus*, the body tubercles are oval in outline, and have a longitudinal keel. In *Echinosaura*, the tubercles are more like spines, nearly circular in outline; if they are keeled, the scale is much more convex than in *Neusticurus*, and usually is rectangular in outline.

Generally, the species of *Neusticurus* have flattened tails; some, such as *N. bicarinatus* and *N. tatei*, conspicuously so. The tail of *Echinosaura* is only slightly flattened, in no case conspicuously so.

The differences between *Echinosaura* and *Neusticurus* are more convincing than the similarities. Detailed studies of the internal anatomy may reveal that the external similarities are convergent. At present, however, there seems to be no other plausible ally for *Echinosaura* within Group II.

Many of the species of *Neusticurus* are diurnal and semiaquatic. *Echinosaura*, on the other hand, is largely terrestrial and at least partly nocturnal. The weakly compressed tail of *Echinosaura* almost certainly reflects the greater terrestriality of the genus compared to *Neusticurus*. The greater irregularity of the scales on the head and throat of *Echinosaura* are quite possibly terrestrial adaptations. Dunn (1944) reported that these lizards play dead when found or when handled, and that their general appearance is then much like a twig. Perhaps some of the unusual scalation of *Echinosaura* is related to concealment.

The hemipenial spines of *Neusticurus* and *Echinosaura* are widespread in members of Group II; I have observed them in 12 of the 20 or so genera. The others have not been examined. In only three of the 12 genera is the situation unusual. *Alopoglossus* and *Ptychoglossus* share the same arrangement, and in *Neusticurus* only some of the species have spines. To my knowledge, hemipenial spines are not found in other groups of teiids, despite Cope's statement (1896) that he observed them in *Bachia*. Such spines apparently do not occur in the other families of the Scincomorpha. The presence of the spines in Group II is almost certainly a derived condition.

The large basal spines are a further development of the trend in Group II and also represent a derived condition. Several other characters that distinguish *Echinosaura* from *Neusticurus* also distinguish it from the other genera of Group II. In particular, most members of Group II have a well-developed collar fold and regular posterior head scales. The conditions in *Echinosaura* seem to be derived from more widespread conditions. I believe

that the similarities between *Echinosaura* and *Neusticurus* are unlikely to be convergences. On the other hand, each genus has distinctive morphological characteristics. If the two genera had a close common ancestor, it seems almost certain that *Echinosaura*, which is less like other representatives of Group II, is the derived genus, and that *Neusticurus* more nearly resembles the original stock.

ZOOGEOGRAPHY AND HISTORY OF *ECHINOSAURA* AND *NEUSTICURUS*

THE RANGE OF *Echinosaura* is more or less continuous, and forms a triskelion (fig. 5), one arm extending westward into western Panamá, another south along the Pacific lowlands and slopes of Colombia and Ecuador, and the third extending eastward into the Atlantic slopes of Colombia. The genus has not been found in the Sierra Nevada de Santa Marta or in the lowlands surrounding that massif (Uzzell, 1965).

Echinosaura appears to be a derivative of the stock that gave rise to *Neusticurus*. Probably a population of that stock became isolated west of the Andes, developed terrestrial habits, and gave rise to the present *Echinosaura*.

Echinosaura contains three recognizable races (fig. 5; Uzzell, 1965). The southern form (*E. h. horrida*) is very distinctive, suggesting that it has been longer or more completely isolated from the other populations. The population on the Atlantic and Pacific slopes of western Panamá (*E. h. panamensis*) may be isolated from the rest of the species by the lowlands of central Panamá. The population in eastern Panamá and in the Chocó and Atlantic slopes of Colombia (*E. h. palmeri*) resembles the western Panamá form more than it does the southern form. *Echinosaura h. palmeri* occurs at low altitudes in the Chocó, but is apparently absent from the lowlands of the Atlantic drainages of Colombia.

