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RECENT EPIDERMAL SCALES FROM
NORTH AMERICAN LIZARDS OF THE
GENUS *SCELOPORUS*
(REPTILIA, IGUANIDAE)

CHARLES J. COLE AND THOMAS R. VANDEVENDER

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ABSTRACT

More than 2000 fossil epidermal scales from lizards of the genus *Sceloporus* have been found in the American Southwest (Arizona, California, Nevada) in 35 fossil packrat (*Neotoma*) middens, ranging in age from $21,700 \pm 500$ to 2720 ± 100 radiocarbon years. We compared the surface structure (using a scanning electron microscope), dimensions, and shapes of the fossil scales with scales from seven Recent species of *Sceloporus* (*S. occidentalis*, *S. undulatus*, *S. graciosus*, *S. jarrovi*, *S. orcutti*, *S. clarkii*, and *S. magister*). Our objective was to identify the species of *Sceloporus* represented by the fossil scales, with a view to improving our understanding of the communities that formerly inhabited the fossil localities. In addition, we discovered several fossil scales that are referable to *Sauromalus obesus*, *Crotaphytus*, and *Cnemidophorus*.

Controlled observations demonstrate that the scales of the seven Recent species we examined have rather similar surface micro-ornamentation, as do the fossils. Such specific differences as do exist are subtle and difficult to resolve on most of the fossils. Work with living and preserved *S. occidentalis* and *S. undulatus* revealed extreme intraspecific variation in scale surface ornamentation that is correlated with the shedding cycle. Scale surfaces that are newly exposed upon molting are highly ornamented with spinules, pits, and partitions that represent superficial cell boundaries. This ornamentation disappears or deteriorates drastically in time, but reappears after the animal molts. This extreme variation must be accounted for in making interspecific comparisons. The most reliable method for studying surface micro-ornamentation on *Sceloporus* scales is to work with living captives and examine their newly exposed scale surfaces immediately following molting.

Burstein, Larsen, and Smith (1974) proposed that certain characteristics of surface micro-ornamentation of *Sceloporus* scales may be very useful in systematics at lower levels of the taxonomic hierarchy and are unidirectional in evolution; they also concluded which traits represent primitive character-states. These authors, however, worked strictly with scales from preserved specimens, and they did not properly account for variation. Our direct comparisons of shed scales with newly exposed scale surfaces

obtained concurrently from the same living individuals demonstrate that many of the character-states utilized by these authors are nothing more than differences that normally appear on a single scale at different periods in the shedding cycle.

Examination of gross features revealed that, when isolated, certain scales with distinctive morphology (dimensions, shapes) are useful for distinguishing among the seven Recent species, but even at best their utility is limited. Small scales cannot be identified with certainty because most of the small scales on large lizards cannot be distinguished readily from the larger scales on small lizards. Certain large scales can be determined as not having been deposited by the smaller species if the sizes and shapes of the scales clearly exceed the maximum limits observed on the smaller species. Thus, gross morphology can be used to limit the number of candidate species represented by certain large scales in a given sample of fossils, and in some instances geographic distribution is useful to limit the possibilities further.

The scales in 11 samples of fossils were such that we could not confidently identify the species of *Sceloporus* they represented. However, 24 samples ranging in age from 9770 ± 160 to $17,610 \pm 290$ radiocarbon years, from Coconino, Mohave, and Yuma counties, Arizona, and from San Bernardino County, California, contained large scales that probably were deposited by *Sceloporus magister*, which is found today at or very near each of the fossil localities. *Sceloporus magister*, and some other species of reptiles (*Sauromalus obesus*, *Gopherus agassizi*) whose remains have been found in some of the same fossil packrat middens, occur primarily in desert and chaparral communities today. However, plant fossils from the same deposits suggest that in the Pleistocene these reptiles occurred often in relatively mesic woodland in which the lowest winter temperatures were not very different from those at the same sites today, but in which summer temperatures were cooler than those prevailing today.

Scale functions are discussed briefly. We suspect that one of the important functions of the large, keeled, spinose and imbricating scales of *Sceloporus*, and possibly of their micro-ornamentation, is to provide the proper surface contact

with the environment, particularly in regard to friction. This scutellation may be particularly advantageous to lizards that seek shelter from predators in deep crevices among rocks and vege-

tation, where efficient entry into cover and the ability to cling there may be enhanced by the structure of the scales.

INTRODUCTION

In terms of specific diversity and geographic distribution, the genus *Sceloporus* is one of the largest and most widespread genera of lizards in North America. These lizards, commonly called scaly or spiny lizards, are characterized in part by the presence of large, keeled, spinose and imbricating epidermal scales on their body, limbs, and tail (fig. 1A). Some of these scales are unique among those of all North American lizards. In addition to interspecific morphological variation, the scales of *Sceloporus* vary considerably according to their location on the individual (fig. 1). The nature of variation in scutellation in *Sceloporus* is such that the scales are useful taxonomically not only in defining the genus, but also in recognizing species groups and in diagnosing species (Smith, 1939).

Sceloporus, as many genera of Recent lizards, is represented but poorly in the fossil record, and until most recently, all fossils known were small skeletal remains (e.g., Robinson and Van Devender, 1973). These were identified to genus and sometimes to species on the basis of compar-

isons with apparently homologous bones of extant species from geographically relevant localities. The discovery of fossil epidermal scales that clearly are referable to *Sceloporus* and sometimes are associated with fossil lizard bones, adds considerable credence to the generic identification of certain Pleistocene lizards (Van Devender, 1973). In addition, we have discovered several fossil scales that clearly are referable to *Sauromalus obesus*, *Crotaphytus*, and *Cnemidophorus*, which we report here for the first time. The fossil scales were found in fossil packrat (*Neotoma*) middens, closely associated with various plant remains that have been dated from 21,700±500 (the oldest deposits) to 2720±100 (the youngest deposits) YBP (radiocarbon years before the present). Most of the scales are excellently preserved, which probably is due to the low humidity of the Southwest deserts (Long and Martin, 1974) and to the preservative action of packrat urine, which indurated or cemented the fossil materials into a hard mass.

We undertook the investigations reported here

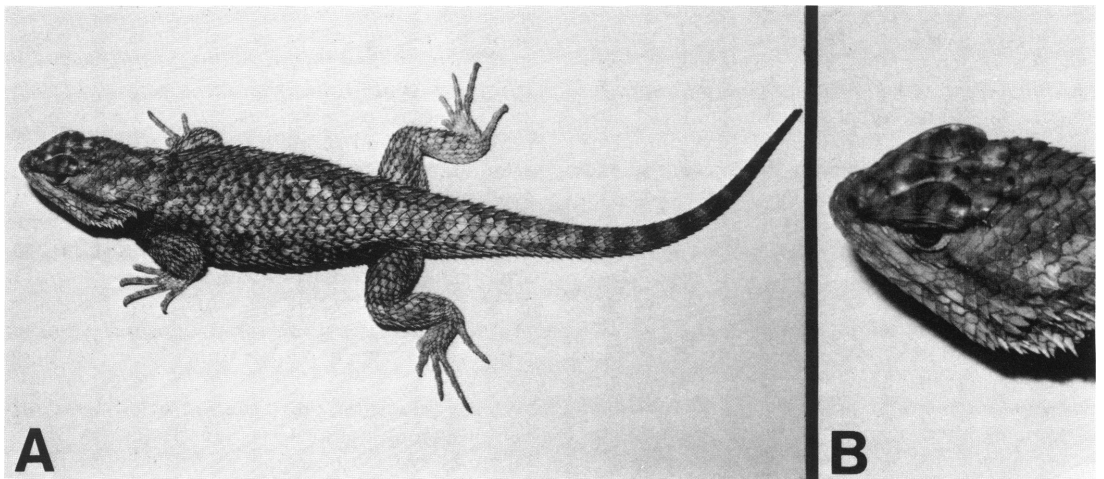


FIG. 1. *Sceloporus magister*, AMNH 111139, adult male, snout-vent length 109 mm. A. Whole animal. B. Head.

