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CYTOTAXONOMIC STUDIES ON SOME UNUSUAL IGUANID LIZARDS ASSIGNED TO THE GENERA *CHAMAELEOLIS*, *POLYCHRUS*, *POLYCHROIDES*, AND *PHENACOSAURUS*, WITH BEHAVIORAL NOTES

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INTRODUCTION

ABSTRACT. Chromosome data are presented for four species of iguanid lizards. *Phenacosaurus heterodermus* has a diploid number of 36, with 12 metacentric macrochromosomes and 24 microchromosomes. *Chamaeleolis porcus* also has 12 metacentric macrochromosomes. The exact number of microchromosomes was not ascertained, but it is quite similar to that in *Phenacosaurus*. The karyotypes found in these two species resemble the primitive iguanid condition and that most frequently found in alpha *Anolis*. *Polychrus femoralis* has an apparent diploid number of 26, with 10 pairs of acrocentric and one pair of submetacentric macrochromosomes, and two pairs of microchromosomes. *Polychrus peruvianus* has 20 acrocentric macrochromosomes and 8 microchromosomes ($2n = 28$). A karyotype with low diploid number ($2n = 30$ or less) and few metacentric macrochromosomes is very unusual in iguanid lizards—previously reported only for *Polychrus marmoratus*. Its presence in the two presently studied *Polychrus* confirms their very close relationship *inter se*, but gives no clue to their relationship to other members of the family Iguanidae. *P. peruvianus* has previously been assigned to the monotypic genus *Polychroides*. However, osteological and cytological data show its very close relationship to *Polychrus*, and we formally propose the synonymy of *Polychroides* with *Polychrus*. Notes on behavior and ecology are appended for the four species. Although there may be a nomenclatural problem surrounding the use of the name *P. femoralis*, our Peruvian animal resembles *P. femoralis* from Loja,

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Ecuador. This is the first record of an apparent *Polychrus femoralis* from Peru.

We have recently obtained several poorly known iguanid lizards on field trips to Peru (RBH), and Cuba and Colombia (GCG). Although our observations and chromosome data are meagre, they provide insight into the relationships of these lizards. Field and behavioral notes are appended because of the paucity of information on these species and because we have the first record of an apparent *Polychrus femoralis*³ from Peru.

The genus *Chamaeleolis* is endemic to Cuba and the adjacent Isle of Pines. Long considered monotypic, Garrido and Schwartz (1968) have demonstrated that there are two distinct species.

Both are arboreal, moderate-sized lizards (snout-vent of adult males 155 mm), quite closely related to *Anolis*. They share with anoles extensible dewlaps and adhesive lamellae on the toes but differ in a number of osteological features, the most conspicuous of which is a parietal crest that extends far back over the neck (Etheridge, 1960), giving the animals a marked resemblance to true old-world chamaeleons.

Phenacosaurus is an iguanid genus with very close affinities to *Anolis*. Dunn (1944) listed a series of characters by which the genus was supposed to differ from *Anolis* (e.g. a prehensile tail, a heterogeneous scutellation with large and small scales intermixed, a dorsal crest of enlarged scales), but Etheridge (1960) pointed out that all of these characters occur individually in a number of species of *Anolis*. However, because of a number of osteological peculiarities (low number of sternal ribs, high number of parasternal chevrons), Etheridge retained the genus.

Phenacosaurus is known predominantly from high altitudes (1800-3500 m) in the Eastern Andes of Colombia. There are currently four recognized species, but *richteri* and *paramoensis* are undoubtedly synonyms of *P. heterodermus*, and there is at least

³The single specimen reported here runs down to *P. femoralis* in the key provided by H. W. Parker (1935: 516). Examination of comparative material (all of it *femoralis* by Parker's key) indicates that there may be as many as three distinguishable populations. A specimen in the United States National Museum from Guayaquil, the type locality of *femoralis*, has markedly larger scales than Parker's Loja specimens, which closely resemble the Peruvian animal. Pending revisionary studies, we believe it to be preferable to use the name *femoralis* for all this material, including our Peruvian animal.

one undescribed species from Ecuador (J. D. Lazell, Jr., personal communication).

