

THE SCLERAL OSSICLES OF SCELOPORINE IGUANIDS: A REEXAMINATION WITH COMMENTS ON THEIR PHYLOGENETIC SIGNIFICANCE

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ABSTRACT: A reexamination of the scleral ossicles of sceloporine iguanids was undertaken after conflicting data sets were discovered in the literature. The scleral ossicles of certain other iguanids were also studied for comparative purposes. Sceloporines exhibit much greater variation in ossicle configuration than has previously been reported. This variation is often too great within genera and species to provide useful characters for inferring intergeneric relationships, although a few derived characters do suggest monophyletic groupings of genera. A large number of iguanids exhibit an ossicle arrangement in which there are 14 ossicles of approximately equal size in each eye; three positive and three negative ossicles occupy the same positions in the scleral rings of all these iguanids. This condition is thought to be either the direct or indirect precursor to all patterns of ossicle configuration seen in sceloporines. These patterns seem to have been derived from their presumed precursor by both reductions and losses of ossicles in the dorsal portion of the ring.

Key words: Eye; Homology; Iguanidae; Phylogeny; Sceloporines; Scleral ossicles

THE outermost sheath of the vertebrate eye is the scleroid coat or sclera, which is composed primarily of fibrous connective tissue and functions to preserve the shape of the eyeball. In many vertebrates, this function is enhanced by a ring of small bones lying within the scleroid coat, the scleral ossicles (Romer, 1970). Among living reptiles, these ossicles are known to occur in turtles, most lizards, some amphisbaenians, and *Sphenodon*, but they are absent in snakes and crocodilians. Scleral ossicles are also known from various extinct reptiles, including certain crocodilians (Romer, 1956; Underwood, 1970). The scleral ossicles of lizards are thin, sigmoidally flexed plates that overlap one another in a fashion resembling the leaves of a camera's iris diaphragm. The number of ossicles in lizards varies from 6–40 in a single eye, with 10–17 being most common (Underwood, 1970).

Gugg (1939) proposed a standardized method for counting and numbering the individual ossicles. He defined three types of ossicles on the basis of their pattern of overlap with adjacent ossicles (Fig. 1 below). When viewed from the corneal aspect, positive ossicles overlap

their neighbors on either side; negative ossicles are overlapped by their neighbors on either side; and halfway (or imbricating) ossicles overlap ossicles on one side but are overlapped by ossicles on the other side. The positive ossicle in the temporoventral corner of the eye is designated as number 1, and consecutive ossicles are numbered up the temporal side of the eye and down the nasal side. Underwood (1970) modified this convention slightly so that only the ossicles immediately adjacent to the ossicle in question are taken into consideration when scoring an ossicle as positive, negative, or imbricating. In addition, he noted that certain lizards have ossicles with S-shaped margins and mutual overlap between two adjacent ossicles. In such cases, the overlap nearer the corneal end is scored.

Using Underwood's (1970) modified system of scoring, Presch (1970) described the scleral ossicles of the sceloporine lizards (family Iguanidae; see Etheridge, 1964; Presch, 1969). He divided the sceloporines into two groups based on the configuration of their scleral ossicles. Members of Group 1 (*Sceloporus*, *Sator*, *Urosaurus*, *Uta*, and *Petrosaurus*)

have a total of 14 ossicles in each eye. Numbers 1, 6, and 8 are positive; numbers 4, 7, and 10 are negative; and the remainder are imbricating (as in Fig. 1A below).

Members of Presch's Group 2 are *Phrynosoma*, *Uma*, *Callisaurus*, and *Holbrookia* (including *Cophosaurus texanus*). They were reported to have 12 scleral ossicles in each eye. Presch divided this group into two subgroups. Members of Group 2B (*Phrynosoma*) were stated to differ from those of Group 2A (*Uma*, *Callisaurus*, and *Holbrookia*) in that the eighth ossicle of the former is overlapped by the ninth but fails to reach the edge of the seventh. In Group 2A, the eighth ossicle was reported to extend beyond the edges of both immediately adjacent ossicles and to be negative. In Group 2A, ossicles 1, 5, and 7 were said to be positive; 4, 6, and 8 were said to be negative.

While practicing the technique of exposing the scleral ossicles, I noticed an ossicle arrangement in *Uma* different from that reported by Presch (1970). The number and configuration of scleral ossicles reported for various sceloporines by Presch (1970) are similarly incongruent with reports on the same taxa by Underwood (1970). Prompted by these apparent inconsistencies, I have undertaken a reexamination of the scleral ossicles in sceloporus lizards. This reexamination has also resulted in a reassessment of the significance of the different configurations of these ossicles in attempts to reconstruct sceloporus phylogeny.