Neusticurus, with several species, presents a complex picture. The two subgroups apparent in the genus each have geographic continuity. In the Andean region, *N. cochranæ* has a very restricted range (fig. 6). It has been found only in eastern Ecuador, at elevations of 200 to 1300 meters above sea level. *Neusticurus strangulatus* is also restricted to the eastern Andean slopes, but extends from central Peru to Ecuador, at altitudes of 200 to 1300 meters above sea level (fig. 6). There is considerable geographic and altitudinal variation in this species, and two subspecies are recognized, the northern and central *N. s. strangulatus* and the southern *N. s. trachodus*. The most widespread member

of the Andean group is *N. ecpleopus*. It is known from central Bolivia north to southern Colombia, at elevations of 100 to 1500 meters above sea level (fig. 1). This species is found farther out on the floor of the Amazon Basin than the other two Andean species. There is considerable altitudinal and geographic variation in the species *N. ecpleopus*, but subspecies have not been recognized.

Evidence for ecological differences between the Andean species of *Neusticurus* is scanty. *Neusticurus cochranæ*, geographically the most restricted, is possibly the least aquatic member of the genus. *Neusticurus ecpleopus* is known to be semiaquatic and diurnal. The subdigital lamellae and male femoral pores are more numerous than in *N. cochranæ*, but less numerous than those in *N. strangulatus*. *Neusticurus ecpleopus* has better-developed caudal crests than *N. strangulatus*. These features suggest some ecological displacement between *N. ecpleopus* and *N. strangulatus*. It is possible that *N. ecpleopus* is found largely along the valleys of the larger streams, while *N. strangulatus* is found more often on the ridges between the major streams.

Neusticurus apodemus is isolated from the main range of the genus *Neusticurus*, although it is closely related to the widespread *N. ecpleopus* (fig. 5). Possibly the isolation is only apparent—the result of insufficient collecting in intervening areas. *Neusticurus ecpleopus* is a diurnal animal and, in collections, is by far the most abundant species. If it occurred outside the Amazon Basin in Colombia, it almost certainly would have been observed.

The available data indicate that *N. apodemus* is active both by day and at night. Specimens active by day were found in leaf litter. The general habitus of *N. apodemus*, with its weakly compressed tail, weak dorsal crests, generally depressed body and head, weak limbs, and generally delicate build, is very reminiscent of that of *E. h. panamensis* and *E. h. palmeri* rather than that of *N. ecpleopus*. The coloration of *N. apodemus* differs from that of *N. ecpleopus*. In general, *N. apodemus* is much darker both above and below than *N. ecpleopus*. There are conspicuous

light areas on the upper arms of *N. apodemus*, but not of *N. ecpleopus*. Ocelli are present in *N. apodemus*, but they are indistinct. The coloration in many ways resembles that of *E. h. palmeri* and *E. h. panamensis*. It seems possible that *N. apodemus* has habits more like those of *Echinosaura* than like those of *N. ecpleopus*.

Possibly the isolation of the range of *N. apodemus* is in part a result of competition with *Echinosaura*. Further, it may be that the partly nocturnal habits of *N. apodemus* and of *Echinosaura* resulted from competition with the two or more species of the iguanid genus *Basiliscus* that occur in this part of Central and South America (Maturana, 1962), and occupy a niche perhaps similar to that of many species of *Neusticurus*. *Basiliscus* does not occur in Amazonian South America and thus is absent from most of the range of *Neusticurus*.

To the extent that these speculations are correct, it appears that some *Neusticurus*-like stock, isolated by the Andes from the main range of the present *Neusticurus*, gave rise to the terrestrial *Echinosaura*. At a later date, the far-ranging and successful *N. ecpleopus* was able to cross the Andes in northern Colombia, reaching Costa Rica. The annectant populations have since disappeared, leaving *N. apodemus* isolated in Costa Rica, west of the range of *Echinosaura* (fig. 5).

A distribution analogous to that of *N. apodemus* and *N. ecpleopus* occurs in the iguanid genus *Morunasaurus*. Dunn (1933) described *Morunasaurus groi* from El Valle de Antón, in Coclé, Panamá. The closest relative, *M. annularis* (O'Shaughnessy), occurs in Amazonian Ecuador. The genus seems to be disjunct, although, as Dunn pointed out, the secretive habits of *Morunasaurus* may result in its being overlooked.