Polychrus is a genus of arboreal lizards from Central and South America (including Trinidad) comprising about five distinct species (Parker, 1935). Etheridge (1960) compared 22 characters in *Anolis* and *Polychrus* (excluding characters unique to *Anolis* or common to the family Iguanidae) and found that 20 were shared by *Anolis* and *Polychrus*. He wrote, "Although there appears to be a close correspondence between *Polychrus* and the anoles, there are striking differences. Most of these differences, however, are features which are either unique to the anoles or unique to *Polychrus* and therefore tell us little more than that the anoles are separated from other members of the family, including *Polychrus*, by a wide morphological gap" (Etheridge, 1960: 111). He also pointed out that *Polychrus* and *Chamaeleolis* are highly arboreal, "and unusual in their habit of slow, deliberate movement. The similarities of these genera may well be parallel adaptations to a similar way of life, yet the occurrence of multiple parallel developments may, in itself, be an indication of relationship between the groups in which it occurs" (Etheridge, 1960: 113).

The monotypic genus *Polychroides* was erected by Noble (1924) when describing a new species of iguanid lizard (*P. peruvianus*) from the provinces of Cajamarca and Piura, northern Peru. Noble's comments on the affinities of the new genus were quite confused and are here quoted verbatim. On p. 109 in "Remarks" following the generic diagnosis he wrote: "The generic status of many of the slow-moving arboreal iguanids is very uncertain. The species described below cannot be referred to either *Enyalius*, *Enyalioides* or *Polychrus* as at present defined. It seems most closely related to *Polychrus* with which it agrees in its femoral pores, large head scales, subequal third and fourth toe and its sacculated lung. I have seen both *Polychrus* and *Polychroides* alive and have been struck by their great similarity in behavior. The pronounced nuchal crest of the latter readily distinguishes it from the former."

On p. 110, however, in the "Remarks" which follow description of the species he stated: "This species is closely allied to *Enyalioides festae* Peracca from which it differs in its larger head scales and gular sac, also in certain differences in the scutation of the digits and head. I would not hesitate to refer it to the genus *Enyalioides* were it not that this procedure would require a considerable modification of our present conceptions of that genus."

Etheridge (1960) was unable to find any skeletal differences between *Polychrus* and *Polychroides* in X-ray studies of iguanid genera, and he therefore cited *peruvianus* in his list of material examined as another species of *Polychrus*. Only the external character of a dorso-nuchal crest distinguished *peruvianus* from other *Polychrus*.

Chromosomes have been useful in elucidating relationships of iguanid lizards. The majority of species studied have a karyotype consisting of six pairs of metacentric macrochromosomes and eleven or twelve pairs of microchromosomes (Gorman, Atkins and Holzinger, 1967; Gorman and Atkins, 1967, 1968). One species, *Plica plica*, showed apparent centric fissioning with four pairs of acrocentric macrochromosomes. The chromosomes of the single species of *Polychrus* examined, *P. marmoratus*, were so different from all other species of iguanids of which karyotypes are known that it was difficult to relate this genus to any of the others (Gorman, Atkins, and Holzinger, 1967). Female *P. marmoratus* have a diploid number of 30, consisting of 20 acrocentric macrochromosomes and 10 acrocentric microchromosomes. Males have a diploid number of 29, with 1 metacentric and 19 acrocentric macrochromosomes, and 9 acrocentric microchromosomes. In both *Anolis* (Gorman, 1967) and *Sceloporus* (Lowe, Cole, and Patton, 1967), species have now been found with high numbers of acrocentric macrochromosomes. These species, however, are characterized by high diploid numbers, greater than $2n = 30$, the formula which appears primitive for the family Iguanidae (Gorman, et al., 1967). The probable explanation for these high numbers is centric fission of the metacentric macrochromosomes (Gorman, Baptista, and Bury, 1969).

MATERIALS AND METHODS

Chromosome preparations were made by tissue culture of whole blood following methods already outlined; by culture of marrow obtained from the femur and treated in the same fashion as blood; and by direct testis preparations (see Gorman, et al., 1967). The specimens used were one female *Polychrus peruvianus* (Museum of Vertebrate Zoology, no. 82834), one female *Polychrus femoralis* (M.V.Z. 82835), one male *Chamaeleolis porcus* (Museum of Comparative Zoology, 100472), and one male *Phenacosaurus heterodermus* (M.C.Z. 104409).

Chromosome spreads were photographed and karyotypes analyzed as best we could. Unfortunately, for *Chamaeleolis*, *Polychrus peruvianus*, and *P. femoralis*, we obtained few mitotic divisions.

and we are unable to present fully definitive karyotypes or diploid numbers, though the material permits interesting comparisons. Numerous divisions from the testis of *Phenacosaurus* were studied.