MATERIALS AND METHODS

I employed two methods for obtaining intact scleral rings that had been partially freed of associated tissues. Some scleral rings were obtained from skeletons cleaned by dermestid beetles; most, however, were removed from wet specimens. Longitudinal incisions were made anteriorly and posteriorly from the nasal

and temporal corners of the eye, respectively. The skin was then peeled back and the eyeball removed. The orbital hemisphere of the eyeball was cut away, and much of the remaining tissue was removed with fine forceps. By leaving some of the tissue on the orbital surface of the scleral ring intact, the ring was less likely to disarticulate upon further processing.

After the ossicles were partially freed of associated tissues by either of the methods described above, they were immersed in 5% sodium hypochlorite (bleach) for 20–30 s to remove additional tissue. The action of the sodium hypochlorite was arrested by immersion in 95% ethanol.

The techniques described above have certain drawbacks. Identification of ossicle number 1 depends in part upon its location in the intact eye. The techniques used in this study preclude determination of the orientation of individual ossicles as they would appear in the intact eye. Only the spatial relationships of the ossicles to one another were studied. The configuration of the ossicles, however, is conservative enough that ossicle number 1 can be determined by the pattern of overlap alone. Whether or not the entire ring has been rotated was not determined. The number and overlap pattern of the ossicles are described using Gugg's (1939) conventions as modified by Underwood (1970).

Representatives of all genera of sceloporus lizards and certain members of other iguanid groups (Etheridge, reproduced in Paull et al., 1976) were examined using the above techniques. Because members of the sand lizard group (Smith, 1946) exhibited a high degree of variation in ossicle pattern, all species in this group of related genera (Etheridge, 1964) were examined. The genus *Sator* is here regarded as a member of *Sceloporus*, following Wyles and Gorman (1978). Generic nomenclature for sand lizards follows Clarke (1965) for

ease of discussion, though his classification is regarded by some as oversplit (Adest, 1978; Wyles and Gorman, 1978).

In order to be able to infer genealogical relationships based upon the distributions of particular features of the scleral ossicles among the sceloporine taxa, something must be known about the probable pathways of evolutionary change in various characteristics of these ossicles. In order to make such evolutionary inferences, I have relied solely on the method of outgroup comparison, in which the condition of a variable character in the sceloporines that is found in the majority of closely related taxa is inferred as being primitive for the sceloporines. Only shared, derived characters (synapomorphies) are taken to be indicative of close genealogical relationship (Hennig, 1966).

Although the numbering system used here provides an unambiguous method for describing the number and pattern of ossicles in a scleral ring, ossicles of the same number in rings that differ in total ossicle number are not necessarily homologous. A second numbering system is used to indicate homologies between ossicles in different rings: individual ossicles are numbered to indicate their presumed homologies with ossicles in rings containing 14 ossicles numbered according to the first system. Homology between ossicles in different rings is inferred by assuming (1) a consistent pattern of overlap in all rings, and (2) that ossicles in a state of reduction are more likely to be lost than those that are not reduced.

RESULTS

This study revealed nine patterns in the scleral rings of sceloporines and other iguanid lizards (see also Underwood, 1970). These patterns are as follows:

Pattern A.—14 ossicles: 1, 6, 8 positive; 4, 7, 10 negative; all ossicles contribute to the corneal margin of the ring (Fig. 1A).

Pattern B.—14 ossicles: 1, 6, 8 positive; 4, 7, 10 negative; number 8 reduced so as not to reach the corneal margin (Fig. 1B).

Pattern C.—14 ossicles: 1, 6, 8 positive; 4, 7, 10 negative; ossicles 6 and 8 reduced so as not to reach the corneal margin (Fig. 1C).

Pattern D.—14 ossicles: 1, 6, 8 positive; 4, 7, 10 negative; numbers 6, 8, and 9 reduced so as to be excluded from the corneal margin. Number 8 is usually the smallest, followed by 6, then 9 (Fig. 1D).

Pattern E.—13 ossicles: 1, 6, 8 positive; 4, 7, 9 negative; 6 and 8 reduced so as not to reach the corneal margin. Number 6 is smaller than 8 (Fig. 2A).

Pattern F.—13 ossicles: 1, 5, 7 positive; 4, 6, 9 negative; 7 reduced so as to be excluded from the corneal margin (Fig. 2B).

Pattern G.—13 ossicles: 1, 5, 7 positive; 4, 6, 9 negative; neither 7 nor 8 reaches the corneal margin. Number 7 is smaller than number 8 (Fig. 2C).

Pattern H.—12 ossicles: 1, 5, 7 positive; 4, 6, 8 negative; all reach the corneal margin (Fig. 2D).

Pattern I.—12 ossicles: 1, 5, 7 positive; 4, 6, 8 negative; 7 reduced and excluded from the corneal margin (Fig. 2E).

The distribution of these ossicle patterns in various sceloporine taxa is presented in Table 1.