The species group composed of *Neusticurus tatei*, *N. rudis*, and *N. bicarinatus* is centered in the ancient Guayana uplands. *Neusticurus tatei* seems to be restricted to this area, at altitudes of 400 to 1400 meters above sea level (fig. 2). The specimens examined form three groups, and there is considerable local variation between the groups.

Neusticurus rudis occurs in the Guayana uplands and in the coastal region of the Guianas, at altitudes from near sea level to 1800

meters above sea level (fig. 2). The Venezuelan material is relatively uniform. The lowland specimens, from British Guiana and Surinam, are different from the Venezuelan specimens in several characters. In some, the British Guiana specimens are intermediate between the Venezuelan and Surinam specimens, but in others, the Venezuelan specimens are intermediate between the British Guiana specimens and those from Surinam.

Neusticurus bicarinatus has the greatest range of any species of the genus (fig. 1). It occurs in the lowlands of the Guianas, as well as along the streams stretching south into the uplands. Specimens are also known from Venezuela and the Brazilian states of Pará and Rondonia. Altitudinal records associated with *N. bicarinatus* are mainly low, from near sea level to 300 meters above sea level; one record (M.B.U.C.V. No. 8011) is from 1000 meters above sea level.

Evidence for ecological diversity among these species is scanty. *Neusticurus tatei* and *N. bicarinatus*, the two most closely related species of this group, are essentially allopatric. *Neusticurus rudis*, which overlaps the range of both, is smaller and has a less conspicuously flattened tail. This geographic arrangement may reflect ecological similarity between *N. tatei* and *N. bicarinatus*, and a dissimilarity of *N. rudis* to both.

Although the history of the development of the three species within this group is unclear, that *N. bicarinatus* is the widespread and successful member of the group seems unquestionable.

There are no localities known where one of the species with hemipenial spines occurs with one that lacks them. In fact, the great differences between these two groups of species suggest that they have been isolated for a long time, with each group undergoing a separate radiation, into three (Guianan) or four (Andean and Costa Rican) species.

The isolation of these two groups of species in northern South America is perhaps partly a result of the savanna area that separates the Venezuelan uplands from the Andes of Colombia and Venezuela (fig. 1). Apparently the galeria forests of the affluents of the Río Orinoco have not provided an adequate avenue for exchange between these two areas.

To the south, the vast expanse of the Am-

azonian Basin is herpetologically *terra incognita*. The picture that emerges after a consideration of the available data, however, is plausible. Of the Guianan species, *N. tatei* is restricted to the Venezuelan uplands; the lowlands of the Amazon apparently are a barrier that this species cannot pass. *Neusticurus rudis* occurs on the lowlands of the Guiana coast and is also found in the uplands. It does not, as far as is known, reach the Amazon Valley. The tail of *N. rudis* is less flattened than the tail of *N. tatei* and *N. bicarinatus*, and, although it is partly aquatic, *N. rudis* is apparently less aquatic than those two species. It is possible that for this species, too, the Amazon lowlands serve as a barrier.

The only member of the Guianan group that is widespread is *N. bicarinatus*. This species has a much compressed tail. Altitudinal records for *N. bicarinatus* suggest that it is well adapted for living in areas that flood; the species is spread widely throughout the Amazon Valley. It seems plausible that the spe-

cial adaptations of this species that allow it to occur widely in the Amazon Basin prevent it from moving up the slopes of the Andes at the edge of its range.

Among the Andean species, the short tail and limbs suggest that *N. cochranæ* is less aquatic than most members of the genus *Neusticurus*. Probably the Amazon Valley is an effective barrier for this species. Similarly, there is some suggestion that *N. strangulatus*, although it reaches low altitudes, is an animal that avoids larger streams. Only *N. ecpleopus*, of the Andean group, is known to occur any distance out into the Amazon Valley, and the strikingly flattened tail of *N. bicarinatus* is absent from this species.

Although it is possible that *N. bicarinatus* and *N. ecpleopus* occur sympatrically at the edge of the Amazon Basin, the respective adaptations that have allowed these two species to become the most widespread of the genus may also tend to keep their ranges from overlapping broadly.

SUMMARY

EXAMINATION OF 310 SPECIMENS, including type material of eight of the 12 previously proposed names, indicates that lizards of the genus can conveniently be separated into seven species and eight forms.