RESULTS AND DISCUSSION

Only four clearly resolved metaphase plates were found in *P. peruvianus*, all with 28 chromosomes, all acrocentric. There is not a sharp break in size between macro- and microchromosomes; however, 20 might be termed macrochromosomes and 8 microchromosomes (Fig. 1a). This is very similar to the karyotype of female *Polychrus marmoratus*, and this is only the second species of iguanid reported to date that has a karyotype of all acrocentric chromosomes. So few cells were seen that we cannot safely assume that the diploid number is 28 — but it is quite clear that the karyotype of *P. peruvianus* resembles that of *P. marmoratus* to such a great extent that considering these forms as members of separate genera obfuscates their close relationship. We formally propose the synonymy of *Polychroides* with *Polychrus*.

Few divisions were obtained in our specimen of *P. femoralis* — but, again, there are enough data to establish both its close relationship to the other *Polychrus* in the similarity of the specialized karyotype and its uniqueness among the species thus far examined. The diploid number appears to be 26. (This is based upon only four metaphase plates; additional spreads were seen, but, because of overlaps, precise counts could not be made.) In all cells, there is one pair of submetacentric chromosomes (Fig. 1b). Within the genus *Polychrus*, a submetacentric chromosome had previously been seen only in the male of *P. marmoratus*, where it is quite clearly the Y chromosome (Gorman, et al., 1967). In *P. femoralis* also, the largest chromosome pair is clearly subacrocentric with minute short arms present. There is a total of 11 pairs of macrochromosomes and 2 pairs of microchromosomes in the cells that were carefully analyzed. The karyotype of *P. femoralis* is most likely derived from a *marmoratus*-like karyotype of $2n=30$. Centric fusions of microchromosomes to macrochromosomes would account for the reduction in diploid number and the appearance of submetacentric and subacrocentric chromosomes.

Numerous metaphase plates were observed in *Chamaeleolis porcus*, but we lack definitive information on the number of microchromosomes. It is quite clear that the karyotype resembles the “typical” iguanid in having six pairs of metacentric macrochromosomes and a series of more than 20 microchromosomes (Fig. 2).