primarily in an attempt to identify the species of *Sceloporus* represented by the fossil scales, with a view to improving our understanding of the communities that formerly inhabited the fossil localities. To this end, we examined the surface structure of the fossils with a scanning electron microscope (SEM). In order to understand the fossils in proper perspective, however, we also examined scales from the Recent species of *Sceloporus* now living at or near the localities where the fossils were found (Arizona, California, and Nevada). We conducted our observations on Recent scales in a controlled fashion in order to minimize the probability of misinterpreting our observations on the fossils. Thus, we conducted observations designed to determine whether variables such as sex, ontogenetic development, geographic variation, location on the body, and the skin shedding cycle had significant effects on the surface structure of *Sceloporus* scales.

We are aware of only three publications concerning details of surface structure of *Sceloporus* scales. Ruibal (1968) and Stewart and Daniel (1973) compared some aspects of microornamentation on scales of *Sceloporus occidentalis* with those of several other species of lizards belonging to several families, in an attempt to elucidate structure and functions. Most recently, while the present investigation was being completed, Burstein, Larsen, and Smith (1974) published a taxonomically oriented study of *Sceloporus* scales, based on samples from preserved specimens of 51 species. These papers did not include controlled observations on the variables we investigated, among which we have determined that the skin-shedding cycle is exceedingly important, and none of these papers considered fossil scales.

MATERIALS AND METHODS

This report is based on an examination of nearly 100 *Sceloporus* scales with the SEM. In addition, we examined with a dissecting microscope more than 2100 fossil scales from 35 deposits and untold numbers of scales *in situ* on series of lizards that were preserved in formalin and alcohol by standard methods. Scales of the following Recent species were examined: *Sceloporus occidentalis* Baird and Girard, *S. undulatus* (Latreille), *S. graciosus* Baird and Girard, *S. mag-*

ister Hallowell, *S. clarkii* Baird and Girard, *S. jarrovi* Cope, and *S. orcutti* Stejneger. This includes all the species of *Sceloporus* that presently occur at the fossil localities. Indeed, these are the only species of *Sceloporus* presently inhabiting any portions of the states where the fossil scales have been found, excepting *S. scalaris* Wiegmann and *S. virgatus* Smith, two species we did not examine because of their small size and occurrence southward from extreme southeastern Arizona. We also examined a few scales from a living *S. olivaceus* Smith for data pertaining to the shedding cycle.

FOSSIL PACKRAT MIDDENS

Fossilized middens of packrats (genus *Neotoma*) are hardened, dark, shiny masses that contain various biotic remains. Plant macrofossils including leaves, seeds, spines, and twigs are especially abundant and are used in reconstructing past vegetations and climates (Wells and Jorgensen, 1964; Wells and Berger, 1967; Van Devender and King, 1971; Phillips and Van Devender, 1974). Animal remains preserved in the ancient middens include fecal pellets, insect fragments, bones, hair, and lizard scales. Fossil middens represent the portion of the packrat house or den where waste materials accumulate and become hardened through trampling and urination (Finley, 1958). Packrats are habitual gatherers and eventually they bring samples of most of the local flora into their houses. The materials preserved in a fossil midden presumably were collected within one home range of a packrat, which is within approximately 100 meters of the midden (Raun, 1966; Stone and Hayward, 1968). When the midden deposits are built in protected dry sites, they can be preserved for long periods of time and have been dated at more than 30,000 radiocarbon years old (Van Devender and King, 1971).

Fossil packrat middens are found in rock shelters and crevices. At desert localities, middens of Pleistocene age usually can be distinguished from the more common Holocene middens in the field because they contain readily visible fossils of plants (usually juniper) that today are restricted locally to higher and moister elevations. Since a midden may have several distinct stratigraphic units, samples are collected

carefully to prevent mixing materials of different ages. In the laboratory, each sample is soaked in water, screened through a 20 mesh/inch soil sieve, and carefully sorted. The fossil lizard scales considered in this paper were collected in the general sorting of midden fossils. Approximately 50 percent of the middens investigated contained one or more scales.

The fossil lizard scales could have reached the fossil middens in several ways. Probably the most likely way is that the lizards used the packrat dens for shelter. For example, *Sceloporus magister* and *Sceloporus undulatus* today commonly inhabit packrat houses that are constructed in open areas, and they enter those in rocky situations also. Some of the scales appear to be from shed skins and some from lizards that died within the shelters. Another possibility is that the scales or some of them were transported to the shelters in part by predators, either in the feces of small carnivores, such as the coyote (*Canis latrans*) or ring-tailed cat (*Bassariscus astutus*), or in the regurgitated waste pellets of raptorial birds, such as hawks and owls. Packrats often collect dung and raptor pellets and add them to the pile of debris forming their house. Intact carnivore dung or raptor pellets have not been found in the fossil middens, however; if the scales are from these sources the dung and pellets are decomposed and thoroughly mixed into the other organic materials and the morphology of the scales was essentially unaffected by the digestive processes involved.

AGE OF THE FOSSILS

The fossils in ancient packrat middens can be placed in a time framework using the radiocarbon dating technique, and most of the middens containing fossil lizard scales have been dated (table 5). Fossils of plant species that now are restricted to higher woodland communities were submitted for dating to prevent contamination by younger materials. Most of the dates were obtained from twigs and seeds of *Juniperus* sp. (juniper), but *Pinus* (pine), *Fraxinus anomala* (single-leaf ash), two species of *Nolina* (bear-grass), *Ephedra nevadensis* (Mormon tea), *Larrea divaricata* (creosote-bush), and midden debris were dated also (table 5).

Pleistocene middens containing fossil lizard

scales have yielded radiocarbon dates ranging from $21,700 \pm 500$ YBP (years before present) to 2720 ± 100 YBP. This time period extends from the Wisconsin glacial maximum to the Holocene or postglacial period. The confidence interval given for each radiocarbon date is a standard deviation (sigma) indicating a 67 percent probability that the true age lies within the range of the stated date plus or minus one sigma (Long and Rippeteau, 1974). This probability is 95 percent for the interval of the stated date plus or minus two times sigma.

Fossil packrat middens are never absolutely free from the possibility of contamination resulting from the addition of spurious materials by rats at some point in time subsequent to the age determined by radiocarbon dating. The technique of attempting to date a single, ecologically restricted species greatly reduces the likelihood of erroneous dating but cannot totally preclude the possibility that younger lizard scales may be worked into a deposit. We conclude that the lizard scales reported here are contemporaneous with the Pleistocene floral assemblages dated because of their characteristic staining, their localized occurrence and abundance within the fossil middens, and because of the care taken in collecting and processing the samples.