On the basis of characters of the hemipenis, the seven species form two quite distinct groups. *Neusticurus bicarinatus*, *N. tatei*, and *N. rudis* have few flounces (eight to 12), no calcareous spinules in the flounces, a reduced dorsal welt in the inverted organ, and zigzag flounces in the inverted organ. *Neusticurus ecpleopus*, *N. strangulatus*, *N. cochranæ*, and *N. apodemus* have more flounces (11–20), numerous calcareous spinules in the flounces, the free ends in the edge of the flounce, a well-developed dorsal welt in the inverted organ, and chevron-shaped flounces.

These two groups have discrete ranges: *Neusticurus tatei* is known only from the Guayanan uplands; *N. rudis* occurs there and in the lowlands of the Guianas. *Neusticurus bicarinatus* occurs in these areas and widely throughout the Amazon Valley. On the other hand, *N. cochranæ* is known only from the eastern Andean slopes of Ecuador. *Neusticurus strangulatus* occurs on the eastern Andean slopes from Ecuador to central Peru. *Neusticurus ecpleopus* is widely distributed on the eastern Andean slopes from central Bolivia to southern Colombia. *Neusticurus apodemus* is isolated in southwestern Costa Rica.

Additional characters unite the species in these two groups. *Neusticurus bicarinatus*, *N. tatei*, and *N. rudis* have more (24–32) transverse rows of ventral scales; usually the canthus rostralis is angular. *Neusticurus ecpleopus*, *N. apodemus*, *N. strangulatus*, and *N. cochranæ* have fewer (19–26) transverse rows of ventral scales; usually the canthus rostralis is more rounded. *Neusticurus ecpleopus*, *N. apodemus*, *N. strangulatus*, and *N. cochranæ* have poorly to well-developed, black-bordered, white-centered ocelli; ocelli do not occur in *N. bicarinatus*, *N. rudis*, or *N. tatei*.

Neusticurus bicarinatus and *N. tatei* share a recessed tympanum, strongly compressed tails, and complex hemipenial flounces; they appear to be closely related. *Neusticurus ecpleopus* and *N. apodemus* have longitudinal

rows of tubercles on the upper sides of the neck and tubercles on the sides of the body and posterior end of the head. They are closely related.

Lizards of the genus *Neusticurus* apparently lay two eggs per clutch. Nineteen of 20 females with oviducal eggs contained one egg in each oviduct; the single exception had an egg in one oviduct only. Observations are not available for *N. apodemus*.

Many species of *Neusticurus* are diurnal and semiaquatic. Observations are available for *N. ecpleopus*, *N. rudis*, *N. tatei*. *Neusticurus apodemus* is semiaquatic and partly nocturnal. The very short tail of *N. cochranæ* suggests that it is not aquatic; it may be partly nocturnal. The strongly compressed tail of *N. bicarinatus* suggests that it is semiaquatic; it is probably diurnal. The habits of *N. strangulatus* are not known, but the well-developed ocelli of some specimens suggest that it may be diurnal.

Within Group II of the family Teiidae, *Neusticurus* appears to be most closely related to *Echinosura*. The present distribution of the forms of these two genera suggests an early division into *Echinosaura* in the Caribbean and Pacific lowlands of northwestern South America, and two groups of *Neusticurus*, one on the eastern Andean slopes and another in the Guayana highlands area. It seems likely that the respective adaptations of these two groups serve to prevent extensive contact between them. The widespread Guayanan species *N. bicarinatus* seems well adapted to the Amazon lowlands. This specialization probably keeps it from moving far into the Andean region. The most widespread Andean species (*N. ecpleopus*) does not occur far into the Amazon lowlands. It seems to lack special adaptations for this habitat. The lack of morphological intermediates between these two groups suggests that they have been long isolated.

Neusticurus ecpleopus and *N. apodemus* are closely related. The present range of *N. apodemus* represents a past transgression of the Andes by *N. ecpleopus* or its immediate ancestor. The partly nocturnal habits of *N. apodemus* and the partly nocturnal and more

terrestrial habits of *Echinosaura horrida* may reflect competition of both with iguanid lizards of the genus *Basiliscus*, which occur in Pacific and Caribbean Central America and South America, and which are semiaquatic.