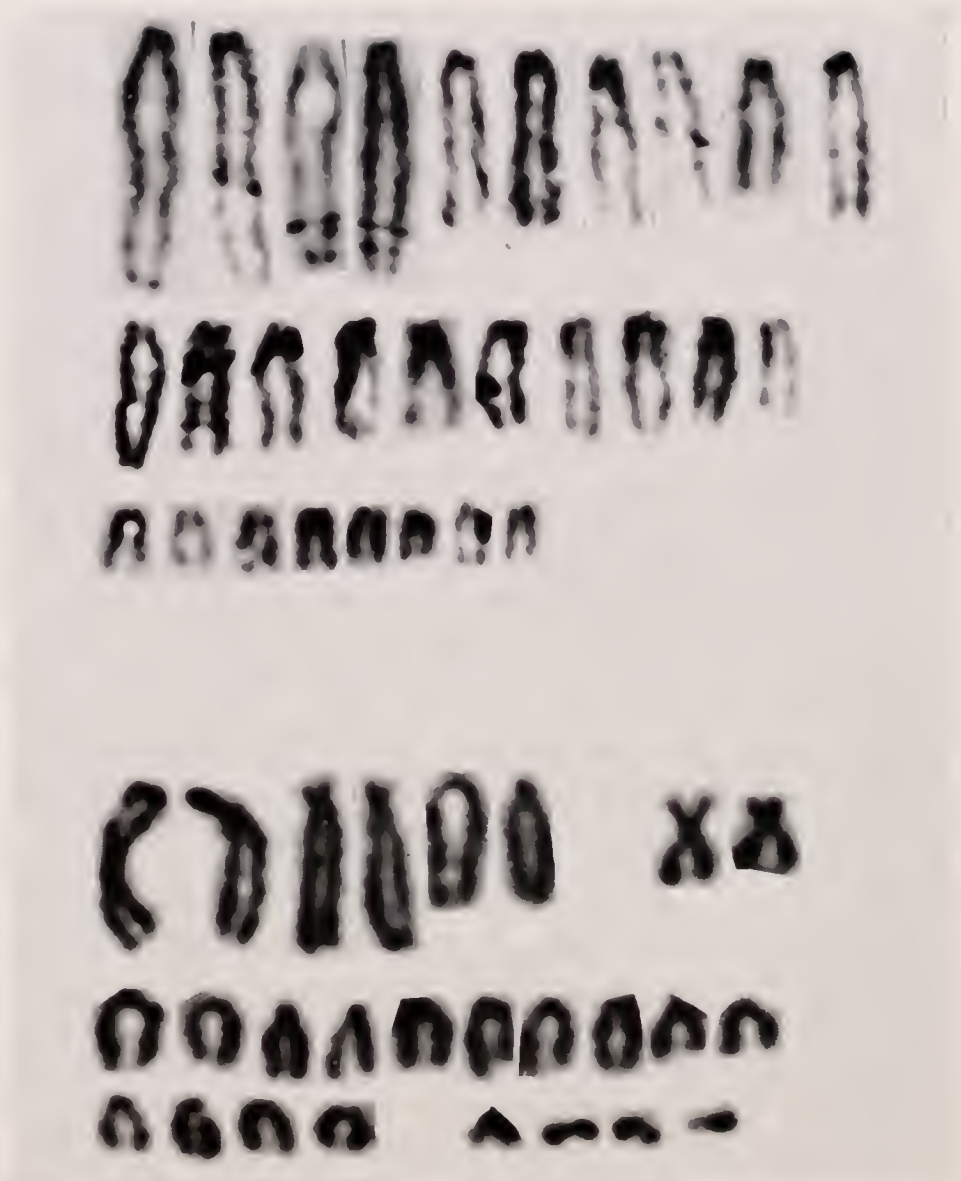


Fig. 1. Karyotypes of *Polychrus*. a., *P. peruvianus* female. There are 28 acrocentric chromosomes. Bone marrow preparation, Giemsa Stain. b., *P. femoralis* female. There are 26 chromosomes; one pair (top row, far right) is submetacentric. Leukocyte culture, Giemsa stain.

Only testis preparations were made for *Phenacosaurus heterodermus*. There were numerous meiotic and mitotic divisions. In meiosis we can clearly see six large macrobivalents and 12 considerably smaller microbivalents (Fig. 3). In mitosis, it was quite clear that the macrochromosomes were metacentric. Thus, the diploid number is 36, with 24 microchromosomes.