SEM PREPARATIONS

The following procedure proved most reliable for preparing individual scales for examination with the SEM, particularly in terms of cleaning the scales efficiently for clear viewing without introducing artifacts: (1) place scale (fossil, molt, or keratinized outer scale surface lifted with fine insect pins from the skin of a preserved or living lizard) into 75 percent ethanol; (2) for fossils or scales from living lizards, wait 24 hours or more, but for others soaking for a few minutes is sufficient; (3) transfer scale to a small beaker of 100 percent ethanol, and cleanse for 20 minutes in a Cole-Parmer Ultrasonic Cleaner (Model 8845-4); (4) rinse briefly in fresh 100 percent ethanol; (5) place scale on a dry cloth (folded over scale for protection from dust) and let dry for 20 minutes; (6) place scale on sticky side of a piece of Scotch copper electrical tape, which previously has been affixed to a clean aluminum SEM stub with silver colored conducting paint; (7) coat with approxi-

mately 75 angstroms of carbon and then with approximately 100 angstroms of gold-palladium (60% and 40%, respectively), in a Denton vacuum evaporator (DV-515); (8) examine with an S4 Stereoscan SEM (Kent Cambridge Scientific Co.), usually with a LaB6 (lanthanum hexaboride) emitter in the electron gun; for magnifications less than $\times 1500$ we used 5 kv. and for greater magnifications we used 10 kv.

Aspects of the procedure were modified on various occasions in a controlled fashion to determine the most efficient procedure and to ascertain that we did not inadvertently introduce artifacts into our observations. In experimenting, we attempted to change only one variable, and usually we compared the results with those obtained using the standardized procedure on other scales from the same individuals, often prepared concurrently. Such experiments were conducted with scales from living or preserved lizards. Thus, we determined that surface structure of untreated scales, lifted from living lizards and placed directly into the SEM, is consistent with that observed after following the standardized procedure, but few details can be observed before the scales deteriorate in the machine. Scales coated after removal from living lizards and examined without going through the steps of preservation, soaking and ultrasonic cleaning had surface details similar to those prepared by the standardized procedure, but they were not very clean. Scales that were lifted from preserved lizards, air-dried, coated, and examined without ultrasonic cleaning had surface details similar to those prepared by the standardized procedure, but they were not very clean either. Acetone can be used as a soak prior to and during ultrasonic cleaning, but this is not necessary and 100 percent ethanol does not leave a surface film that may result from acetone. Scales subjected to ultrasonic cleaning for only 20 minutes showed better surface details than one cleaned for an hour, suggesting that ultrasonic cleaning can be destructive if overdone. One scale that was subjected to critical point drying lost most of the surface details that were visible on other scales prepared from the same lizard by other techniques, indicating that critical point drying can be destructive also. Although the first coating all scales received was of carbon, we found that this could be followed by aluminum, gold-palladium,

or silver, and all showed similar results as far as surface details were concerned. Some scales charged quickly (perhaps due to faulty coating), and giving them a thin second coat did not produce any noticeable artifacts. In addition, scales lifted from specimens that had been preserved for several years had surface structures that were consistent with those lifted from living lizards and then preserved by the procedure normally used for preserving entire lizards (two days in 10% formalin followed by one day in water followed by two months in 75% ethanol). Experimentation with the techniques of preparation has convinced us that the results we present here are properly descriptive of the scales and cannot reasonably be considered artifacts of preparation.

Nearly all the fossils examined with the SEM were prepared by the standardized procedures, but a few received ultrasonic cleaning in acetone rather than 100 percent ethanol. The standard procedure is remarkably effective in cleaning these aged scales, particularly considering that many of them had adobe-like dried mud and plant remains rigidly adhering to their surfaces before cleaning.

SPECIMENS EXAMINED

Specimens of Recent lizards examined for this investigation are in the herpetological collections of the American Museum of Natural History (AMNH) and the Department of Biological Sciences at the University of Arizona (UAZ). All the fossil scales presently are deposited in the herpetological collection of the American Museum of Natural History, and the fossil bones cited in the text are in the collection of the University of Arizona Laboratory of Paleontology (UALP).

Specimens of Recent species from which scales were examined with the SEM are: *Sauromalus obesus*, AMNH 57724 (♂); *Sceloporus clarkii*, AMNH 84602 (♂), 111138 (♂); *Sceloporus graciosus*, AMNH 109109 (♂); *Sceloporus jarrovi*, AMNH 109117 (♂); *Sceloporus magister*, AMNH 97781 (♂), 108053 (♂), 111139 (♂); *Sceloporus occidentalis*, AMNH 107494-107496 (1♂, 2♀), 108047 (♂), 111140 (♂); *Sceloporus orcutti*, AMNH 75597 (♂); *Sceloporus undulatus*, AMNH 108099 (♂), 108104 (♂), 111136 (♀), 111141 (♀).

Complete locality data for all the samples of fossil scales are presented in the text (pp. 490-503).

Large specimens of Recent species whose scales were examined for comparison with the fossil scales include: *Sauromalus obesus*, AMNH 57723-57724 (1♂, 1♀); *Sceloporus clarkii*, AMNH 295 (♀), 2556 (♂), 84605 (♂); *Sceloporus graciosus*, AMNH 22953 (♀), 109109, 109110 (2♂); *Sceloporus jarrovi*, AMNH 63787 (♂), 84626 (♂), 111582 (♂); *Sceloporus magister*, AMNH 26696 (♂), 27641 (♂), 68486 (♂), 97781 (♂), 111139 (♂); *Sceloporus occidentalis*, AMNH 107494, 107495 (♂, ♀), 108047 (♂); *Sceloporus orcutti*, AMNH 20479 (♂), 60531 (♀); *Sceloporus undulatus*, AMNH 64768 (♀), 97777, 97778 (2♂), 107511 (♀), 109205-109215 (5♂, 6♀), 111117 (♂), 111131 (♀).

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Arizona Laboratory of Paleoenvironmental Studies, kindly permitted us to examine and report on fossil scales from middens they are investigating. Dr. Austin Long, Radiocarbon Laboratory, Department of Geosciences, the University of Arizona, provided all but one of the radiocarbon dates reported here; the exception was provided by Dr. C. Wesley Ferguson, Laboratory of Dendrochronology, University of Arizona. Dr. E. H. Lindsay, UALP, provided us with catalogue numbers for the fossil bones cited in the text. Drs. Charles H. Lowe and Michael D. Robinson, UAZ, provided the most recently available distributional data for *Sceloporus clarkii*, *S. jarrovi*, and *S. magister* in Arizona. Mr. Donald McBee of the Lake Mead National Recreational Area, gave considerable assistance in collecting specimens of packrat middens. Mr. David C. Ochsner, Chief of Environmental Activities and Systems Evaluations at Grand Canyon National Park, provided permits for field work undertaken at the Grand Canyon. We are grateful for the assistance contributed by all these individuals, and for the partial financial support of grant number GB-27406 from the National Science Foundation to Dr. Paul S. Martin, University of Arizona Laboratory of Paleoenvironmental Studies.¹

SURFACE DETAILS OF *SCELOPORUS* SCALES

Most of the scales examined with the SEM were lifted from the dorsal or dorsolateral aspect of the body at a point approximately midway between the axilla and groin. While examining and photographing surface details, all scales were oriented in the same way, and care was taken to ensure that all photographs reproduced here are printed with the same orientation, to eliminate concern for introducing artifacts resulting from the pseudoscopic effect. This effect is well illustrated in figure 6B, in which the pits may appear as low, rounded tubercles when the photograph is held upside down. Figure 2 illustrates how the dorsal scales were oriented for detailed examination and indicates the various regions that were selected as standards for comparative photography. Although some large scales were oriented differently for efficient use of space in photo-

graphing the entire scale (e.g., fig. 26A), they were then oriented immediately as in figure 2 for all viewing and photography thereafter, unless specified otherwise.