Using the modal number of eyes for each taxon, the sceloporine taxa in Table 1 can be characterized by ossicle pattern as follows: pattern B: *Petrosaurus*, *Sceloporus*, *Urosaurus*, and *Uta*; pattern C: *Cophosaurus*; pattern D: *Callisaurus*, *Uma notata* (including races formerly recognized as *U. inornata*, *U. notata*, and *U. scoparia* now included within a single species [Adest, 1977; Zalusky et al., 1980]), and *U. paraphygas*; pattern F: *Holbrookia maculata*; pattern H: *Holbrookia lacerata* and *H. propinqua*; pattern I: *Phrynosoma* and *Uma exsul*. None of these taxa exhibits a statistical mode for ossicle pattern A, E, or G, although pattern A is the most common pattern in iguanids other than sceloporines and is

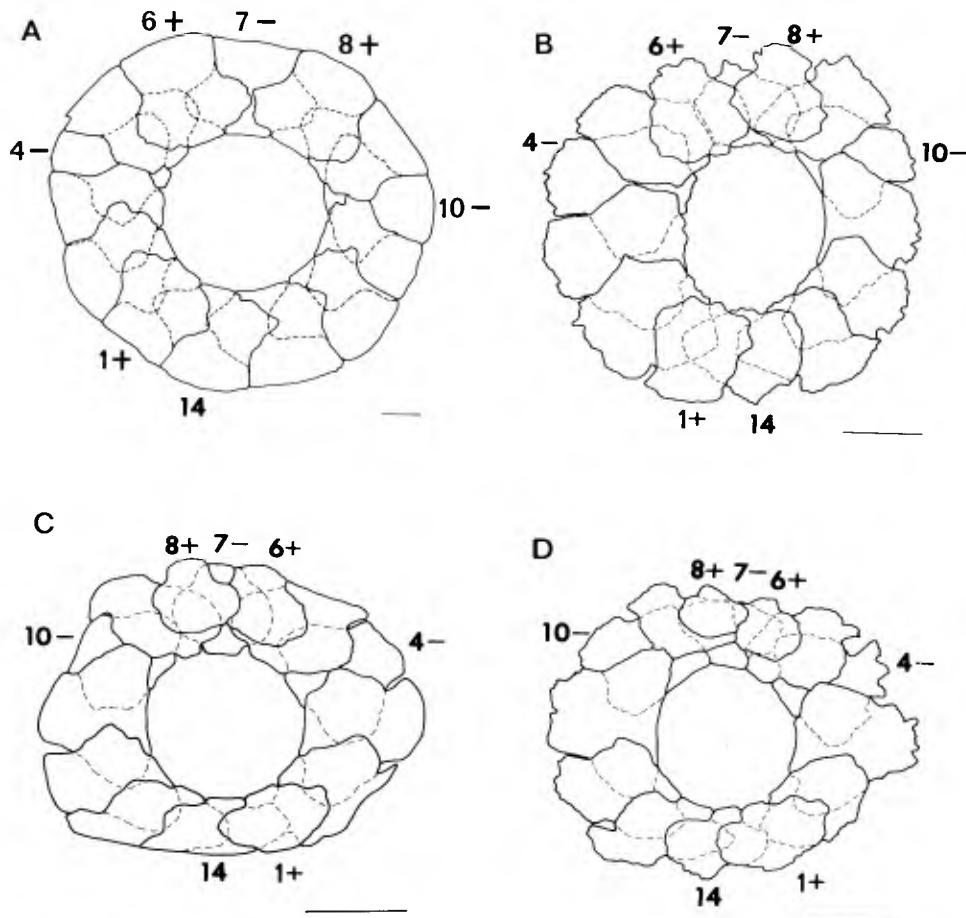


FIG. 1.—Patterns of ossicle configuration: (A) right scleral ring of *Chamaeleolis chamaeleonides* (SDSU 488); (B) right scleral ring of *Sceloporus orcutti* (CKD 53); (C) left scleral ring of *Cophosaurus texanus* (SDNHM 15422); (D) left scleral ring of *Callisaurus draconoides* (CKD 36). Individual ossicles are numbered to indicate relative position and total number. Ossicles of the same number in different rings are presumed to be homologous. Except for the final ossicle, only positive and negative ossicles are numbered. Scale equals 1 mm.

known to occur in a number of other lizard families (Underwood, 1970).

The ossicles in the sceloporine scleral ring are noticeably unequal in size (Fig. 1B–1D; Fig. 2A–2E). Ossicles 3 and 11, and to a lesser extent the ossicles immediately adjacent to them, are larger than those removed by 90° from them. In many iguanids (anolines, basiliscines, iguanines, and morunasaurines), all the ossicles of the ring are of approximately equal size (Fig. 1A), though ossicle 11

sometimes exhibits slight enlargement. In others (crotaphytines and tropidurines), a condition resembling that of sceloporines is evident. In general, arboreal species have larger scleral ossicles for a given body size, and more even scleral rings (Fig. 1A). These species also have relatively larger eyes.

