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CONTRIBUTIONS TO THE CONCEPTS OF REPRODUCTIVE CYCLES AND THE SYSTEMATICS OF THE *SCALARIS* GROUP OF THE LIZARD GENUS *SCELOPORUS*

Hobart M. Smith and William P. Hall¹

ABSTRACT.— The concept of parity type is proposed as a criterion of relationship among members of the *Sceloporus aeneus-scalaris* complex, with members of *S. aeneus* being regarded as viviparous and those of *S. scalaris*, as oviparous. The viviparous *S. goldmani* is regarded as a relative of *S. aeneus*, and *S. a. subniger* is not regarded as intermediate between *S. scalaris* and *S. aeneus*. The proposal by Davis and Smith that *S. a. aeneus* is oviparous and specifically distinct (as *S. aeneus*) from *S. a. bicanthalis* (as *S. bicanthalis*) is rejected. *S. aeneus* is hypothesized to have a biennial reproductive cycle. *S. scalaris slevini* auctorum is segregated into two subspecies: *S. s. samcolemani* subsp. nov. in the Sierra Oriental (northern end), and *S. s. slevini sensu stricto* in the Sierra Occidental (also northern end) of Mexico and of the adjacent United States.

The systematics and phylogenetic history of the *scalaris* group of *Sceloporus* has long been viewed as enigmatic, beginning with the statement of the quandary by Smith (1939: 347-348) in explanation of the allocation of the northwestern member, *slevini*, to the species *scalaris* despite some contrary evidence. However, Smith and Poglayen (1958: 13-15) allocated *slevini* to the species *aeneus* after another population exhibiting certain features of intermediacy between the two polytypic species *scalaris* and *aeneus* was described (*S. a. subniger*).

Neither of the preceding accounts placed any overt emphasis upon parity types. Smith (1939: 332) made a passing comment that both oviparous and "ovoviviparous" species occur in the group. Evidence now available makes it certain that members of the *scalaris* complex are oviparous, and we here postulate that members of the *aeneus* complex are viviparous (a broader term, more certainly applicable than ovoviviparity, which has come to imply absence of placental structures, whereas "euviviparity" implies their presence; both conditions exist in viviparous reptiles and only by microscopic techniques can they be determined). Anderson (1962) has demonstrated that *slevini* is oviparous, and accordingly its allocation with the *scalaris* complex is correct.

The most critical doubt cast upon this hypothesis is the proposition by Davis and Smith (1953: 102) that *S. a. aeneus* is oviparous, whereas *S. a. bicanthalis* is incontrovertibly viviparous (Smith, 1939: 356, and personal data). On this basis these taxa were elevated to specific status (*S. aeneus*, *S. bicanthalis*). The data provided in Davis and Smith, however, strongly suggest that in *S. a. aeneus* viviparity does occur, but on a two-year cycle. Ten of 28 females collected from 25 July to 15 August "contained from 3 to 5 (average 4) large ova, the largest measuring 6 x 12 mm. . . . In none . . . was there any recognizable evidence of embryonic development. . . . Many of these

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specimens were taken at an elevation of 10,000 feet. . . ." Obviously these eggs could not be laid, at that elevation, and hatch before winter or survive the winter without hatching. Almost certainly they would be carried *in utero* through the winter, the embryos developing and the young being born in the spring. Indeed, further observations in Davis and Smith support this contention: "12 of the others appeared to have oviposited and in the others (6) the ova were minute, less than 1 mm. in diameter." The logical inference is that after the young are born in spring or early summer, ova start to develop but do not reach large size until the following year, and the embryos are not ready for birth until the spring or summer after that.

We are not aware of any previous record of occurrence of a biennial reproductive cycle in lizards, although Fitch (1970) records the occurrence of biennial or triennial cycles (his opinion being that they are sometimes more properly interpreted as irregular cycles, their length being determined by environmental variables) in several species of northern snakes (*e.g.*, *Crotalus viridis*, *Vipera aspis*, and *V. berus*). Drs. Frank N. and Frieda C. Blanchard thought (personal communication) that a biennial cycle occurs in northern Michigan populations of *Thamnophis sirtalis* (Oliver, 1955: 244), and there is considerable evidence (obtained by Dr. Althea Gerrard of the Laboratory of Comparative Reproduction of the University of Colorado, under the direction of Dr. Richard Jones) that a biennial cycle occurs in populations of *Thamnophis radix* occurring at the extreme periphery of the range of the species in the foothill area near Boulder, Colorado. Reproductive cycles exceeding one year in length require, as a rule, considerable longevity, which is not ordinarily attributed to small lizards such as *Sceloporus aeneus*. Regardless of the apparent improbability of relative longevity in *S. aeneus*, a biennial viviparity does appear to occur in both subspecies of the species. Definitive investigation of this apparently unique phenomenon is of high priority.

