INTERSEXUALITY IN A MEXICAN COLUBRID SNAKE (*PSEUDOFICIMIA*)

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ABSTRACT: Females of the colubrid snake *Pseudoficimia frontalis* (Cope) have well-developed hemipenes. This is the first example of a snake in which the adult females universally possess primary sex characteristics of males and are, in this sense, intersexual. Young females contain epoöphorons and *ductus deferens*, and young males contain oviducts. Sexual dimorphism in several parts of the reproductive system is demonstrated. The name *Pseudoficimia pulcherrima* is placed in the synonymy of *P. frontalis*.

POPE (1935:378) reported a specimen of *Amblycephalus stanleyi* (AMNH 29943) that had well-developed hemipenes and oviducts that contained ". . .six fully formed and apparently normal eggs." This may be the record referred to in a review of intersexuality in vertebrates by Ponse (1949:120), who listed one example of ". . .hermaphrodisme accidentel. . ." in snakes, but gave no reference. White (1954) reported that the only hermaphroditic forms of vertebrates are a few species of fishes and that there is no genetic evidence as to the nature of the sex determining mechanism nor is the heterogametic sex known for any species of reptile. More recently, Gorman and Atkins ("1966" [1967]) and Cole et al. (1967) have demonstrated sex chromosomes in lizards. Beçak (1965) demonstrated a ZW:ZZ sex determination mechanism with female heterogamety in colubrid snakes. He also identified ZW-sex chromosomes in an intersex specimen of *Bothrops insularis* which was a normal female according to its sex chromosomes.

Hoge et al. (1954) reported a population of *Bothrops insularis* in which most of the females contained hemipenes (bilateral or unilateral), but the rest lacked them; males appeared normal. The frequency of intersexes increased in the population during a 30-year period, and the frequency of adult males decreased. Only "intersexual females" and males are fertile; "true females" appear to be sterile (Hoge et al., 1959). Maclean (1968) reported a specimen of *Bothrops moojeni* containing 12 embryos, a well-developed right hemipenis, and a small left hemipenis. In a summary of intersexuality in reptiles by Forbes (1964), intersexuality in adult snakes was recorded only for *Bothrops insularis*. Thus far the *Bothrops insularis* population has been the only known example of recurring intersexuality in reptiles, but even in these snakes primary sex characteristics (gonads, hemipenes, oviducts, etc.) of both sexes are not present in all members of either sex. The term intersexuality refers to the existence in one sex of structures which are considered to be appropriate to, and functional in, the other sex (Forbes, 1964).

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In their diagnoses of *Pseudoficimia frontalis* (Cope, 1864) and *P. pulcherrima*, Taylor and Smith (1942) separate the species on the bases that *P. frontalis* has: smaller hemipenial spines; 141–156 ventrals in males, 160–161 in females (146–155 in *pulcherrima* males); 39–45 subcaudals in males, 35–38 in females (41–43 in *pulcherrima* males); 7 or fewer infralabials (7 in *pulcherrima*); and more of rostral plate visible from above. They examined six specimens of *frontalis* and two of *pulcherrima*. In this paper I report only the characteristics of the reproductive system; analyses of other characteristics will appear later.