Sceloporus occidentalis

We examined a total of 20 dorsal scales from five individuals of *S. occidentalis*. Usually we examined dorsal surfaces, but also we examined the underside of two scales and in several instances we tore scales in order to examine torn edges.

The first scales were from an adult male, AMNH 107494, from Utah. Prominent features visible at low magnifications (fig. 3A, B) are the

¹Contribution Number 614, Department of Geosciences, the University of Arizona, Tucson 85721.

keel, the spine projecting from the posterior edge, a notch on each side of the spine (we have seen as many as one notch on one side and two notches on the other), a very inconspicuous troughlike depression anterior to midscale that approximately parallels the curvature of the anterior edge of the scale, and a conspicuous ridge comprising the anterior edge of the scale and having a distinct posterior overhang above the anterior surface of the scale. *In situ* the anterior ridge borders the hinge region, which connects the scale to those anterior to it. The preceding scales loosely overlapped the scale approximately to the place marked by the troughlike depression. Posterior to this, the scale surface was the fully exposed external surface of the lizard. Also *in situ* the distinct, high anterior ridge limits the surface contact between the imbricating scales.

The entire surface of the scale is covered with variably shaped polygons (fig. 3C, D), including the dorsal surface of the keel and spine, where the polygons are less distinct than elsewhere. At approximately X1000 in Region 1, these polygons are seen to be distinct because of the

approximately vertical partitions that comprise their borders (fig. 4A, B). Generally the partitions are highest along the anterior edges of the polygons, where often they have a slight but evident slant posteriad. Within the polygons and crossing their partitions there is a very inconspicuous pattern of smaller partitions (fig. 4). We agree with Stewart and Daniel (1973), who suggested that the conspicuous polygons are Oberhäutchen cells, the conspicuous partitions representing the cell boundaries; we shall refer to them as such hereafter. Stewart and Daniel (1973) interpreted the inconspicuous partitions as being traces of cell outlines remaining from the clear layer cells that overlaid these Oberhäutchen cells prior to the preceding molt. The surface structure illustrated for Region 1 (fig. 4) exemplifies that of the entire scale surface posterior to the troughlike depression on both sides of the keel.

At higher magnifications (*ca.* X6000), the surfaces of the cells are seen to be ornamented with numerous spinules situated on inconspicuous ridges that form a fine reticulum such that there are inconspicuous pits between the spinules; this structure is not clear unless viewed from various angles (fig. 4C, D). In places where the spinules are least abundant, the pits are more conspicuous than elsewhere. Some spinules may (or may not) be found also on the cell boundaries (fig. 4C, D). We did not see the extreme undulating nature of these surfaces described and illustrated by Stewart and Daniel (1973) unless scales remained in the SEM for some time and began to deteriorate; then their surface bubbled (undulated) and cracks appeared, but these clearly were artifacts.

Region 2 is similar to Region 1 but has larger cells (fig. 5). Note again that the surface structure is not clear unless it is viewed from various angles. On most scales Region 2, which is overlaid by the preceding scales *in situ*, is considerably cleaner and shows more detail than Region 1. The surface structure illustrated for Region 2 exemplifies that of the entire surface immediately posterior to the ridge comprising the anterior edge of the scale, but in viewing from Region 2 toward the troughlike depression, one sees a gradual decrease in cell size until reaching the size occurring in Region 1.

In Region 3 the cell outlines are clear also, as

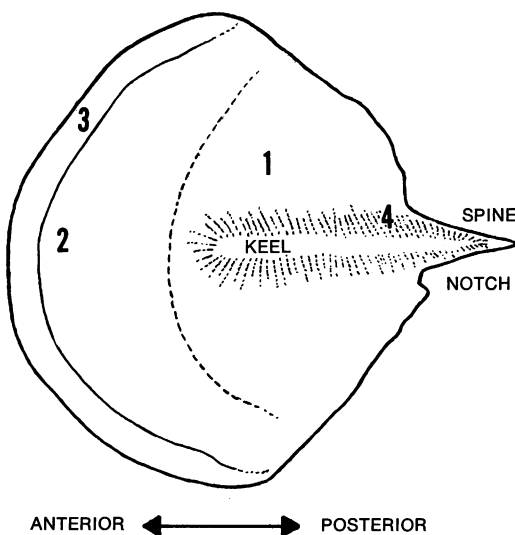


FIG. 2. Dorsal scale of *Sceloporus occidentalis* (fig. 3). All dorsal scales were oriented in this position in the SEM for viewing details of surface structure. The various standard Regions selected for comparative photography (subsequent figures) are numbered.