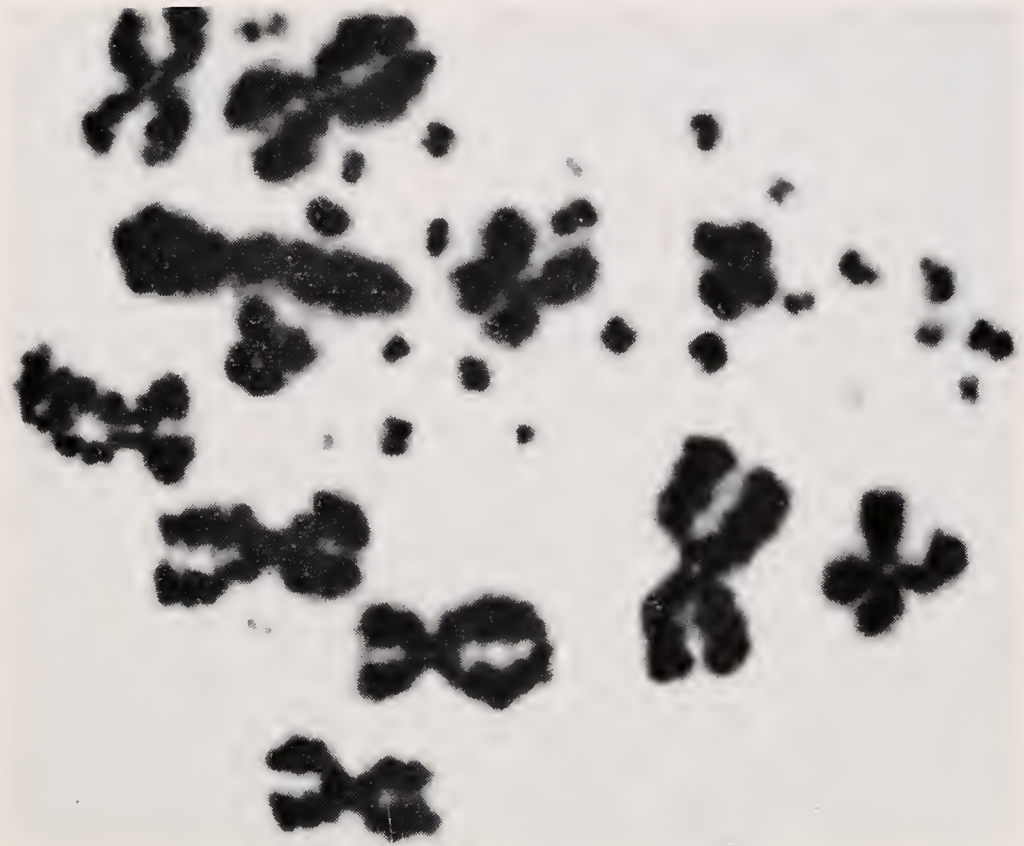


Fig. 2. Mitotic metaphase of *Chamaeleolis porcus* male showing the "typical iguanid" condition of 12 metacentric macrochromosomes, and a sharp break in size between the macro- and microchromosomes.

Among *Anolis*, Etheridge (1960) defined two major groups termed *alpha* and *beta*. Chromosome studies (Gorman, et al., 1967) have shown that the primitive *alpha* karyotype is identical with that of the primitive iguanid condition (12 metacentric macrochromosomes, 24 microchromosomes). In a recently proposed classification of iguanids on the basis of structure of the caudal vertebrae (Etheridge, 1967), *Chamaeleolis* and *Phenacosaurus* were placed in a group with the *alpha* anoles; chromosomes support this classification.

Polychrus remains a puzzle within the iguanids. Now that three species have been studied it is quite clear that they are close to each other *inter se*, but distinctly different from anoles and anoline genera such as *Chamaeleolis*, *Phenacosaurus*, and *Anisolepis* (Gorman, et al., 1967).

Since this paper was originally written, we have received the following new data.

On November 26, 1968, Dr. John Wright of the Los Angeles County Museum collected a male *Polychrus peruvianus* at 3.5 km east of the junction between Bagua Grande and Bagua Chica, 15.5 km west of Bagua Grande, Amazonas Dept., Peru, at an altitude of 2,000 feet. (Field catalog number P-927; to be deposited in L.A.C.M.)

Testes were minced and allowed to settle in a hypotonic citrate solution (as no centrifuge was available), the citrate was removed with an eye-dropper, and fixative was added. This field preparation was then brought back to the United States, where slides were made some two months later.

Dr. Wright has kindly consented to our examination of the slides and utilization of the data. At diakinesis there are 13 bodies.



Fig. 3. Diakinesis in *Phenacosaurus heterodermus*. There are six large bivalents, and 12 microbivalents. $n = 18$. Large round black area is a sperm head, not part of the meiotic figure.

12 bivalents, and a trivalent. The male diploid number is thus expected to be 27. One mitotic metaphase was seen, and 27 chromosomes were counted. Position of the centromere could not be ascertained. One clear metaphase II cell had 14 chromosomes, all acrocentric.

These data are consistent with the sex chromosome situation known in *Polychrus marmoratus*, in which the males have a diploid