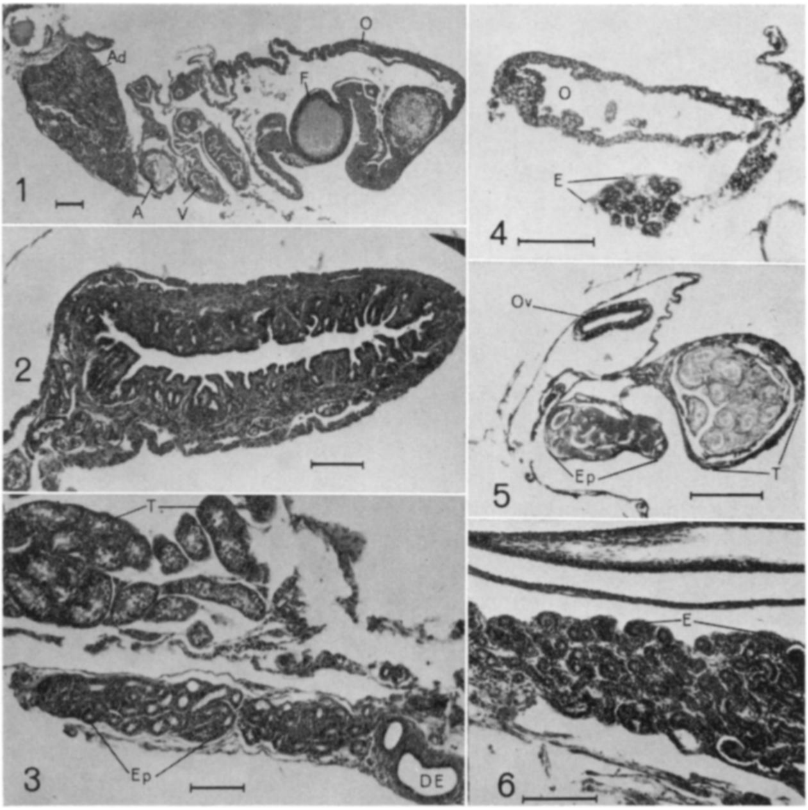
Materials and Methods

I have examined 46 specimens (including the cotypes of *P. frontalis* and the paratype of *P. pulcherrima*): 23 males, 22 females, and 1 small specimen of undetermined sex. All specimens have been dissected to determine the structure of the hemipenes and other reproductive organs. Parts of the reproductive tracts of certain specimens were removed for histological examination. Tissues were sectioned at 8 microns thickness, stained with hematoxylin and eosin, and permanently mounted.

The sex of any individual can be ascertained by determining the point of origin of the *musculus retractor penis magnus* even if viscera and hemipenes have been destroyed. The combined lengths of the hemipenis and the *m. retractor penis magnus* can be indicated by counting the subcaudals between the base of the tail and the point of the muscle's origin. Since the muscle originates on a caudal vertebra, its position can be easily determined and is independent of the condition of the hemipenis, which on some specimens is dried or partially everted, causing any measurement of hemipenial length to be in error.

Initially, gross dissection revealed epoöphorons and *ductus deferens* in young females and oviducts in young males; these specimens contained normal reproductive organs for their respectively designated sexes. Examination of histological sections supports these findings.

The smallest females (UMMZ 104496, S-V = 155; UMMZ 104687, S-V = 146), the sex of each of which was determined by locating the point of origin of the retractor muscle, have ovaries and epoöphorons (Figs. 4 and 6), and the smallest male (USNM 24961, S-V = 94) has a testis, an epididymis, and an oviduct (Fig. 5); these individuals are probably in their first season of growth. The epoöphoron of the young female (Figs. 4 and 6) is similar to the epididymis of a large (and older) male (Fig. 3). The oviduct of the young male (Fig. 5) is a flattened tube with a large lumen lined with simple columnar epithelium. Although this specimen is in a poor state of preserva-



FIGS. 1–6.—(1) Ovary (O) and follicle (F) with small ovum of large female (KU 68939, S-V = 376). Ad = adrenal; A = artery; V = vein. (2) Oviduct of large female (KU 68939, S–V = 376). (3) Testis (T), epididymis (Ep), and *ductus epididymis* (DE) of young male (LACM 7041, S-V = 278). (4) Epoöphoron (E) and ovary (O) of young female (UMMZ 104496, S-V = 155). (5) Testis (T), epididymis (Ep), and oviduct (Ov) of young male (USNM 24961, S-V = 94). (6) Epoöphoron (E) of young female (UMMZ 104496, S-V = 155). The horizontal line represents 0.1 mm.

tion, the flattened tube is similar in structure and position to the oviduct of a young female. The epoöphoron in Fig. 4 is continuous with that in Fig. 6.

Results

All large females have ovaries with ova (Fig. 1), oviducts (Fig. 2), and uteri, and all females have unmistakable hemipenes (Fig. 7). The following hemipenial muscles are present in females: *retractor penis magnus*, *posterior constrictor sacculi ani*, *anterior constrictor sacculi ani*, *retractor penis parvus*, and *retractor penis basalis*.