Systematic changes include transfer of *Arthrosaura tatei* to *Neusticurus*; *N. racenisi* is considered a synonym of *N. tatei*. *Neusticurus dejongi* and *N. surinamensis* are both considered synonyms of *N. rudis*. *Neusticurus ocellatus* and *N. tuberculatus* are both considered synonyms of *N. ecpleopus*. *Neusti-*

curus rudis, *N. tatei*, and *N. ecpleopus* all vary geographically, but subspecies are not recognized nomenclatorially. *Neusticurus apodemus*, an isolated species from Costa Rica, is described; it is closely related to *N. ecpleopus*. *Neusticurus cochranæ* is recognized as a species different from *N. ecpleopus*. *Euspondylus festae* is considered a synonym of *Neusticurus strangulatus*; a subspecies with tubercles from central Peru (*N. s. trachodus*) is described.

SPECIMENS EXAMINED

Neusticurus bicarinatus

Locality unknown: U.U.L. No. 70, holotype of *Lacerta bicarinata*. **Brazil:** Pará: Road, Belem to Brasilia, Kilometer 93, 0–100 meters, D.Z.S.P. No. 8073; Cachimbo, 0–100 meters, D.Z.S.P. Nos. 6310, 6311. Rondonia, Mutum-Paraná, 100–200 meters, D.Z.S.P. Nos. 6308, 6309. **British Guiana:** Kamakusa, 0–100 meters, A.M.N.H. No. 25069; Kartabo, 0–100 meters, A.M.N.H. No. 21259; Kuyuwini Landing, 206 meters, A.M.N.H. Nos. 61238, 61240; Malali, 60 meters, A.M.N.H. No. 58975, U.M.M.Z. No. 77818; Marudi, 200–300 meters, A.M.N.H. Nos. 61380, 61387, 61388; Shudikar-wau, 200–300 meters, A.M.N.H. Nos. 61361, 61363–61366; Unorowo-wau River, 100–200 meters, A.M.N.H. Nos. 61288–61290. **French Guiana:** M.N.H.N. No. 4181. **Venezuela:** Bolívar: Cerro Lema, 1000 meters, M.B.U.C.V. No. 8011.

Neusticurus tatei

Venezuela: Bolívar: Auyantepui, 400 meters, A.M.N.H. Nos. 61008, 61040, holotype and paratype of *Neusticurus racenisi*; Urúyén, 460 meters, M.B.U.C.V. No. 3541. Territorio Federal de Amazonas: Casa de Julián, 609 meters, M.C.Z. Nos. 62207, 62208; La Culebra, about 1000 meters, M.C.Z. No. 62206; Temiche, Cerro Marahuaca, 1215 meters, M.C.Z. No. 66933; Ugueto, 400 meters, M.B.U.C.V. No. 8014, M.C.N. No. 1281; Vegas Falls, 1400 meters, A.M.N.H. No. 36649, holotype of *Arthrosaura tatei*.

Neusticurus rudis

British Guiana: Kartabo, 0–100 meters, A.M.N.H. Nos. 29925–29927. **Surinam:** Z.M.A. No. 10241, holotype of *Neusticurus dejongi*. **Venezuela:** Bolívar: Arabopó, 1216 meters, U.M.M.Z. Nos. 85243–85249; Auyantepui, A.M.N.H. No. 61025; Auyantepui, 1800 meters, M.B.U.C.V. Nos. 8008, 8015, 8017, 8019; Auyantepui, El Oso, 1800 meters, M.B.U.C.V. No. 3066; Guayaraca, 1020 meters, M.C.Z. Nos. 54722, 54723; Guayaraca, 1200 meters, M.B.U.C.V. No. 3067 (2); La Laja, 109 kilometers south of El Dorado, 600 meters, M.B.U.C.V. No. 8010.