It should be noted that although small size and probable short life (assumed on the basis of longevity records for related species: no records are available for members of the *scalaris* group of *Sceloporus*) mitigate against a biennial reproductive cycle (which might not be productive enough to offset the mortality rate), the very short season of activity and the perpetual coolness have the effect of increasing longevity. It has been amply documented that in squamatan reptiles and anurans, the members of subpolar or high-altitude populations of any species or group, subjected to cold-induced inactivity much of the year, are longer-lived and have more protracted reproductive cycles than do their more temperate or subtropical relatives, which are active most of the year and have shorter reproductive cycles. Indeed, if other lizards with biennial reproductive cycles exist, they are almost certainly high-altitude or subpolar in distribution. Andean lizards would be particularly suspect, since the reproductive cycles of the northern temperate lizards are well known and are consistently annual. However, *S. aeneus* and its viviparous rela-

tives may truly be unique in this respect: whereas most, if not all, other high-altitude lizards are conspicuously heliotherm arboreals or saxicoles, *aeneus* is secretively terrestrial and graminicolous. *S. scalaris* is equally terrestrial and graminicolous but occurs at lower altitudes and is less secretive. *S. microlepidotus* occurs at altitudes as great as *aeneus*, but it lengthens its activity period conspicuously by insolation above ground, usually on trees; and insolation on rocks would have the same effect. Thus *S. microlepidotus* and other high-altitude species of arboreal or saxicolous habits may, through extreme heliophily, so protract their activity that an annual reproductive cycle may be maintained, whereas the terrestrial, seemingly much less heliophilous, *S. aeneus* has been forced to adopt a biennial reproductive cycle to survive. Even if it were known to have a lower optimum activity temperature (not yet established) than do other sympatric species, it would not thereby necessarily escape the need for a biennial cycle; *Sphenodon*, with the lowest optimum activity temperature of any living reptile, has a protracted reproductive cycle (± 13 months), although its freedom from temperatures in the freezing range permits a more rapid development of embryos than would be possible in the strongly seasonal weather to which *S. aeneus* is exposed. *Sphenodon* in the habitat of *S. aeneus* would undoubtedly also require two years for completion of one reproductive cycle.

Although *subniger* was interpreted when described as occupying an ancestral position relative to the *scalaris* and *aeneus* complexes (Smith and Poglayen, 1958: 14), the clear evidence of intergradation between *subniger* and *a. aeneus* (and absence of such evidence for *subniger* and *scalaris*) leads to the assumption that viviparity occurs in *subniger*, conclusive evidence that it is not an ancestral member of the *scalaris* complex.

An important link in considerations of relationship and phylogeny in the *scalaris* group is *goldmani*, which possesses a mixture of derived and primitive characters. Its viviparity—indicated by the occurrence of 9 well-developed young in the uteri of the holotype and one paratype of the species (Univ. Michigan Mus. Zool. 80896 and 77266, respectively, both from Charcas, San Luis Potosí)—is critical. Obviously *goldmani* falls with the *aeneus* complex, not with the *scalaris* complex, and it seemingly constitutes the northernmost member of its complex. However, the species is known from only the hypodigm (Charcas, S. L. P.; Carneros, Coah.) localities and Ojo de Agua, Pablillo, Nuevo León (Liner and Olson, 1973: 54). One of us (Hall) has surmised that the species is a grassland inhabitant whose existence has been critically attenuated by destruction of habitat through grazing by goats. A character progression from minimal derived states in northern populations (*goldmani*) to maximal derived states in southern populations (*a. aeneus*), through the intermediate populations of *subniger* and *bicanthalis*, supports Larsen's (1973) hypothesis of a northern origin for the group.

Sympatry of the *scalaris* and *aeneus* complexes is extensive in central parts of the Mexican plateau, although to the west the *sca-*

laris complex occurs without the other. A puzzling area of overlap occurs in the northern part of the Sierra Oriental, where populations referred to *slevini* are reported from areas occupied also by *goldmani*. It appears that the *scalaris*-complex representatives of that area are isolated from their closest relatives (*scalaris slevini*) in the western Sierra Occidental, Arizona, and New Mexico (Dixon and Medica, 1965: 73). Re-examination of material from the isolated northeastern populations reveals the existence of constant differences from paratotypic *scalaris slevini* that justify recognition of a distinct taxon we here name:

Sceloporus scalaris samcolemani, subsp. nov.