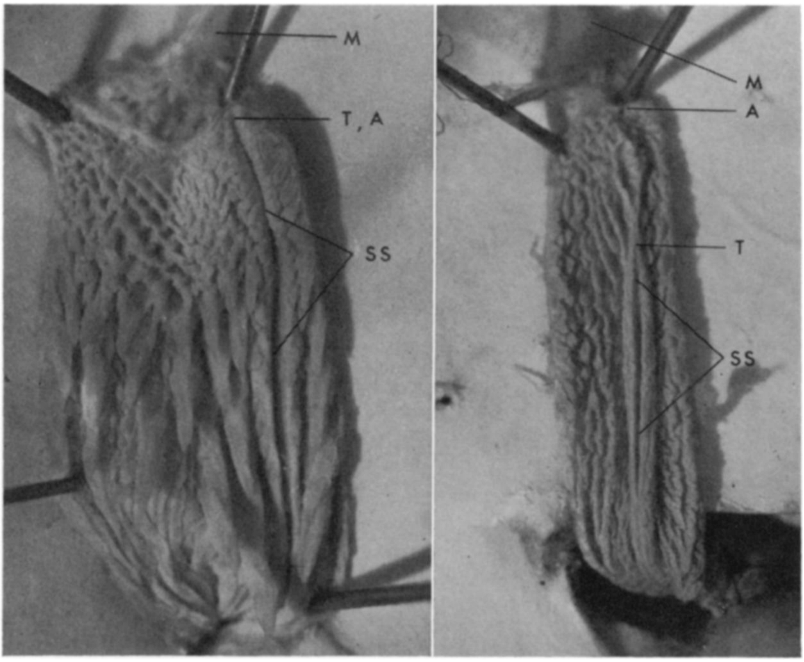


FIG. 7—Hemipenis of male (UIMNH 35052, S-V = 360) on left and female (FMNH 106366, S-V = 365) on right. Taylor and Smith (1942) examined the female hemipenis (original number EHT-HMS 5204) and referred this specimen to *P. frontalis* as a typical male. SS = *sulcus spermaticus*; T = terminus of *sulcus spermaticus*; A = apex of hemipenis; M = *m. retractor penis magnus*. The *sulcus spermaticus* of the female appears to continue beyond the termination indicated; however, close examination reveals that the true termination is proximal to two large flounces that continue distally almost to the apex.

The values for the length of the hemipenis, in numbers of subcaudals, are 3–8 ($\bar{x} = 6.4$; SE = 0.3) in 19 females and 6–14 ($\bar{x} = 9.8$; SE = 0.5) in 17 males. The position of origin of the *m. retractor penis magnus* is 11–18 ($\bar{x} = 13.8$; SE = 0.4) in 23 females and 25–37 ($\bar{x} = 30.3$; SE = 0.6) in 21 males with no overlap in the ranges. Large males have testes, epididymides, *ductus deferens* (Fig. 3), hemipenes (Fig. 7), and all of the muscles listed above.

There is distinct sexual dimorphism in the combined lengths of hemipenis and muscle. Although the combined lengths of hemipenis and muscle are greater in males, the hemipenis length (relative to the muscle) is greater in females. In 18 females the hemipenis length is 23.0–63.6% ($\bar{x} = 46.3$; SE = 2.6) of the combined lengths of the hemipenis and the retractor muscle. In 15 males the hemipenis length is 19.3–40.6% ($\bar{x} = 31.7$; SE = 1.5) of the combined lengths of the hemipenis and the retractor muscle.

TABLE 1.—Occurrence of certain structures of the reproductive tract in *Pseudoficimia frontalis*.

Specimens examined	Number of specimens: Hemipenis — Present	Hemipenis — Absent	Extent of *sulcus spermaticus*: Terminates at apex	Terminates proximal to apex	Unknown[a]	Ova in oviducts: Present	Absent	Unknown[c]
23 ♂♂	23	0	10	0	13	0	15	8
22 ♀♀	22	0	0	9	13	15	2[b]	5
1?	1	0	0	0	1	0	0	1

[a] The extent of the *sulcus spermaticus* cannot be determined on some incompletely everted hemipenes.

[b] UMMZ 104496 and 104687 are small specimens with empty oviducts. They were examined histologically.

[c] Scavengers, probably ants, had completely eviscerated some specimens.

In 9 females the *sulcus spermaticus* occupies about four-fifths of the length of the hemipenis and never terminates at the apex; in 9 males the *sulcus spermaticus* terminates at the apex (Fig. 7). The spines are smaller in all females than in males; other structures are similar to those on normal male hemipenes. The occurrence of certain structures of the reproductive tract in *Pseudoficimia frontalis* is summarized in Table 1.

Hemipenes were not found in any of the 41 females of 39 other species (23 genera) of colubrid snakes that I examined; however, some species have vestiges of hemipenial muscles. This survey is continuing.

DISCUSSION

The embryogeny of reproductive systems in vertebrates is characterized, in general, by a sexually indifferent stage, during which the future sex of the gonads cannot be determined by either gross or microscopical examination. Later in embryogeny, when sex is expressed, each reproductive system contains both mesonephric and Müllerian ducts. In males the mesonephric ducts give rise to the *ductus deferens* and *ductus epididymides*, and the Müllerian duct is vestigial in an adult as the appendix testis. In females the mesonephric duct in an adult is vestigial as the epoöphoron and is functional as the ureter while the Müllerian duct becomes the functional oviduct and uterus. In most vertebrates the male Müllerian and the female mesonephric ducts are vestigial or absent in postfetal individuals. Normally, mammalian embryos develop as females until the presence of hormonal substances produced by a dominant testis prevents a genetic male from developing into a female (Arey, 1965). The testis (or its hormones) has a determining influence for the development of maleness.