Neusticurus ecpleopus

Bolivia: La Paz or Territorio de Colonias: Rurenabaque, 227 meters, A.M.N.H. No. 22512, holotype of *Neusticurus ocellatus*. **Colombia:** Comisaria de Amazonas: Araracuara, Río Caqueta, 200 meters, U.M.M.Z. No. 124692; Puerto Nariño, 70 kilometers west of Leticia, 50–100 meters, M.C.Z. No. 61150. Vaupés: mouth of Río Cananari, Cerro Isibucurí, 100–200 meters, U.M.M.Z. Nos.

124693, 124694. **Ecuador:** Moruna-Santiago: Chinghasa, 210 meters, A.M.N.H. No. 56241; Río Cenipa, 225 meters, A.M.N.H. No. 56232; Riobamba-Macas trail, 1100 meters, A.M.N.H. Nos. 14563–14570, 14572, M.C.Z. No. 34871; between Río Santiago and Río Pastaza, south of Macas and north of Gualiquiza, C.N.H.M. Nos. 42471–42483. Napo-Pastaza: Anga-Cocha, Río Bobonaza, 100–500 meters, A.M.N.H. No. 60629; Canelos, 500 meters, M.C.Z. No. 37748; Río Capequaria, 250–500 meters, A.M.N.H. No. 60626; Río Coto-pino, 400 meters, U.M.M.Z. No. 90786; Cuni-bundo, 1100 meters, C.N.H.M. Nos. 27660–27662; Mera, 1000 meters, C.N.H.M. No. 28047; Río Napo, 300 meters, U.M.M.Z. Nos. 90783, 90784 (2); Río Pastaza, Canelos to Río Marañón, 100–500 meters, M.C.Z. Nos. 37264–37266, paratypes of *Neusticurus tuberculatus*: between Riobamba and San José: A.M.N.H. No. 28806; San Francisco, 200 meters, U.M.M.Z. Nos. 84748–84750; San José de Sumaco, 700–1000 meters, A.M.N.H. Nos. 28890, 28899; south of San José de Sumaco, A.M.N.H. No. 28882; Sarayacu, 400 meters, M.C.Z. No. 37711, holotype of *Neusticurus tuberculatus*; 2 kilometers south of Shell Mera, 1066 meters, U.S.N.M. No. 157106. Tungurahua: Abitagua, 1300 meters, A.M.N.H. Nos. 24145, 38813, C.N.H.M. Nos. 25807, 27659, 28059, U.M.M.Z. No. 90785. **Peru:** Ayacucho, La Mar: Ayna, C.N.H.M. No. 39634. Junín: Chanchamayo, 1000–1500 meters, A.M.N.H. Nos. 23162–23166, 23168–23170, 23172–23181, paratypes of *Neusticurus ocellatus*; Chontilla, 33 kilometers north-northeast of Oxapampa, 780 meters, L.A.C.M. Nos. 8527, 8530–8532, 8536–8540; La Victoria, 700–1000 meters, M.C.Z. Nos. 45854–45856; Pan de Azucar, 39 kilometers north-northeast of Oxapampa, 380 meters, L.A.C.M. Nos. 8522–8526, 8528, 8529, 8533–8535; Perené, 1000–1500 meters, A.M.N.H. Nos. 23183, 23184, 23187, 23189, 23199, 23201, 23204, 23206, 23208, 23211, 23214, 23215, 23225, 23226, 23229, 23231, 23234–23244, M.C.Z. No. 34870, paratypes of *Neusticurus ocellatus*; Valle de Perené, 1000–1500 meters, A.M.N.H. Nos. 23155–23159, paratypes of *Neusticurus ocellatus*; trail, Satipo to Puerto Ocopa, M.C.Z. Nos. 45857, 45858. Loreto: Río Aquaytia, 165 meters, A.M.N.H. No. 56256; upper Río Cushabaty, 200–300 meters, A.M.N.H. No. 56237; Iquitos, 106 meters, C.N.H.M. No. 45476; Monte Alegre, 300 meters, A.M.N.H. Nos. 56303–56306; Ollanta, 200–300 meters, A.M.N.H. No. 56252; Pampa Hermosa, mouth of Río Cushabaty, 176 meters, A.M.N.H. No. 56258; Utoquinia region, 100–300 meters,