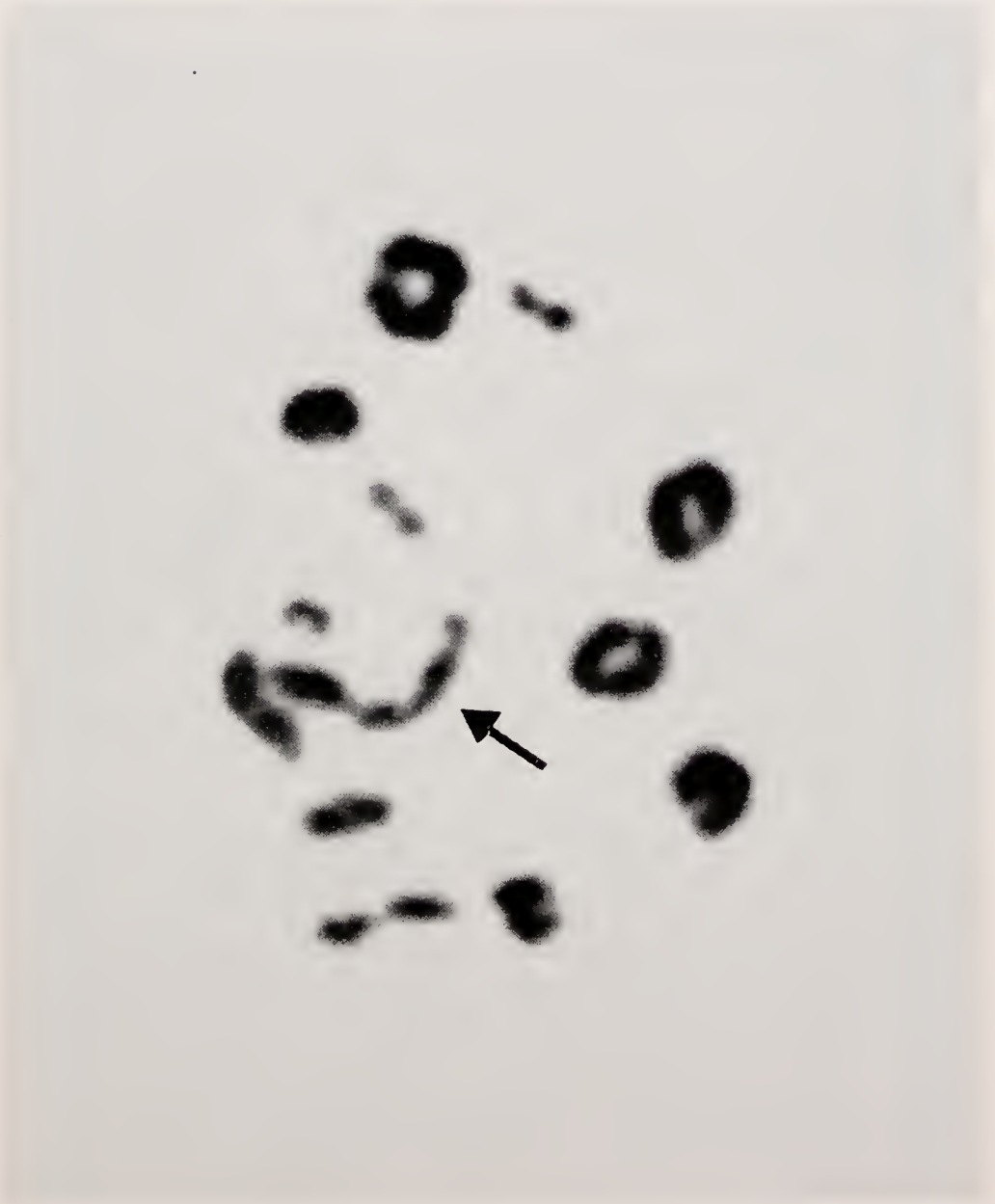


Fig. 4. Diakinesis of *Polychrus peruvianus* male. There are 13 bodies, 12 bivalents, and a sex trivalent (arrow).

number one lower than the females, the Y chromosome is meta-centric (not demonstrated for *P. peruvianus*), and a sex trivalent is clearly evident at meiosis (Gorman, Atkins, and Holzinger, 1967).

The finding of 12 bivalents and a trivalent in *P. peruvianus*, with an expected male $2n$ of 27, gives further strength to our assumption that female $2n = 28$ (the latter figure having been arrived at with the examination of relatively few cells). Figure 4 illustrates diakinesis in *P. peruvianus*.

NOTES ON POLYCHRUS

POLYCHRUS PERUVIANUS

Five specimens of *Polychrus peruvianus* were collected:

MVZ 82834 El Arenal, Rio Huancabamba, elevation 3000
82388 ft., 7 km N, 50 km E of Olmos, Dept. Cajas-
83678 marca, Peru.

83679

MVZ 82413 (skin and skeleton). Tingo, Rio Utcubamba,
elevation 3000 ft., 30 km S, 41 km E of Bagua,
Dept. Amazonas, Peru.

El Arenal is on a terrace above the Rio Huancabamba. The hillsides are dry and rocky, and the terrace has a predominance of mesquite (*Prosopis*) interspersed with cultivated areas. All specimens were collected on mesquite branches.

The Tingo individual was captured by Dr. Carl Koford at night on a horizontal branch of an unidentified tree. Stomach contents included several Hymenoptera and a leaf fragment. The largest ovarian follicles were less than 2 mm in diameter.

This locality is much wetter than El Arenal. Bromeliad-laden trees up to 40 feet are found on the steep hillsides, and dense second-growth vegetation covers the valley floor.