DISCUSSION

The findings of this study indicate much more variation in the configuration

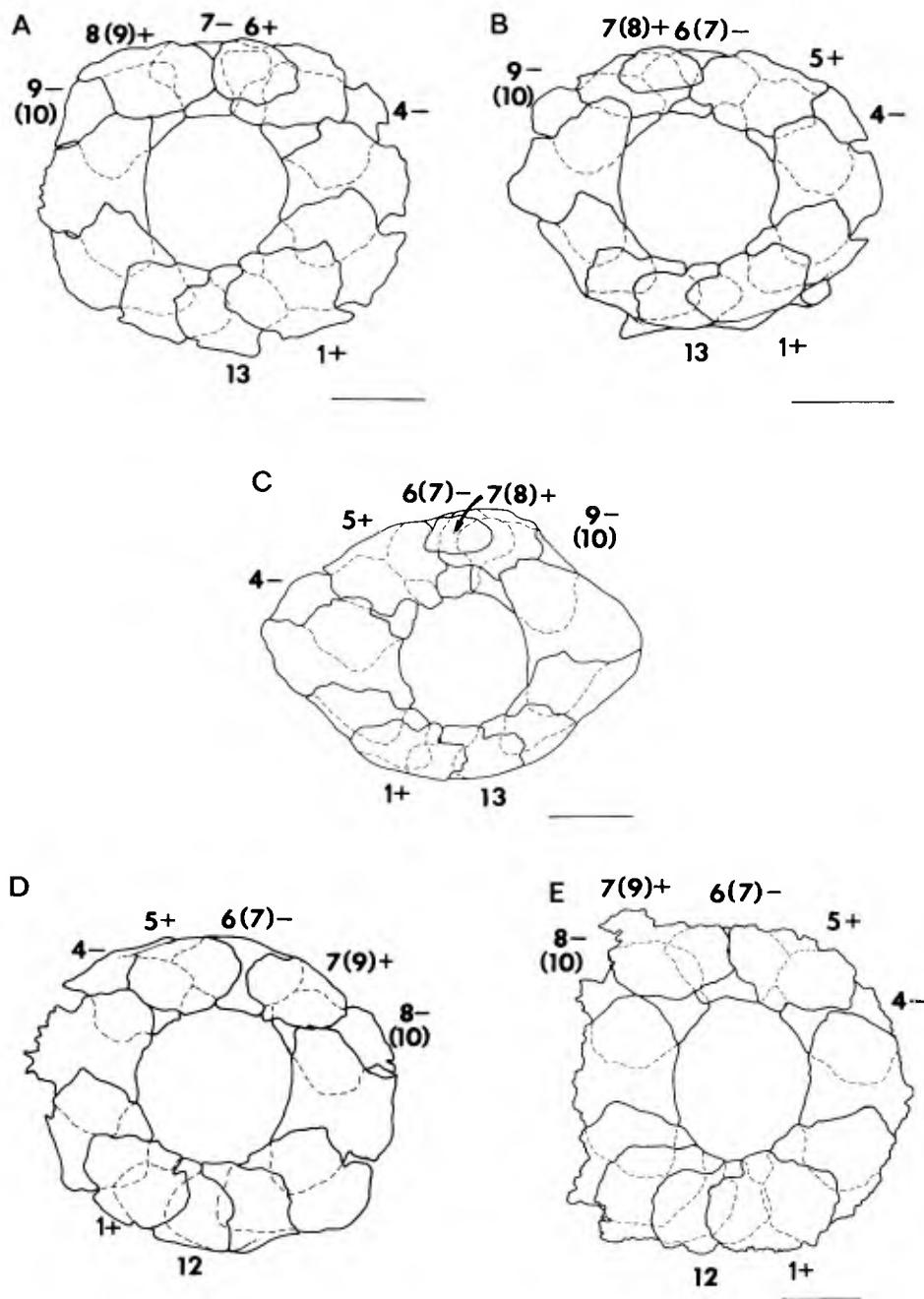


FIG. 2.—Patterns of ossicle configuration: (A) left scleral ring of *Callisaurus draconoides* (CKD 24); (B) left scleral ring of *Holbrookia maculata* (SDNHM 35994); (C) right scleral ring of *Uma exsul* (CU 10163); (D) right scleral ring of *Holbrookia lacerata* (UCLA 1842); (E) left scleral ring of *Phrynosoma coronatum* (CKD 13). Individual ossicles are numbered to indicate relative position and total number as in Fig. 1 (nonparenthetical), and to indicate presumed homologies with ossicles in rings with 14 ossicles where these numbers differ from the former (parenthetical). Except for the final ossicle, only positive and negative ossicles are numbered. Scale equals 1 mm.