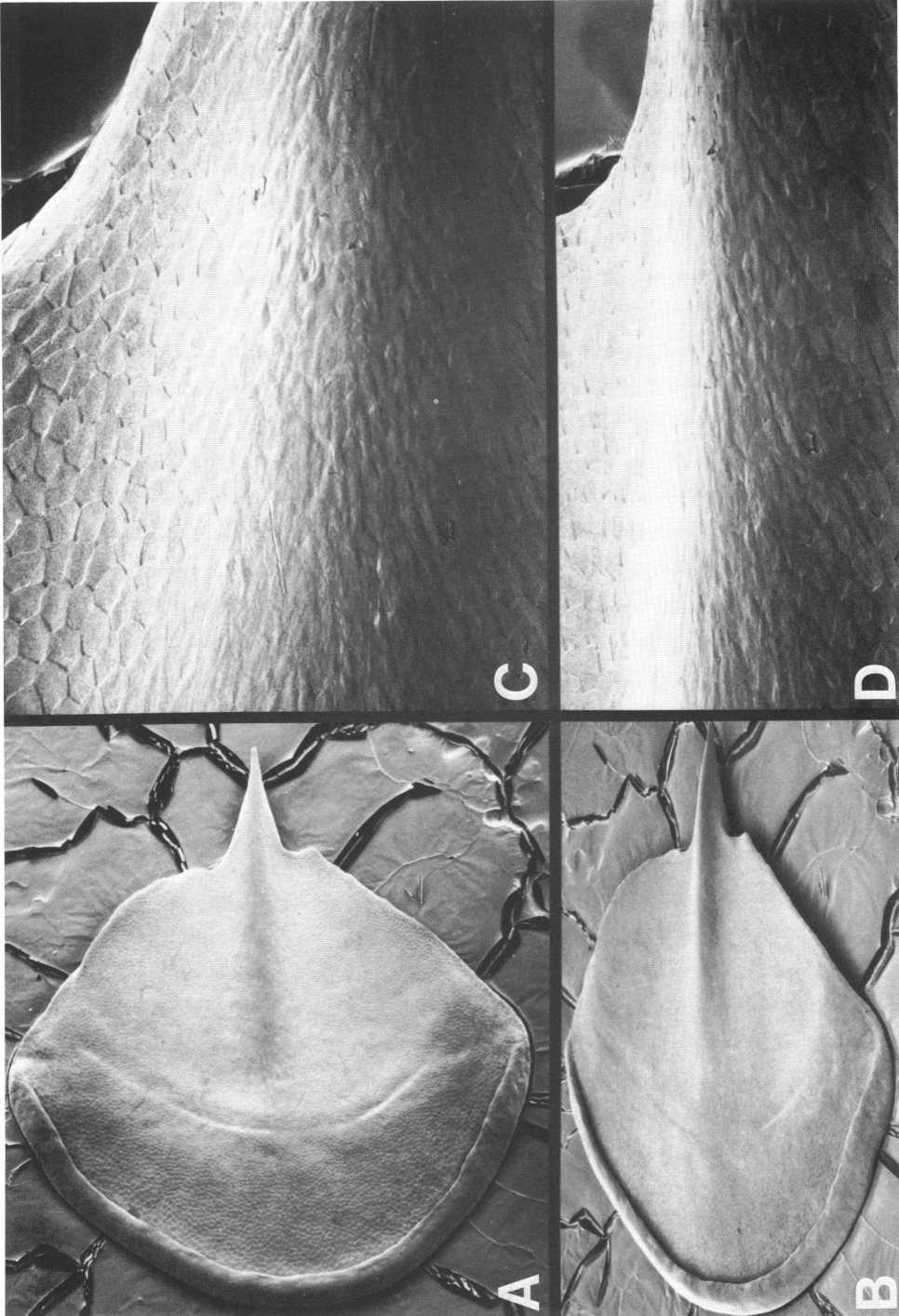


FIG. 3. Dorsal scale of *Sceloporus occidentalis*, adult male, AMNH 107494. A. Entire scale, no angle, $\times 24$. B. Entire scale, 45° angle, $\times 24$. C. Region 4, no angle, $\times 240$. D. Region 4, 45° angle, $\times 240$.

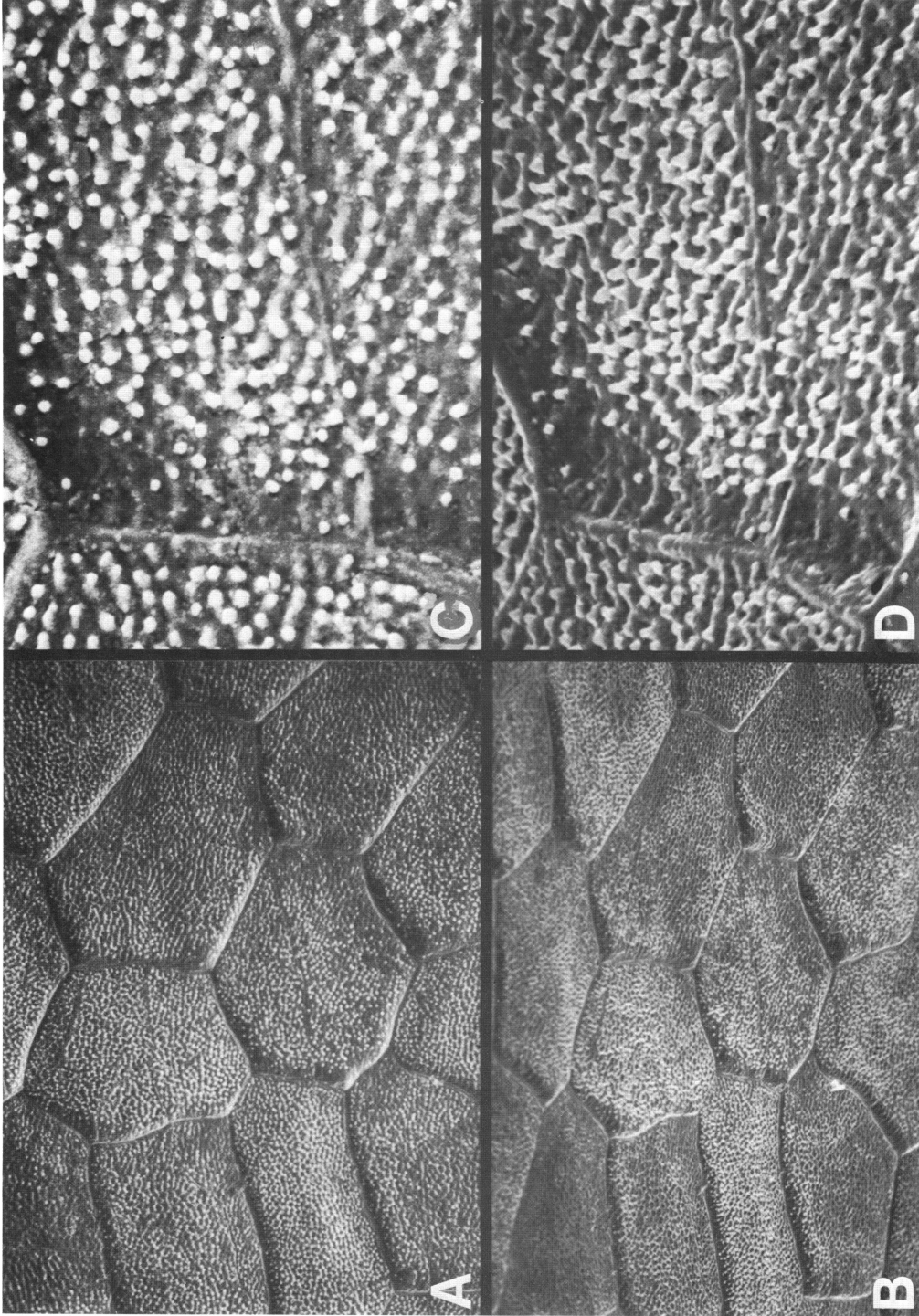


FIG. 4. Same scale of *Seeloporus occidentalis* as in figure 3. A. Region 1, no angle, $\times 1200$. B. Region 1, 45° angle, $\times 1200$. C. Region 1, no angle, $\times 6000$. D. Region 1, 45° angle, $\times 6000$.