Body coloration in life (MVZ 82834) was medium yellow-green with a narrow, pale yellow band running from the eye to the groin and olive-drab saddles on the dorsum and tail. Small irregular yellow marks were spaced between the saddles. Some capacity to darken the body colors was observed in captivity.

The tail of this specimen was slightly prehensile. *P. femoralis* gave no evidence of this ability. Both species emitted a nasal salt solution in captivity (see Templeton, 1967).

P. peruvianus has a more protrusive gular flap than *P. femoralis*. In addition, only *P. peruvianus* possesses a row of raised scales forming a mid-gular crest.

POLYCHRUS FEMORALIS

On 31 August 1967, one gravid female of this species was captured near Molino, elevation 2300 ft., 21 km E, 7 km N of Olmos, Dept. Lambayeque, Peru (5.9° S/ 79.6° W). This specimen (MVZ 82835) represents a considerable range extension from the record in Loja (Parker, 1932) and an apparent Peruvian record.

She was oriented head down on a vertical branch of a plant about 5 ft. tall and remained motionless until capture. The locality is in a narrow river valley. Deciduous woodland alternates with open areas cleared for farming.

She was kept alive and placed in a runway with a temperature gradient beginning 18 September. Water was sprinkled daily at the cool end. On 27 September she laid 12 eggs at the cool, moist end of the runway. The eggs were removed and placed in an incubator. Egg size eight hours later averaged 19.6 mm in length and 11.3 mm in width. The shell texture was soft and leathery. Mold developed on the eggs by 4 October and they subsequently decayed.

In captivity movement was rare. When prodded, she exhibited a leaping form of locomotion described by Boker (1935) as "bipedal leaping" for *Polychrus marmoratus*. Davis (1953) observed a similar method of locomotion in *Corythophanes cristatus*.

In life she was light yellow-green with pronounced brown saddles on the dorsum. The capacity for color change in this specimen was less marked than in *P. peruvianus*.

BEHAVIOR IN CAPTIVITY

Davis (1953) outlined a sequence of four defensive responses used by *Corythophanes cristatus* against apparent predators. These can be grouped into two general categories:

- I. Passive defense
 - A. Behavioral and morphological camouflage
 - B. Catalepsy to eliminate all movement not associated with a positional change and thus decrease the probability of detection
- II. Active defense
 - A. Active postural movements to increase the apparent size of the animal
 - B. Aggressive biting as a last resort

Davis stated that the defensive response given was geared to the relative immediacy of the threat to the animal's safety. The more immediate the threat, the more active the response.

Both *Polychrus peruvianus* and *P. femoralis* exhibited this sequence of defensive traits in captivity but did differ in degree of response. Since only one specimen of each species was observed, these notes should be considered tentative.

Behavioral and morphological camouflaging is well marked in both species. The colors and patterns render detection of these animals difficult in their arboreal habitats. Their relative immobility and capacity for color change accentuate this concealment. In both the field and captivity, *P. femoralis* relied more on immobility than on other defensive responses.

Behavior similar to the catalepsy of walking sticks (Phasmidae) has been reported for several arboreal lizards (reviewed in Davis) and was present in these two species as well. *P. peruvianus* could be easily induced into this behavior by forcibly altering its position, but both used it when coming to rest after voluntary movement. When matched with other types of camouflage, Davis felt that this behavior aided in concealment.

In response to a threat, many animals are recorded to increase the apparent size of the body or parts of the body by behavioral posturing. This behavior is manifest in social encounters, as well. Postural movements common to both *Polychrus* species involve lateral compression of the body, expansion of the throat fan, and head bobbing. The plane of expansion is sagittal and presented broadside for both, as is the case in *Corythophanes*. The expanded area is thus displayed to maximum advantage.

P. peruvianus would often gape when posturing. If approached closely, she would lunge forward, maintaining balance by the two hind legs and tail. She would bite vigorously if given the opportunity. In contrast, *P. femoralis* could rarely be induced to bite. But it would often attempt to escape by leaping.

Of the two species of *Polychrus* under discussion, the behavior of *P. peruvianus* was more similar to that of *Corythophanes* than was that of *P. femoralis*. It is perhaps of significance that *P. femoralis*, having a much less pronounced gular flap than the other two species, relied less on active postural movements and more on passive camouflage.

NOTES ON CHAMAELEOLIS

Although rare in collections, *Chamaeleolis* is widely distributed throughout Cuba. Through the help of Orlando Garrido, we obtained a juvenile male *C. porcus* from La Florida, Sabanilla,

Oriente Province, and a larger (but subadult) male from La Casimba, eight kilometers west of Maisi, Oriente Province.