TABLE 1.—The distribution of ossicle patterns in sceloporine taxa. Numbers under the different patterns are expressed as the percentage of the total number of eyes examined for the taxon.

Taxon	Ossicle pattern								No. eyes	No. ind.	
	A	B	C	D	E	F	G	H			
<i>Callisaurus draconoides</i> ^a				75%	13%				8	4	
<i>Cophosaurus texanus</i>		100%							12	6	
<i>Holbrookia lacerata</i>							100%		6	4	
<i>Holbrookia maculata</i>			10%			50%	20%	20%	10	5	
<i>Holbrookia propinqua</i>				8%			17% ^b	75%	12	7	
<i>Petrosaurus</i> (2 species) ^c	80%								5	3	
<i>Phrynosoma</i> (7 species)							8% ^d	92%	26	13	
<i>Sceloporus</i> (5 species) ^e	100%								13	7	
<i>Uma exsul</i>			13%				19%		69%	16	8
<i>Uma notata</i> ^f			13%	81%	6%				16	9	
<i>Uma parphygas</i>				86%	14%				14	7	
<i>Urosaurus</i> (4 species)	100%								12	7	
<i>Uta stansburiana</i>	100%								5	3	
Most other iguanids	X										

^a One ring (13%) contained 15 ossicles; a small supernumerary ossicle was positive to 6 and 8.

^b In this specimen both eyes contained 13 ossicles, but number 7 was extremely small in both.

^c One eye (20%) had a small supernumerary ossicle positive to 7 and 8.

^d In this specimen of *P. m'calli* there appears to have been a doubling of ossicle 7 so that ossicle number 8 here is not homologous with number 8 in other *Phrynosoma* scleral rings.

^e Includes members of four species groups (Guillette et al., 1980; Smith, 1939) if *Sator* is considered a member of the *utiformis* group.

^f Includes members of populations formerly regarded as three distinct species: *U. inornata*, *U. notata*, and *U. scoparia*.

of the scleral ossicles in sceloporines than has been reported previously. Presch (1970) reported the presence of three ossicle patterns in sceloporines, one of which could not be confirmed in the present study. I found eight patterns, of which six (patterns B, C, D, F, H, and I) appear to be characteristic of taxa or groups of taxa, and two (patterns E and G) appear to be less frequent variants. Underwood (1970) noted some of this variation, but his study was more inclusive taxonomically, prohibiting a detailed examination of the sceloporines.

My findings also differ with certain of those reported by Presch (1970). According to Presch, the scleral ring of *Phrynosoma* is incomplete, owing to lack of overlap between ossicles 7 and 8. I have not been able to confirm this observation despite examining 26 scleral rings of seven species of *Phrynosoma* (see Fig. 2E), six of which were examined also by Presch. His observations seem to be in error.

Presch (1970) also reported that the scleral rings of *Callisaurus*, *Holbrookia* (including *Cophosaurus texanus*), and

Uma contained 12 ossicles. My findings indicate that *Uma exsul* is characterized by 12 ossicles, but the modal number of ossicles for *Callisaurus*, *Cophosaurus*, *Uma notata*, and *U. parphygas* is greater than 12. Although individuals of all three species of *Holbrookia* may possess only 12 ossicles per eye, the only species that can be characterized by this number are *H. lacerata* and *H. propinqua*, neither of which Presch examined.

Presch (1970) also noted that Gugg (1939) reported different patterns of ossicle overlap in *Phrynosoma cornutum* and *P. orbiculare*, the latter having only two positive ossicles. From Gugg's detailed description of the overlap of individual ossicles (Gugg, 1939:363), it is apparent that *P. orbiculare* exhibits the same ossicle pattern as the *Phrynosoma* examined in this study and the *P. cornutum* examined by him. The reported difference results merely from Gugg's consideration of ossicles other than those immediately adjacent to the ossicle in question in his scoring system.