A.M.N.H. Nos. 56239, 56251. Puno, Sagrario: Río Quitón, 1020 meters, C.N.H.M. Nos. 40415-40519. Puno, Sandia: Tambopata, San Juan, 1300 meters, C.N.H.M. No. 64748. San Martín: Achinamisa (= Puerto Arambasa), 100-200 meters, A.M.N.H. No. 56381; Río Cainarache, 160 meters, A.M.N.H. No. 56392; Chasuta, 275 meters, A.M.N.H. No. 56247; Pachisa, 300 meters, A.M.N.H. Nos. 56226, 56234-56236, 56238, 56240, 56242-56246, 56248-56250, 56253. Province unknown: mouth of Río Ayendama, A.M.N.H. No. 56230; mouth of Río Santiago, 200-300 meters, A.M.N.H. Nos. 56228-56229, 56231, 56254, 56259; Peru-Ecuador frontier: Guache, A.M.N.H. No. 60579.

Neusticurus apodemus

Costa Rica: San José: 15 kilometers southwest of San Isidro del General, 865 meters, U.K.-M.N.H. Nos. 67375, 67377-67381, U.M.M.Z. No. 124688, holotype and paratypes.

Neusticurus strangulatus strangulatus

Locality unknown: A.N.S.P. No. 7538, holotype of *Euspondylus strangulatus*. *Ecuador*: E.P.N. Nos. 509, 4482, 6001-6004. Napo-Pastaza: Alpayacu, 1100 meters, M.C.Z. Nos. 8075-8076; Loreto, 600 meters, O.V. No. 1020; Mera, 1000 meters, C.N.H.M. No. 28046; Montalvo, 300 meters, O.V. No. 1191; Río Capahuari, 300-400 meters, O.V. No. 1182; Río Cotopino, 400 meters, U.M.M.Z. No. 90770; Río Napo, 300 meters, U.M.M.Z. No. 90772; Río Oglán, upper part, 600 meters, O.V. No. 3846; Río Pastaza, Canelos to Río Marañón, 200-500 meters, M.C.Z. Nos. 37262-37263; Río Pucayacu, 250-350 meters, O.V. No. 1112; San José de Sumaco, 700-1000 meters, A.M.N.H. No. 28881. Moruna-Santiago:

Chiguaza, 900 meters, O.V. Nos. 1122, 1123, 3838, 4493; Río Yuquipa, Macas, 700-1000 meters, O. V. Nos. 3405, 3406; between Río Santiago and Río Pastaza, south of Macas and north of Gualiquiza, C.N.H.M. Nos. 42485-42500. Tungurahua: Abitagua, 1300 meters, C.N.H.M. No. 26894, U.M.M.Z. No. 90773. *Peru*: Pongo de Manseriche, 245 meters, A.M.N.H. No. 56491; Melendez, 200 meters, A.M.N.H. Nos. 56490, 56492.

***Neusticurus strangulatus*
strangulatus × *trachodus***

Peru: Loreto: front range between Moyobamba and Cahuapanas, about 500-1000 meters, A.M.-N.H. No. 56382. San Martín: Lamas, 800 meters, A.M.N.H. No. 56307.

Neusticurus strangulatus trachodus

Peru: Huánuco: Cordillera Azul, 1300-1600 meters, C.N.H.M. Nos. 55989-55993, holotype and paratypes; Fundo Cinchona, 1300-1600 meters, C.N.H.M. No. 56109, paratype; Hacienda Pampayaco, above 750 meters, M.C.Z. No. 43764, paratype.

Neusticurus cochranæ

Ecuador: Between Abitagua and Mera, 1100 meters, U.M.M.Z. No. 123175. Napo-Pastaza: Alpayacu, 1100 meters, U.M.M.Z. No. 90788; Mera, 1000 meters, A.M.N.H. No. 38814, paratype of *Neusticurus ecpleopus cochranæ*; near Mera, 1000 meters, U.M.M.Z. No. 90787; San José de Sumaco, 700-1000 meters, A.M.N.H. Nos. 28891, 28868, holotype and paratype of *Neusticurus ecpleopus cochranæ*. Tungurahua: Abitagua, 1300 meters, C.N.H.M. Nos. 25806, 26893, U.M.M.Z. No. 90789 (4). Llanganate, C.N.H.M. No. 23524.

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