HOLOTYPE.—University of Michigan Museum of Zoology (UMMZ) 124670, an adult female taken between Providencia and La Paz, Nuevo León, Mexico, by P. H. Litchfield, on 16 July 1960.

PARATYPES.—Seventeen, including the Museum of Comparative Zoology (MCZ) 133167-73, 19 mi. S junction of roads to Doctor Arroyo and San Roberto, Nuevo León, 2250 m; and MCZ field nos. Y-25063 - Y-25071, 12 mi. SSE General Cepeda, 2250 m, Coahuila. All paratypes were slit the full length of the abdomen and rather distorted in preservation, but have retained their color and pattern with little change from life. *Hypoparatypes*. Seven, including UMMZ 95220(7), from Galeana, Nuevo León (all extremely discolored, two juveniles 23 and 23.5 mm s-v), taken 12-17 July 1945, by Hellmuth Wagner.

DIAGNOSIS.—A short-legged (tibia 76-89 percent of snout-occiput length), oviparous member of the *scalaris* group of *Sceloporus* (of Smith, 1939), with essentially parallel rows of lateral scales, and two postrostrals; unique in the combination of usually (90 percent) a single canthal, dorsals 44-50, femoral pores 14-19 (66 percent 16 or more), maximum snout-vent length 51 mm, gular region barred or mottled (prominently in males, variable in females), and a consistently multicolored and patterned dorsum.

DESCRIPTION OF HOLOTYPE.—Smaller dorsal head scales moderately keeled, larger ones smooth or weakly rugose; two postrostrals; four scales between nasals, two between median frontonasal and postrostrals; median and lateral frontonasals broadly in contact with each other, median narrowly separating prefrontals and contacting frontal; frontal divided, broadly contacting interparietal; two frontoparietals on each side; three enlarged supraoculars on each side, separated from median head scales by one row of small scales, from superciliaries by two rows (except rear supraocular, separated by one row); one large subnasal and one canthal on each side; two loreals; one preocular; one subocular; 2-3 large keeled lower postoculars, three small upper ones; two rows of lorilabials ventral to loreals, one ventral to anterior half of subnasal, two ventral to posterior half; lorilabials reduced to one row over a length of 1-2 scales between subocular and labials; 3½ supralabials to below middle of eye.

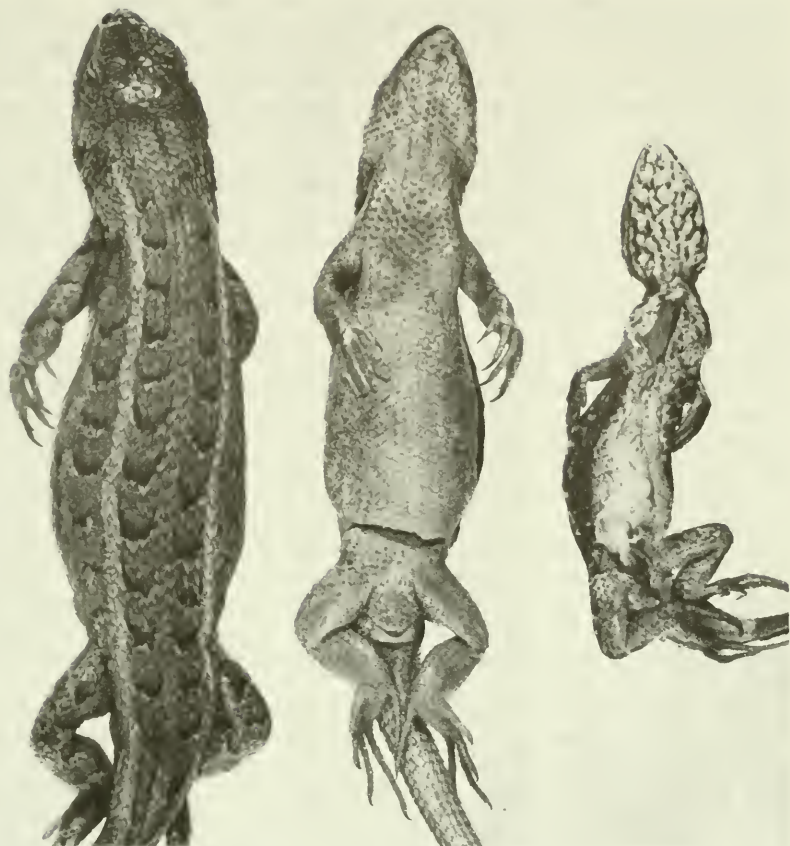


Fig. 1. Dorsal (left) and ventral (center) views of the holotype of *Sceloporus scalaris samcolemani*, UMMZ 124670, 51 mm SVL. Right, ventral view of a male paratype of same, MCZ Y-25066, 41 mm SVL.