As is evident from the large number of ossicle patterns seen in sceloporines,

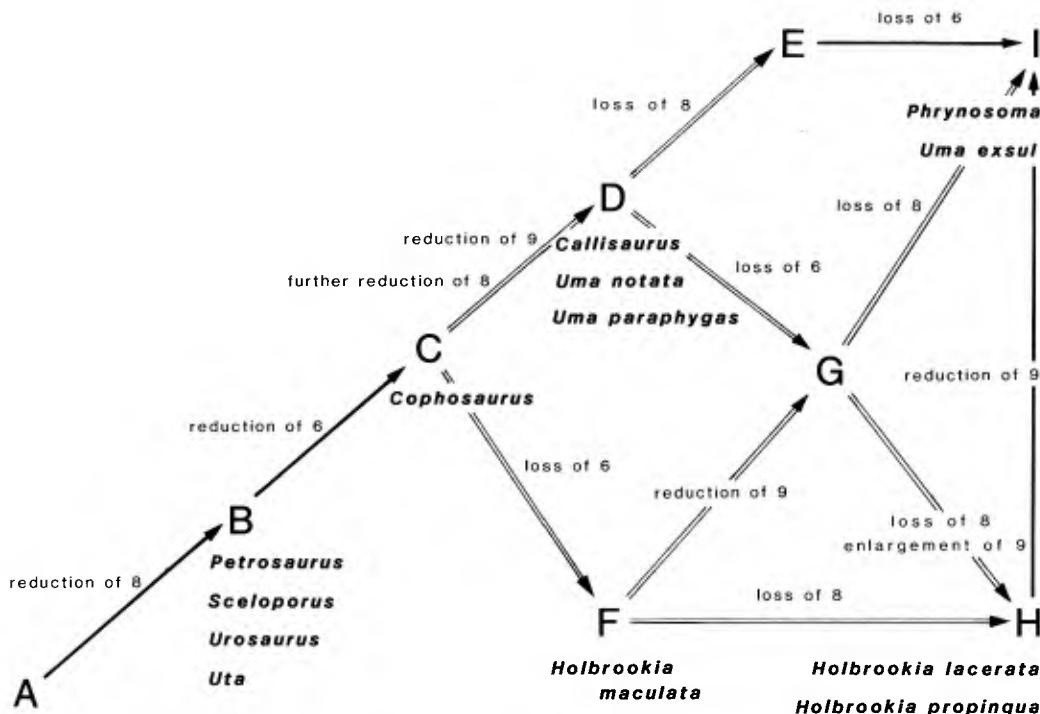


FIG. 3.—Hypothetical evolutionary scheme for patterns of scleral ossicle configuration in sceloporines (see Figs. 1 and 2). Sceloprine taxa are listed under the ossicle pattern for which they exhibit a statistical mode. A double line signifies that the evolutionary step is supported by variation within taxa (Table 1). This scheme of character evolution is not to be interpreted as a phylogeny for the taxa, because convergence in ossicle pattern probably occurs in certain cases. Here each ossicle number refers to the number of the homologous ossicle in the 14-ossicle ring.

evolution has been relatively rapid in this character complex when compared with the rest of the family Iguanidae, nearly all of which possess pattern A. Because ossicle pattern A is widespread in the Iguanidae and is known to occur in other lizard families, I regard this pattern as primitive for the Iguanidae and the precursor to those arrangements occurring in sceloporines. Furthermore, all patterns seen in sceloporines are derivable from pattern A by simple reduction or loss of ossicles in the dorsal portion of the scleral ring.

Figure 3 gives a hypothetical character phylogeny for the different ossicle patterns found in sceloprine iguanids. The evolutionary steps in this figure are intended to be the simplest changes re-

quired to derive one ossicle pattern from another. Variation in ossicle pattern within taxa (Table 1) supports some of these steps (D-E, C-F, F-G, G-H, F-H, D-G, G-I, and C-D), but not others.

Inequality in ossicle size within a scleral ring may be a necessary precursor to the loss of ossicles 6 and 8 in sceloporines. Scleral rings with relatively small ossicles in their dorsal series exhibit greater overlap between ossicles that are not immediate neighbors than do more even rings: compare ossicles 5, 7, and 9 in Fig. 1B-1D with the same ossicles in Fig. 1A. Thus, when ossicle 6 or 8 is lost, the continuity of the ring is preserved, and ossicle 5 or 9, respectively, changes from imbricating to positive.

The hypothetical character phylogeny

(Fig. 3) illustrates some of the ambiguities in the interpretation of character evolution caused by ossicle loss. For example, pattern G seems to be as easily derived from pattern D as from pattern F, and may have been derived from each on different occasions.

This study was initially undertaken with the hope of revealing characters that would be useful for determining phylogenetic relationships among the sceloporine genera. The high degree of variability in ossicle pattern within genera and species precludes the use of much of the variation for such a purpose. Certain conservative statements, however, can be made. All sceloporines are united by the apomorphic reduction (or loss) of ossicle 8 so that this ossicle does not reach the corneal margin of the scleral ring. The sand lizards (*Callisaurus*, *Cophosaurus*, *Holbrookia*, and *Uma*) and *Phrynosoma* share the additional apomorphic reduction (or loss) of ossicle 6. All species of *Holbrookia* are united by the loss of ossicle 6 without reduction of ossicle 9, and *H. lacerata* and *H. propinqua* share the additional apomorphic loss of ossicle 8. The unique ossicle configuration of *Callisaurus*, *Uma notata*, and *U. parvipes* (the pattern in *U. exsul* can be derived from this configuration) suggests a close genealogical relationship between these two genera. This relationship, however, is not supported by the distribution of derived characters in ear morphology and in protein variation studied with electrophoresis (personal observation). For a similar reason, I interpret the common condition of loss of ossicles 6 and 8 with reduction of the ossicle homologous with the original number 9 (now number 7) in *Phrynosoma* and *Uma exsul* as convergent.