Wilson (1957) published a note on the behavior of a captive *Chamaeleolis*. Although he called this *C. chamaeleontides* (sic.), the specimen has been subsequently re-identified by Schwartz as *porcus*. Wilson reported, "its behavior was strikingly chamaeleon-like and quite different from that of several species of *Anolis* (including the giant *A. equestris* Merrem) which the author has observed in captivity." He stated that it was very sluggish even when freshly captured, and that it could be left on a laboratory table without much danger of its wandering. Often, it would remain in the same spot for hours or even days without changing its position. When confronted with food in the form of living insects, it would move deliberately and without hurrying. Experiments using a live male *Anolis equestris* and a cardboard model resembling a male *Chamaeleolis* failed to elicit any aggressive response. Only once, in the year that he had the specimen, did it extend its dewlap — and this was without any apparent external stimulus.

Our observations are not at all in accord with this description. Our specimens would actively jump toward prey (crickets, grasshoppers, and mealworms). They would often scamper away when left out in the open. Garrido and Schwartz (*op. cit.*) point out that *C. porcus* is "at least capable of quick and decisive action." They give a detailed account of the escape behavior of one specimen encountered in the field. Our *Chamaeleolis* were not so quick as *Anolis*, but certainly did not show the incredibly slow movements of true chamaeleons. Furthermore, they were quite aggressive. They would display to each other by extending the dewlap fully, opening the mouth and protruding the tongue. They also displayed in similar manner to *A. equestris*. When handled, they would extend the dewlap and often would bite. Unfortunately, no films were taken of the displays.

It appears, then, that the social behavior of *Chamaeleolis* has been misunderstood. Its reported sluggishness and immobility appear to be facultative rather than obligatory and may well be associated with its cryptic coloration. The ability to move quite quickly, and the fact that anole-like territorial responses were easily elicited implies that the behavior and social structure of *Chamaeleolis* may be quite similar to that of most anoles.

NOTES ON PHENACOSAURUS

Previous notes on *Phenacosaurus* have dealt with specimens in captivity (Osorno-Mesa and Osorno-Mesa [1946], on shedding of skin, incubation of eggs, feeding habits, etc., and Kästle [1965], a detailed ethological study with particular emphasis on social behavior).

On July 10, 1968, Dr. Jorge Hernandez, of the Universidad Nacional, Bogota, led Gorman and J. F. Lynch on a one-day trip specifically to collect *Phenacosaurus* in Chia (Cundinamarca), a semi-rural suburb of Bogota (at about 35 km distance, alt. ca. 2700 m.) and collected between 11 am and 2:30 pm. The day was overcast, with intermittent showers, and cold. A thermometer was not available, but the temperature for most of the time was probably not in excess of 14° C., the mean temperature of that immediate area.

The roads were lined with shrubbery, often blackberries, which separated either pasture-land or homes.

Three *Phenacosaurus* were in the first blackberry bush examined. Two, a male and a female, were collected. In the course of the afternoon, 14 of these supposedly rare lizards were collected. Most often, more than one was taken at a time, usually in groups of two, sometimes of three. One pair was actually in bodily contact—the male's chin was touching the tail of the female.

All but two of the lizards were on blackberry bushes, generally 1-3 feet above the ground, and usually on a bare branch. It is likely that as many were missed as were caught—especially those in leafy parts of the bushes. The escape response is to drop down, often clinging to a branch with the prehensile tail, and then to slink slowly away. The most usual perch position was almost horizontal; only one individual was perched vertically, head down.

In review of body temperatures in reptiles, Brattstrom (1965) listed 18.0° C. as the minimum voluntary temperature for an iguanid lizard. This was *Uma notata*, which, in fact, has a mean body temperature of 38.6° when active, and the 18° probably represents an unusual reading. Normally, iguanids living in cold temperatures bask in sunlight until warmed to a preferred body temperature of $33 \pm 3^\circ$. An extreme example was reported by Pearson (1954) for *Liolaemus multiformis* at high altitudes in Peru. He found that the intense isolation enables these species

to warm to body temperatures of 35°, with shade temperatures as low as 11°.

Phenacosaurus was remarkable for an iguanid lizard because it was normally active at low temperatures with no opportunity to warm up. We consider it quite possible that its preferred body temperature is well below that of any other iguanid reported to date.

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