Five infralabials; 3-4 pairs of chinshields, scales of anterior pair in medial contact, 2 scales between those of 2nd pair; labimentals not reaching mental; one large medial auricular lobule; 6 scales between upper enlarged postocular and ear opening.

Dorsal scales 47 from interparietal to base of tail; 44 ventrals from shoulder level to anus; 44 scales around middle of body; 17-17 femoral pores, the two series in medial contact; dorsal scales straight sided, with a strong medial keel, a short medial mucrone, one or no denticule/scale, no lateral mucrones. All ventral scales smooth; lamellar formula for toes 7-11-13-18-12 (7-11-14-18-13).

Snout-vent length 51 mm; tail 62 mm; snout to occiput, 10.2 mm; hind leg 25 mm; tibia 8.6 mm.

Color a brownish slate gray above, browner on head; a dorso-lateral light line on each side, largely on one scale row, separated by nine scale rows; ten U-shaped markings between shoulders and base of tail, dark-edged and light bordered to the rear, in each of two rows between dorsolateral light lines, separated medially by a space half as wide as markings; a row of similar marks lateral to dorso-lateral light line, bordered laterally by a very faint lateral line; a row of dark dots corresponding in position to the other dark markings, lateral to lateral light line. Ventral surfaces whitish, with scattered gray pigment near chin, on chest, in preanal area and on ventral surfaces of the thigh.

Large, well-developed eggs in the uteri, with no evidence of developing young.

VARIATION.—In the entire hypodigm, the dorsals vary from 44 to 50 (22: 44, six; 45, three; 46, four; 47, six; 48, two; 50, one), mean 46.1; ventrals 36-49 (14: 39, one; 40, one; 42, one; 43, two; 44, five; 45, two; 48, one; 49, one), mean 43.9; scales around mid-body 38-49 (17: 38, one; 39, one; 41, one; 42, three; 43, two; 44, five; 45, two; 47, one; 49, one), mean 43.3; femoral pores 14-19 (41: 14, eight; 15, six; 16, seven; 17, sixteen; 18, two; 19, two), mean 16.2. Scales between femoral pore series 0-1 (none, 11; one, 8); scales between second pair of postmentals 1-3 (1, four; 2, nineteen; 3, one); canthals 1-2 (1, forty-three; 2, five); snout-vent lengths 23-51 mm (23, 23.5, 36, 37(2), 38(2), 40(2), 41(2), 42(4), 43, 44, 45, 45.5, 47(3), 49, 51); tibia/snout-occiput ratio 76-88.8, mean (22) 81.25.

The dorsal pattern in all paratypes is much like that of the holotype, but the ventral markings are more prominent in some females and are conspicuous in males. In males the sides of the abdomen are dark blue, with no darker medial border but with scattered scales and white and irregular borders of scales black. No dark streaks traverse the blue patches. The gular region is conspicuously black-mottled or barred. Some females possess a vestige of the lateral abdominal patches, even with scattered light scales, but the color is gray rather than blue. The gular region is also weakly barred or mottled in some females.

COMPARISONS.—*Sceloporus scalaris slevini* is clearly the taxon that resembles *S. s. colemani* most closely—and indeed is the one with which the latter has long been united. *S. s. samcolemani* is markedly different, however, in having gular bars, in being consistently multicolored above, and in having dorsals 44 or more (100 percent in 22), femoral pores usually (66 percent in 41) 16 or more, and s-v length not exceeding 51 mm. In *S. s. slevini* no gular markings are present, the dorsal pattern is frequently unicolor, the dorsals are usually 43 or fewer (84 percent in 44), the femoral pores usually 15 or fewer (92 percent in 88), and the s-v length frequently exceeds 51 mm (13 in a total of 44 measured), reaching 61 mm. The complete absence of the unicolor phase in *S. s. samcolemani* is of course not a certainty, but that phase is so common in *S. s. slevini*

and *S. s. scalaris* (no precise figures available) that the frequency in *S. s. samcolemani* is assuredly of a much lesser order, since 24 do not exhibit it.