Some features of the scleral ossicles are also suggestive of higher level relationships within the Iguanidae. The crotaphytines, tropidurines, and sceloporines exhibit a similar pattern of inequality in ossicle size. Etheridge (1964, see also his phylogeny reproduced in Paull et al.,

1976) has suggested a close relationship among these groups on the basis of other characters. Although these findings are suggestive, they should not be used as evidence for the relationship mentioned above until the tropidurines and the remainder of the family have been more thoroughly sampled. Furthermore, a similar pattern of inequality in ossicle size is seen in certain distantly related lizards (e.g., *Chamaesaura*, a cordylid; personal observation) where the similarity must be attributed to convergence.

A Note on the Scleral Ossicles of Other Iguanids

Underwood (1970) summarized data on scleral ossicle arrangement in reptiles. His Table 1 (pp. 26–27) lists the following iguanid genera as having a scleral ring consisting of 14 ossicles with numbers 1, 6, and 8 positive, and numbers 4, 7, and 10 negative: *Anolis*, *Aptycholaemus*, *Basiliscus*, *Callisaurus*, *Chalarodon*, *Crotaphytus*, *Cyclura*, *Holbrookia* (2 species), *Iguana*, *Laemancus*, *Liolae-mus*, *Oplurus*, *Petrosaurus*, *Phymaturus*, *Sceloporus* (2 species), *Urosaurus* (2 species), and *Uta*. To this list I now add: *Amblyrhynchus*, *Anisolepis*, *Brachylophus*, *Chamaeleolis*, *Conolophus* (2 species), *Ctenosaura* (3 species), *Dipsosaurus*, *Enyalius* (3 species), *Gambelia*, *Morunasaurus*, *Sauromalus* (5 species), and *Tropidurus*. One species in each genus has been examined unless otherwise indicated. All of the genera newly added to the list exhibit ossicle pattern A, in which all of the ossicles reach the corneal margin of the ring. Occasional variants were detected, but the modal number of ossicles was 14 in all genera mentioned except *Amblyrhynchus*. In *Amblyrhynchus*, 2 of 4 individuals examined had fewer than 14 ossicles in each eye. These two individuals were siblings hatched in captivity and may be exceptional.

Two other genera require further consideration. Gugg (1939) reported 15 scleral ossicles in *Polychrus*. I have examined 8 eyes representing 6 individuals and 2

species of *Polychrus*, including *P. marmoratus*, the species that Gugg examined. All have the ossicle arrangement described here as pattern A. Gugg examined only two eyes of *Polychrus*, and his Fig. 18 (p. 362) shows mutual overlap between ossicles 1 and 2. Judging from the pattern of overlap, the additional ossicle lies within the range of ossicles from 1 to 4. It appears that Gugg examined an anomalous individual in which ossicle 1 had been doubled. I have observed similar apparent doublings on occasion in other iguanids.

Underwood (1970) reported 13 ossicles in the scleral ring of *Corythophanes* which, based on the ossicles designated as positive and negative, seems to be a modification of ossicle pattern A by loss of either ossicle 8 or 9. I have examined 11 eyes from 8 individuals representing 2 species of *Corythophanes*. One of these had a scleral ring with 13 ossicles, but the overlap pattern indicates that this condition was reached by loss of ossicle 5 or 6 rather than 8 or 9. The remaining 10 eyes had 14 ossicles arranged in the typical A pattern. Underwood examined only two eyes, which appear to have been atypical. My observations indicate that aberrant scleral rings are not uncommon in iguanids. Variants apparently derived from other patterns by loss of ossicles, fusion of ossicles, doubling of ossicles, and the addition of small supernumerary ossicles to the outside of the ring (positive ossicles) have all been observed.

Specimens Examined

Nonstandard abbreviations: CKD—Collection of Kevin de Queiroz; SDSU—San Diego State University (Collection of Richard Etheridge); UCLA—University of California, Los Angeles.

Anolines: *Anisolepis undulatus* SDSU 1952; *Anolis equestris* SDSU 448; *Anolis eugenegrahami* SDSU uncataloged; *Chamaeleolis chamaeleonides* SDSU 488; *Enyalius bilineatus* SDSU 1958; *Enyalius brasiliensis* SDSU 1960; *Enyalius iheringi* SDSU 1959; *Polychrus marmoratus* AMNH 72819, 116251, MCZ 8255, SDSU 987; *Polychrus gutturosus* MCZ 77401, SDSU 988.