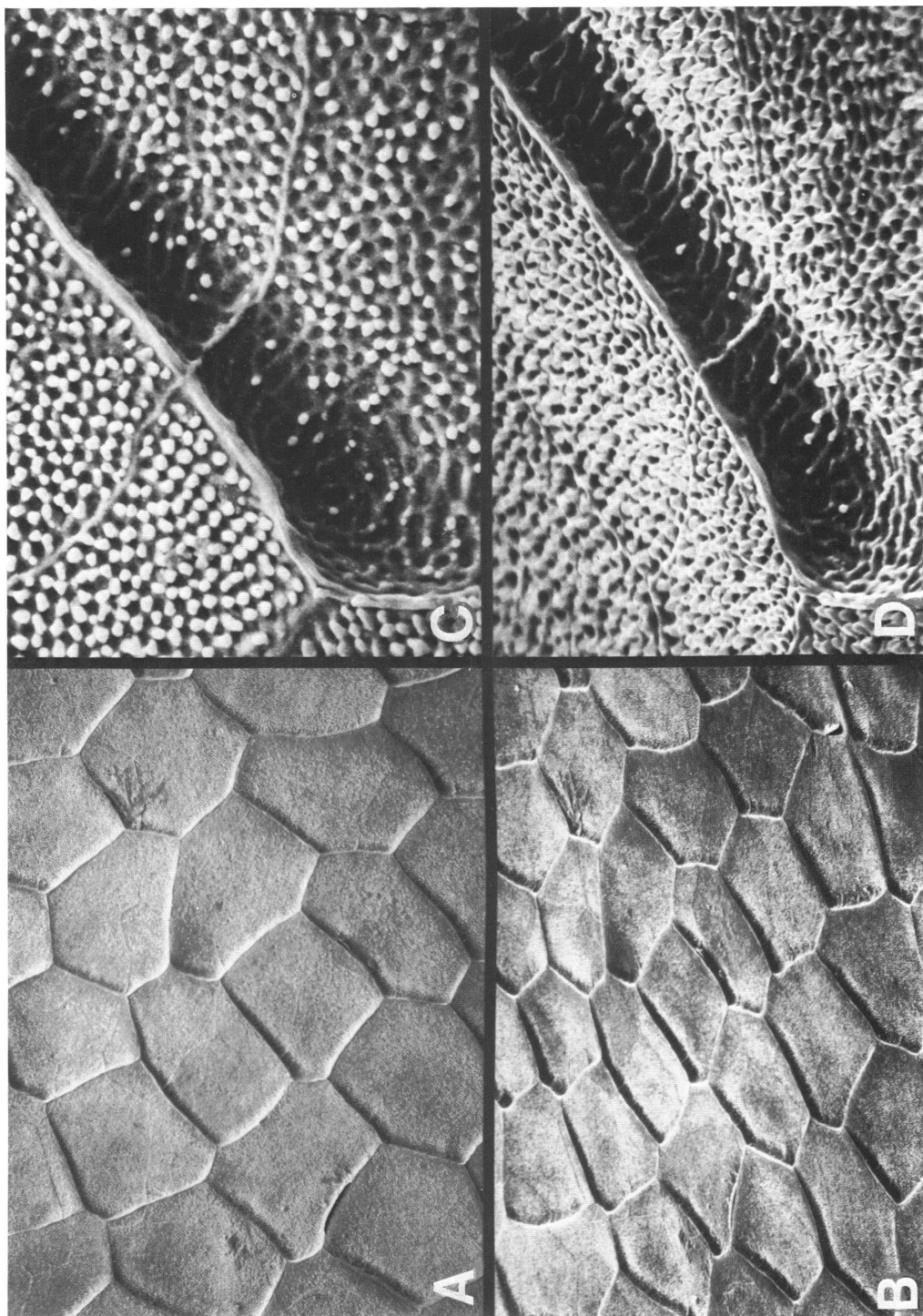


FIG. 5. Same scale of *Sceloporus occidentalis* as in figure 3. A. Region 2, no angle, $\times 600$. B. Region 2, 45° angle, $\times 600$. C. Region 2, no angle, $\times 6000$. D. Region 2, 45° angle, $\times 6000$.

are (in places) the inconspicuous, smaller partitions (fig. 6A). The cells here are large and transversely elongate, with their long axes approximately paralleling the anterior edge of the scale. Surfaces of the cells are covered with numerous pits, and spinules essentially are lacking (fig. 6B). The surface structure illustrated for Region 3 exemplifies that of the entire surface of the ridge comprising the anterior edge of the scale.

Reorienting the scale in the SEM so the spine is pointing downward on the viewing screen and then tilting the stub so the tip of the spine is raised (68° in this instance) clearly reveals a hole at the base of the conspicuous notch to each side of the keel (fig. 6C). Nearly all dorsal scales examined had conspicuous notches and usually there was a single hole at the base of each notch (range 0 to 2). These holes penetrate completely through the scale, and the boundaries of the cells comprising their interior linings are visible (fig. 6D). *In situ* a plug of material occupies the holes. Usually the material remains projecting from the scale that remains on the animal after the outer scale surface has been lifted off for examination, but in some instances this material breaks and a plug of it remains in the hole of the scale being examined (e.g., fig. 27). Clearly, these holes are pores of ducts that extend from areas deeper within the skin. Probably they are sensory pores (Miller and Kasahara, 1967), similar to those on agamid lizards (Scortecci, 1941; Grandison, 1968).

In an effort to add confidence to the conclusion that the large polygons observed are indeed the surfaces of Oberhäutchen cells, we tore several scales into two pieces each and examined their torn edges. The scale illustrated in figures 7 and 8 is from the same male (AMNH 107494) considered above. This scale was torn approximately in half vertically, and oriented in the SEM with the anterior ridge pointing upward on the viewing screen; the stub was tilted for viewing the torn edge at various angles. The scale appears to be composed of layers of flat discs that are approximately the sizes of the superficial polygons (fig. 7A, B), which is consistent with expectations of the appearance of cell outlines in stratified squamous epithelium. Nevertheless, we were unable to follow clearly the cell boundaries

of the superficial cells into the next layer of the skin. In some places the superficial cells were torn and lifted partly or completely away from a surface below, which was ornamented with haphazardly arranged ovoid bodies similar in size to the superficial spinules (figs. 7C, D; 8A, B); perhaps these are the dorsal surfaces of the cells below the superficial layer. Such ornamentation is evident for only one or two cell layers below the surface, after which the cell surfaces appear rather smooth (fig. 8B).

Although our major concern for comparative purposes was with the dorsal surfaces of the scales, we also examined the underside of two scales from the same male as considered above (AMNH 107494). The major gross feature seen on the underside of a scale and not seen from above is the surface along the posterior edge that forms a wide envelope into which fitted deeper layers of the scale (not lifted off) *in situ* (fig. 9A); thus, the posterior spine is hollow in this outer scale material, which actually becomes evident while lifting it from the animal. The interior surface of the scale is rather smooth, although covered with numerous pits (fig. 9B). The surfaces of the envelope and the underside of the spine are covered with polygonal cells (fig. 9C) that are demarcated by conspicuous partitions similar to those in Region 2 (fig. 5A), including the inconspicuous, smaller partitions. The surfaces of these cells consist of scattered spinules situated on ridges that form a reticulum such that there are pits between the spinules (fig. 9D). Boundaries between the cells become less distinct toward the tip of the spine.

Having examined scales from an adult male, we next examined some from two adult females (AMNH 107495, 107496) from the same locality as the male. All of these lizards were collected at the same time and handled similarly both in the field and in the laboratory. The scales from these females (e.g., fig. 10) are similar to one another but strikingly different in detail from those of the male. In Region 1 the cell boundaries are low, bluntly rounded and scarcely discernible; also the scale surface does not appear clean (fig. 10B). Neither spinules nor other micro-ornamentation are discernible at high magnifications. In Region 2 also (fig. 10C), the cell boundaries