The single canthal character-state of *S. s. samcolemani* is shared with *S. s. unicanthalis* as well as with *S. s. slevini*, but *S. s. unicanthalis* is distinctive in usually having the scales of the second pair of postmentals in contact, whereas they are separated by one to three small scales in the other two subspecies. In addition, *S. s. unicanthalis* has a longer tibia and larger dorsals and reaches a larger size than either *S. s. slevini* or *S. s. samcolemani*.

REMARKS.—The southern limit of the range of *S. s. samcolemani* does not reach as far as 12 mi. SW Ahuacatlán, or Ciudad Maíz, both in San Luis Potosí, whence specimens typical of *S. s. scalaris* (UMMZ 126228, Univ. Illinois Mus. Nat. Hist. 21512, respectively) are available. These have 2-2 canthals; 44 and 35 dorsals, 16-19 and

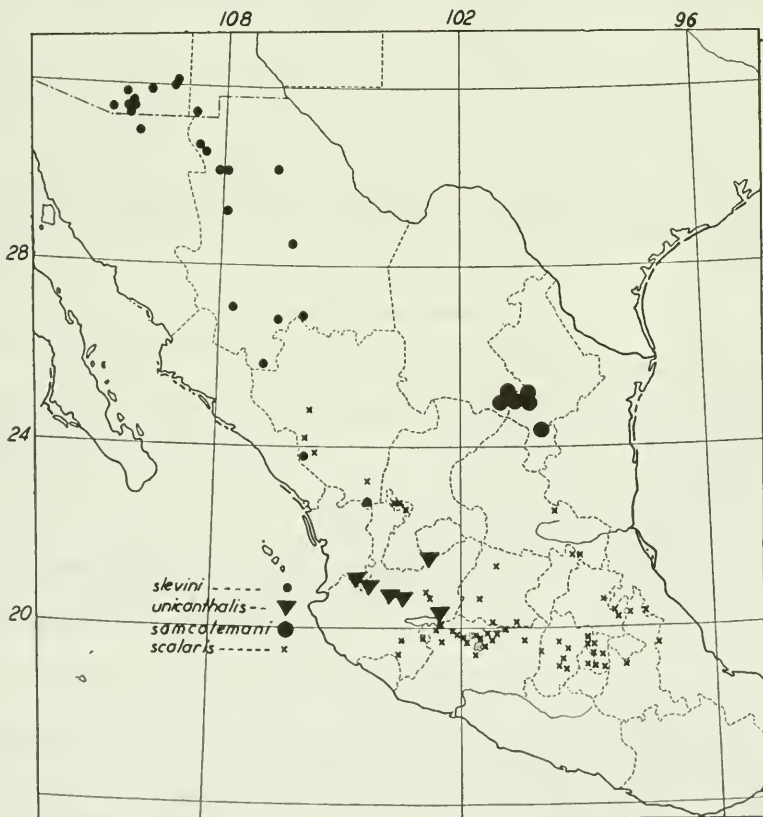


Fig. 2. Distribution of the subspecies of *Sceloporus scalaris*. Localities as given in text for *S. c. samcolemani*, from the literature and museum lists for others: especially Duellman (1961) for Michoacán, Dixon et al. (1972) for Querétaro, and Drake (1950) for Durango records of *S. s. scalaris*, and Grant and Smith (1960: 40) for an Jalisco record of *S. s. unicanthalis*.

14-15 femoral pores, respectively; and s-v measurements of 58 ♂ and 53 ♀ mm, respectively. The female is unicolor above; the male has faint dark gular bars. The female has the smallest dorsal count of any recorded specimen; Smith (1939:347) records counts no lower than 37.

The type series of 24 specimens includes 16 adult females, all with large eggs in the uteri, none showing evidence of embryonic development. In view of the lower altitude and longer season for activity than in *S. aeneus*, the early-middle July dates suggest ample time for egg deposition and hatching later the same year. Apparently, therefore, the population is oviparous and on that basis as well as pattern seems properly allocated with *S. scalaris* rather than with *S. aeneus*.

Localities other than those represented by the hypodigm include Hda. Pablillo, above Galeana, Nuevo León (Smith, 1939:349), the Gomez Farias region, Tamaulipas (Martin, 1955: 173); and Cedritos, Coah. (Amer. Mus. Nat. Hist. 77245).

The subspecies is named for Dr. Sam Coleman, who wrote the programs for processing the enormous quantity of data pertaining to the herpetology of Mexico and who thereby has contributed far more to a synopsis of Mexican herpetology than he realizes.

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