Basiliscines: *Basiliscus basiliscus* CRE 1577, 1583–4; *Basiliscus plumifrons* SDNHM 57098–100,

59467, SDSU 427, 2014; *Corythophanes cristatus* AMNH 75201, 75203, CKD 55, CRE 1701, MCZ 38841, SDSU 1800; *Corythophanes hernandesii* MCZ 53872; *Corythophanes* sp. CKD 10.

Crotaphytines: *Crotaphytus collaris* SDNHM 29122; *Crotaphytus insularis* SDNHM 60109; *Gambeliasila* CKD 35, 38.

Iguanines: *Amblyrhynchus cristatus* SDNHM 45156–7, 47000, SDSU 338; *Brachylophus fasciatus* SDNHM 55289, 55601, 55603; *Conolophus pallidus* CRE 214, SDSU 439; *Conolophus subcristatus* SDNHM 33682; *Ctenosaura acanthura* SDNHM 59542–3; *Ctenosaura hemilopha* SDNHM 48480, 48976; *Ctenosaura pectinata* CRE 696, 704, 1252, SDNHM 55291; *Cyclura cyclura* CKD 47–8; *Cyclura cornuta* SDSU 383, 1841; *Cyclura nubila* SDNHM 42957, 42960; *Cyclura* sp. CRE 269; *Dipsosaurus dorsalis* CKD 22, 41–2, 44–5, SDNHM 57107–9, 59538–9; *Iguana delicatissima* CKD 21; *Iguana iguana* CKD 40, CRE 1545, 1553, SDNHM 59540–1, SDSU 489; *Sauromalus ater* CKD 68–9, SDNHM 6865; *Sauromalus australis* CKD 71–2; *Sauromalus hispidus* CRE 172–3, 436, 915; *Sauromalus obesus* CKD 33, 51, SDNHM 48483, SDSU 244; *Sauromalus varius* CRE 175, 248, SDSU 451.

Morunasaurines: *Enyalioides o'shaughnessyi* SDNHM 1957; *Morunasaurus annularis* SDSU 1956.

Sceloporines: *Callisaurus draconoides* CKD 23–4, 36, SDSU uncataloged; *Cophosaurus texanus* SDNHM 15422, 15427, 29135, 40252–3, SDSU 1528; *Holbrookia lacerata* LACM 53611–2, UCLA 1841–2; *Holbrookia maculata* SDNHM 9042, 9047, 35989, 35994, UCLA 1822; *Holbrookia propinqua* LACM 26925, 26933, SDSU uncataloged, UCLA 16904, 16912, 16914, 16931 (MCZ field numbers); *Petrosaurus mearnsi* SDSU 120A; *Petrosaurus thalassinus* SDNHM 55607, 57101; *Phrynosoma asio* SDNHM 55605; *Phrynosoma coronatum* CKD 13, 50; *Phrynosoma douglassi* SDNHM 5186–7; *Phrynosoma m'calli* SDNHM 16513, 16515; *Phrynosoma modestum* SDNHM 4638; *Phrynosoma platyrhinos* CKD 18, SDNHM 39767, SDSU uncataloged; *Phrynosoma solare* SDNHM 49071, 49346; *Sceloporus (Sator) grandaevus* SDSU 50057–8; *Sceloporus jarrovi* CKD 43; *Sceloporus magister* SDNHM 57112; *Sceloporus occidentalis* CKD 7, 52; *Sceloporus orcutti* CKD 53; *Uma exsul* CU 10140, 10143–5, 10163, 10166, CKD 65, one uncataloged specimen; *Uma notata* LACM 127276–8, SDNHM 10425, 38420, 48486, 49031, 49036, SDSU uncataloged; *Uma parvifigurata* seven uncataloged specimens collected by D. Morafka; *Urosaurus clarionensis* SDNHM 22523, 22529; *Urosaurus graciosus* SDNHM 13541, 28441; *Urosaurus microscutatus* SDNHM 17545, 18122; *Urosaurus ornatus* SDSU 1555; *Uta stansburiana* SDNHM 48488, 57110, 55295.

Tropidurines: *Phymaturus palluma* SDSU 1950; *Tropidurus spinulosus* SDSU 1945.

Acknowledgments.—I am grateful to the following individuals for assistance in obtaining speci-

mens used in this study: Gary Adest, Pere Alberch, Rollin Bauer, Robert Bezy, Mark Dodero, Richard Etheridge, Anne Fetzer, George Foley, Charles Myers, David Morafka, F. Harvey Pough, Jose Rosado, Jay Savage, John Wright, and Richard Zweifel. Richard Etheridge also provided the laboratory space in which most of this study was carried out, and Karen Sitton gave editorial assistance. I thank Arnold Kluge, Gary Packard, Garth Underwood, and an anonymous reviewer for their comments on the manuscript.

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Accepted: 16 January 1982

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