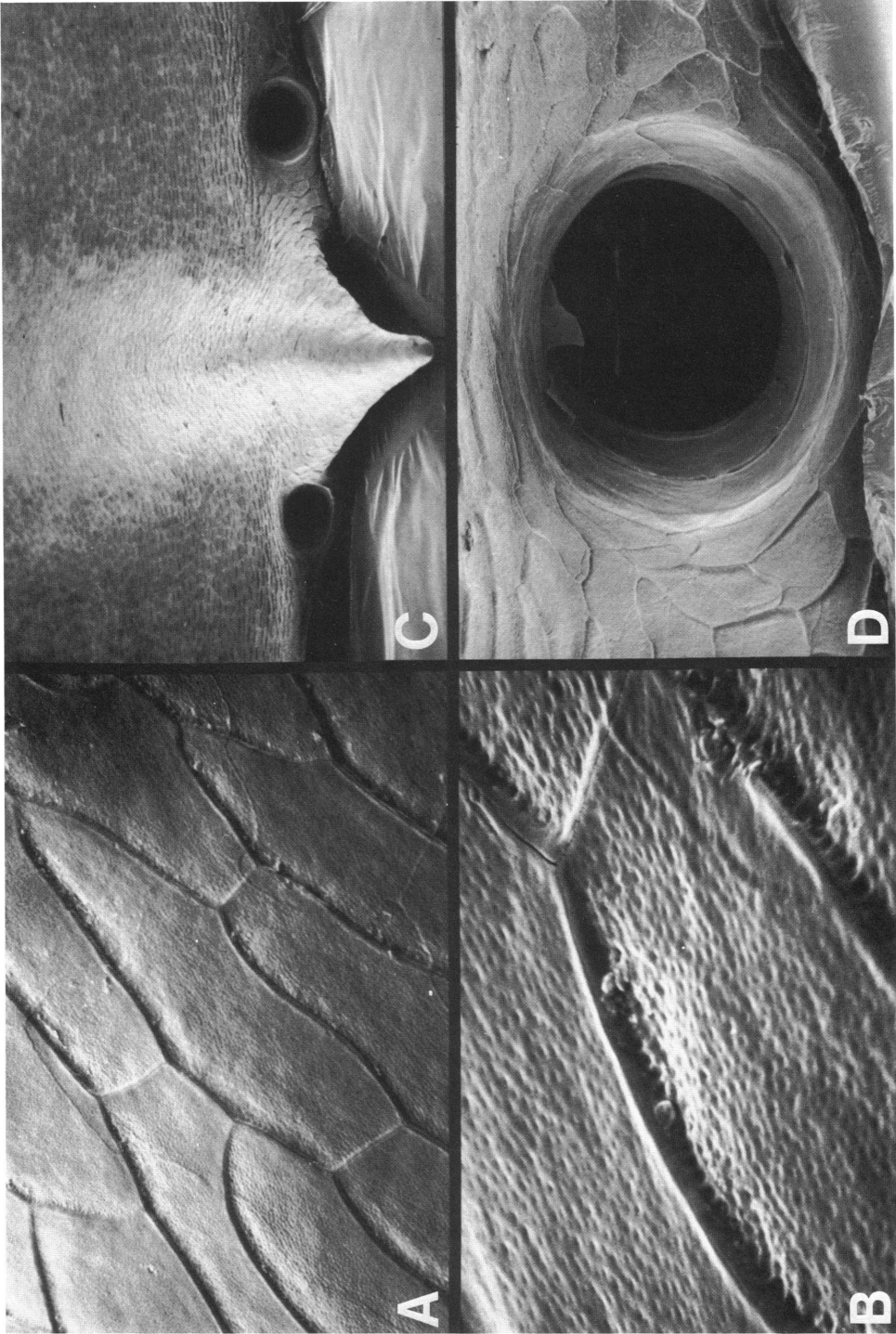


FIG. 6. Same scale of *Sceloporus occidentalis* as in figure 3. A. Region 3, no angle, $\times 1200$. B. Region 3, 45° angle, $\times 6000$. C. Notches and pores in posterior edge of scale, 68° angle, $\times 120$. D. Pore to right of spine in C, 68° angle, $\times 600$.

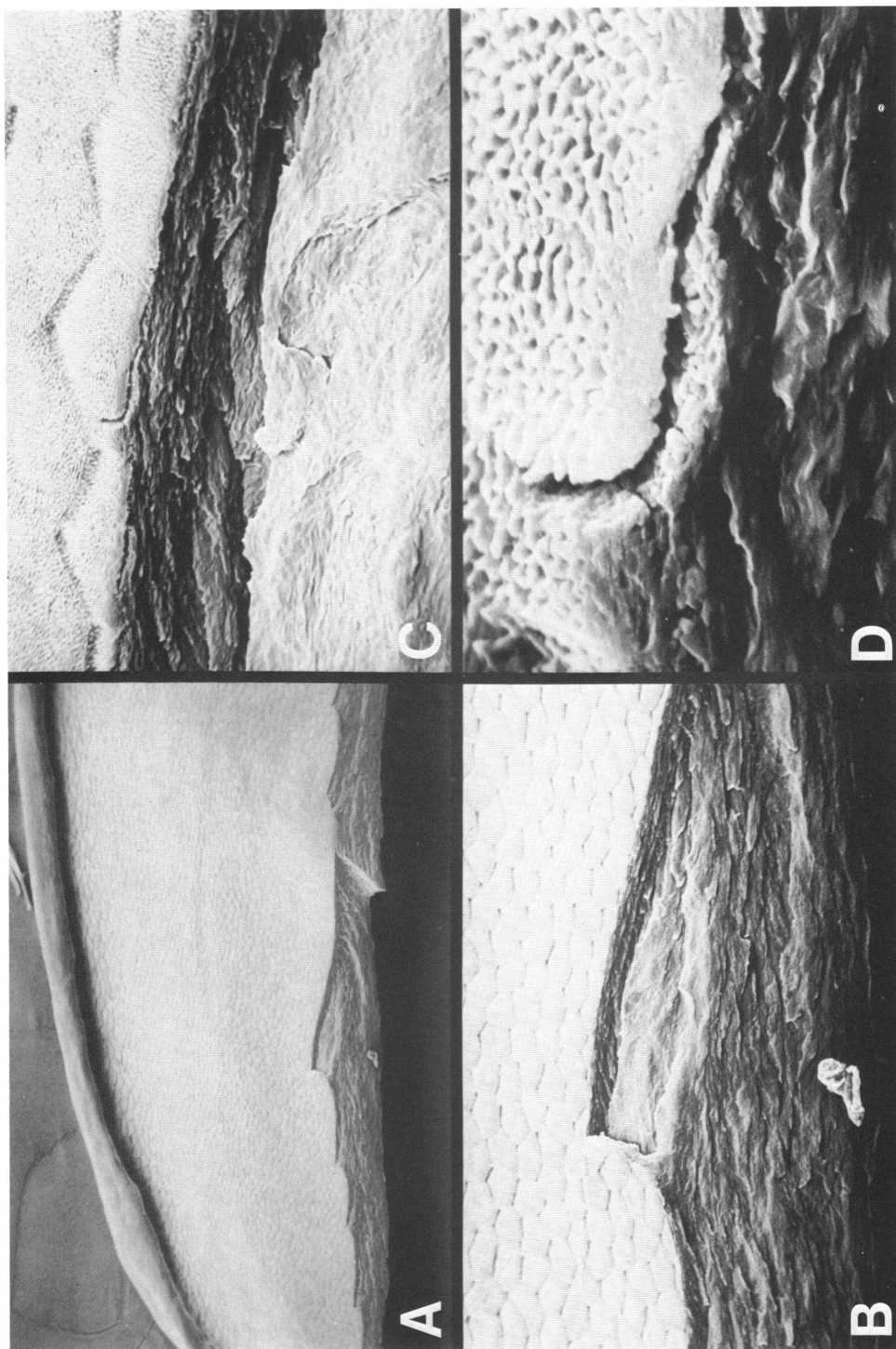


FIG. 7. One area of torn edge of a dorsal scale of *Sceloporus occidentalis*, adult male, AMNH 107494; 45° angle. A. $\times 60$. B. $\times 260$. C. $\times 1200$. D. $\times 6000$.

are low and bluntly rounded compared with those of the male; here also the scale surface is not clean, but at least in places some micro-ornamentation is visible (rounded, irregularly distributed spinules and pits). In Region 3 (fig. 10D) the cell boundaries are low and bluntly rounded also; in places, however, pits are visible on the cell surfaces. The dorsal surface of the keel is essentially smooth on each of these scales.

The differences between the male and females could not be attributed to ontogenetic development or geographic or seasonal variation because all the specimens were adults from the same population sample obtained on one day of collecting. Thus, we suspected that either sexual dimorphism or variation associated with the shedding cycle was responsible for the differences observed, and we examined an additional male (AMNH 108047, from a different locality, in California, due to the presence of only one adult male in the first sample). Surface structure of the dorsal scales from this male (fig. 11) are essentially identical to those of the females (fig. 10), which ruled out sexual dimorphism. In preparing the scales from AMNH 108047 for SEM examination we prepared an additional scale

from the highly ornamented male (AMNH 107494), which ruled out the possibility of artifacts resulting from variations in preparing scales for examination on different occasions.