The presence of both epoöphoron and Müllerian ducts in young snakes suggests that the embryologically indifferent stage of development of the reproductive organs is characterized by the development of both structures, one of which is vestigial and resorbed by the time the snake reaches adult size. Since normal embryological development in vertebrates includes a sexually indifferent stage followed by the disappearance of the vestigial organs prior to parturition, it seems that the presence of structural parts of both sexes in these young snakes results from an unusually prolonged period of development of the otherwise vestigial parts, to the point of histological identification, and delayed regression of the same parts until well after parturition. None of the snakes exceeding 200 mm in snout-vent length has retained any trace of the vestigial organs. Although other male reproductive organs are absent in larger females, the 100% persistence of hemipenes in females may indicate a relatively greater potential for maleness than for femaleness. The hemipenes and associated muscles appear normal in all females and can even be mechanically everted by applying pressure at the base of the tail, just as can male hemipenes.

I am unable to distinguish *Pseudoficimia pulcherrima*, as a population distinct from that of *P. frontalis*, on the basis of the characters used by Taylor and Smith (1942). Taylor and Smith referred six specimens to *P. frontalis*; of these I have not examined the hemipenes of the cotypes (USNM 31424–25). USNM 24961 (incorrectly listed as 24941 by Taylor and Smith) is a young male, and UIMNH 18720 is a female; both were referred to *P. frontalis* by Taylor and Smith. They also referred two females (FMNH 106366–67) to *frontalis* apparently on the basis of the small hemipenes that they described (p. 245; they understandably mistook these specimens for males). The size of the hemipenial spines is one of the most important diagnostic characteristics for these two species according to Taylor and Smith (1942).

It now becomes evident, therefore, that Taylor and Smith proposed the name *P. pulcherrima* for the females, which they mistook for males by virtue of their well-developed hemipenes, of a population of *P. frontalis*. Accordingly, the name *Pseudoficimia pulcherrima* Taylor and Smith (1942) should be placed in the synonymy of *Pseudoficimia frontalis* (Cope, 1864).

A detailed systematic analysis of the genus *Pseudoficimia* will appear later.

Conclusions

1. Females of *P. frontalis* with normal gonads have smaller hemipenes with a subterminal *sulcus spermaticus*, and smaller spines in comparison with males.

2. The gonads of large snakes of both sexes appear to be normal in gross and histological morphology.
3. Young females retain epoöphorons and *ductus deferens* and young males retain oviducts after parturition; both appear to be potentially of either sex. The hemipenis may be a vestige that is never lost in females. There is no evidence of hemipenial regression.
4. *Pseudoficimia pulcherrima* (Taylor and Smith) proves to have been erroneously applied to the males of *P. frontalis* and should, therefore, be placed in the synonymy of *P. frontalis* (Cope).

Specimens examined histologically.—Michoacán: 1.5 mile ESE Coalcoman, Sierra de Camichine (UMMZ 104496); 2 miles NE Coalcoman (UMMZ 104687); Coalcoman (KU 68939); Apatzingan (FMNH 39208). *Jalisco*: Guadalajara (USNM 24961); 5.9 miles E El Rincon (BYU 23940). *Sinaloa*: 18.3 miles N Mazatlán (LACM 7041).

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LATE SUMMER BEHAVIOR OF THE LIZARDS *SCELOPORUS MERRIAMI* AND *UROSAURUS ORNATUS* IN THE FIELD

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ABSTRACT: Late summer behavior of the sympatric iguanid lizards, *Sceloporus merriami* and *Urosaurus ornatus*, was studied in and near Big Bend National Park in southwestern Texas in the summers of 1958–1963 and 1966. Both species are strongly territorial and display toward trespassing members of their own species. No interspecific displays were witnessed between adults. The displays of *U. ornatus* like those of certain other iguanid lizards involve challenging pushups, lateral face-offs, and a terminal chase or fight. *S. merriami* has the same general pattern, but has elaborated it into a preliminary challenge, challenge, circle, and fight. The preliminary challenge consists of the challenging pushups of *U. ornatus* and other iguanids. The challenge is a modified pushup in which the lizard stands motionless at the peak of a pushup with its head and tail elevated and its colors fully exposed. The challenge is slowly and deliberately given in a single pushup, rather than as an extreme peak of several pushups. The circle evolved from the lateral face-off display by both lizards moving in tandem in a circle as they do pushups. The fight or chase-fight is a brief encounter in which one lizard butts the other and both fall a few feet from a boulder or canyon wall. The display in *U. ornatus* lasts only a few minutes and the chase or fight is the most active phase of the encounter, but in *S. merriami* the display may last for over 4 hours and the circle is the most active and lengthy phase of the encounter. Thus, emphasis is on the display in *S. merriami*, and such emphasis may have been favored by selection because it reduces risk from injury or predation and conserves energy.

U. ornatus appears to be polygamous during its breeding seasons, while *S.*