In order to investigate effects of the shedding cycle on surface structure of scales from *S. occidentalis*, we maintained a living adult male in captivity. As soon as we noticed the lizard molting, similar to the *S. undulatus* illustrated (fig. 12), we obtained concurrent samples of the scale surfaces that were cast off as well as the newly exposed scale surfaces from beneath the cast scales of the same individual (AMNH 111140). Surface details of the cast scale (fig. 13) are relatively unclean and include low, bluntly rounded cell boundaries and blunt spinules, which in many areas are so obscure as to be indiscernible; cell surfaces in Region 3 usually are recognized as being pitted, however. All details of the newly exposed scale surfaces, however, are clean and distinct, including tall cell boundaries and spinules that are distributed rather densely on the surfaces of the cells (fig. 14). In places on the same scale, however, the cell boundaries appear lower and inconspicuous, being covered with spinules (fig. 15A). The extremely dense

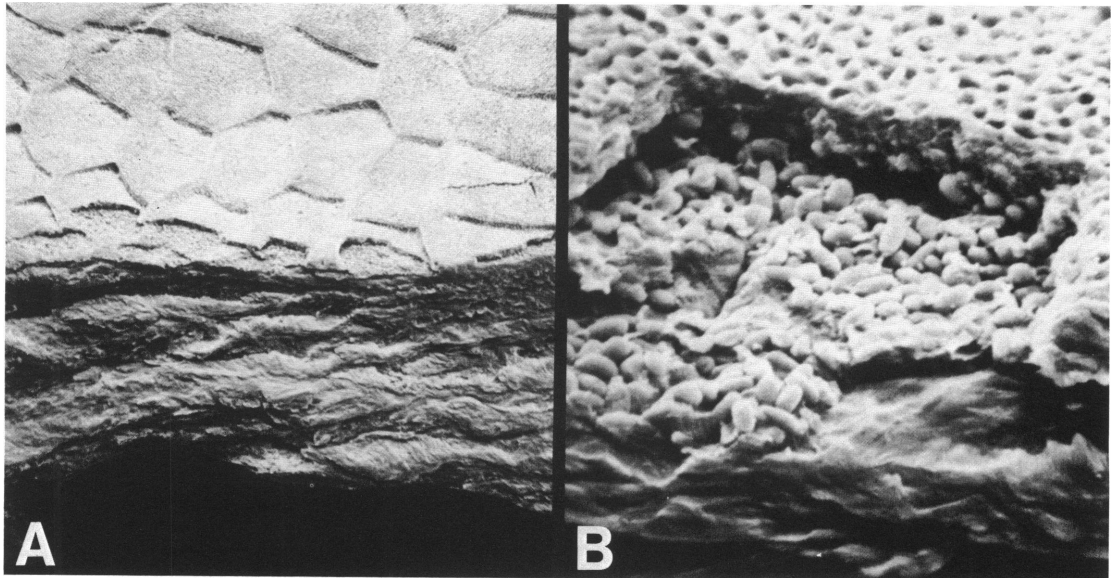


FIG. 8. Another area of torn edge of same scale of *Sceloporus occidentalis* as in figure 7; 45° angle. A. $\times 600$. B. $\times 6000$.

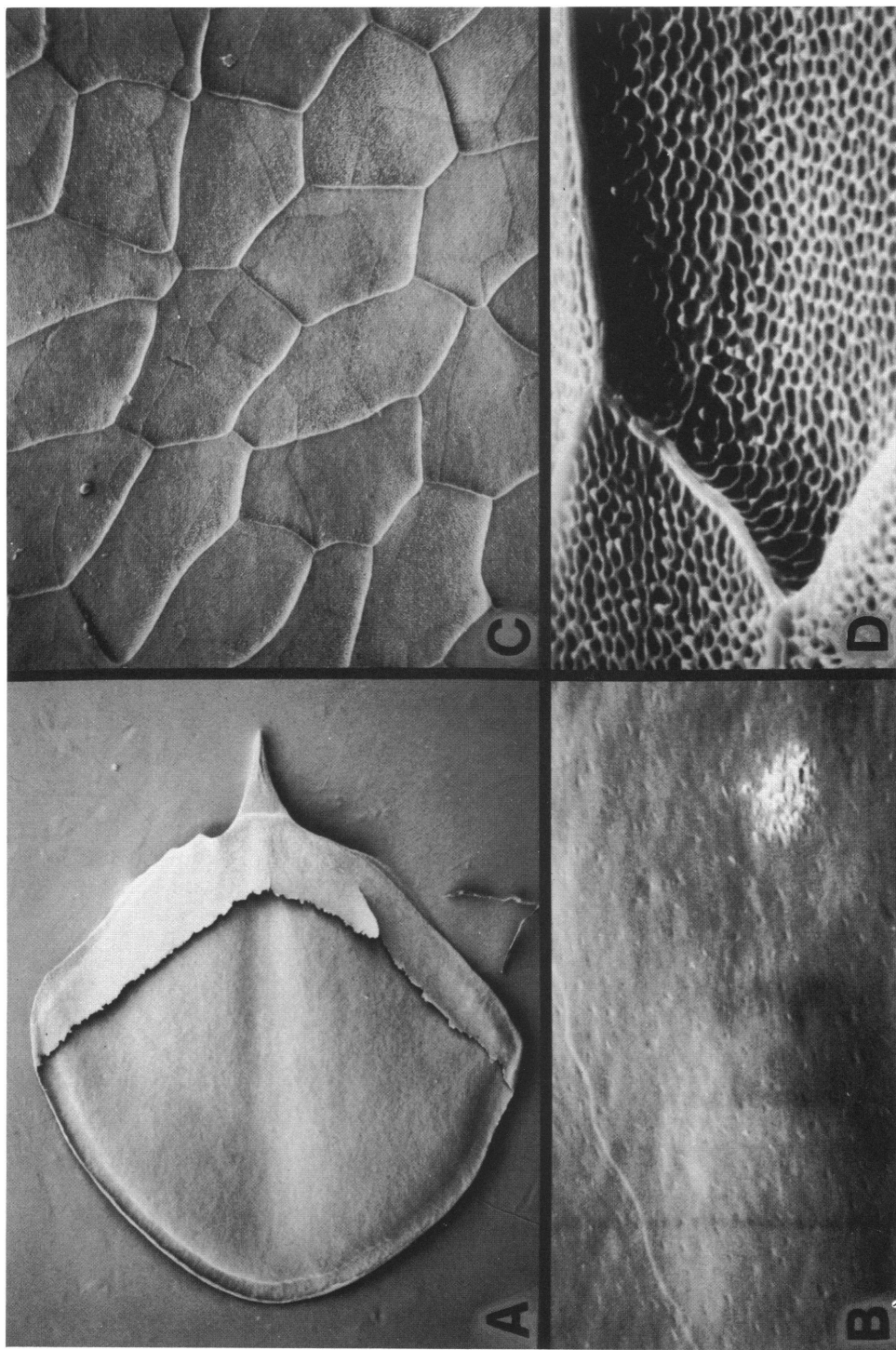


FIG. 9. Underside of dorsal scale of *Sceloporus occidentalis*, adult male, AMNH 107494. A. Entire scale, no angle, $\times 24$. B. Near center, 45° angle, $\times 6000$. C. Envelope, at base of spine, no angle, $\times 6000$. D. Same area as C, 45° angle, $\times 6000$.

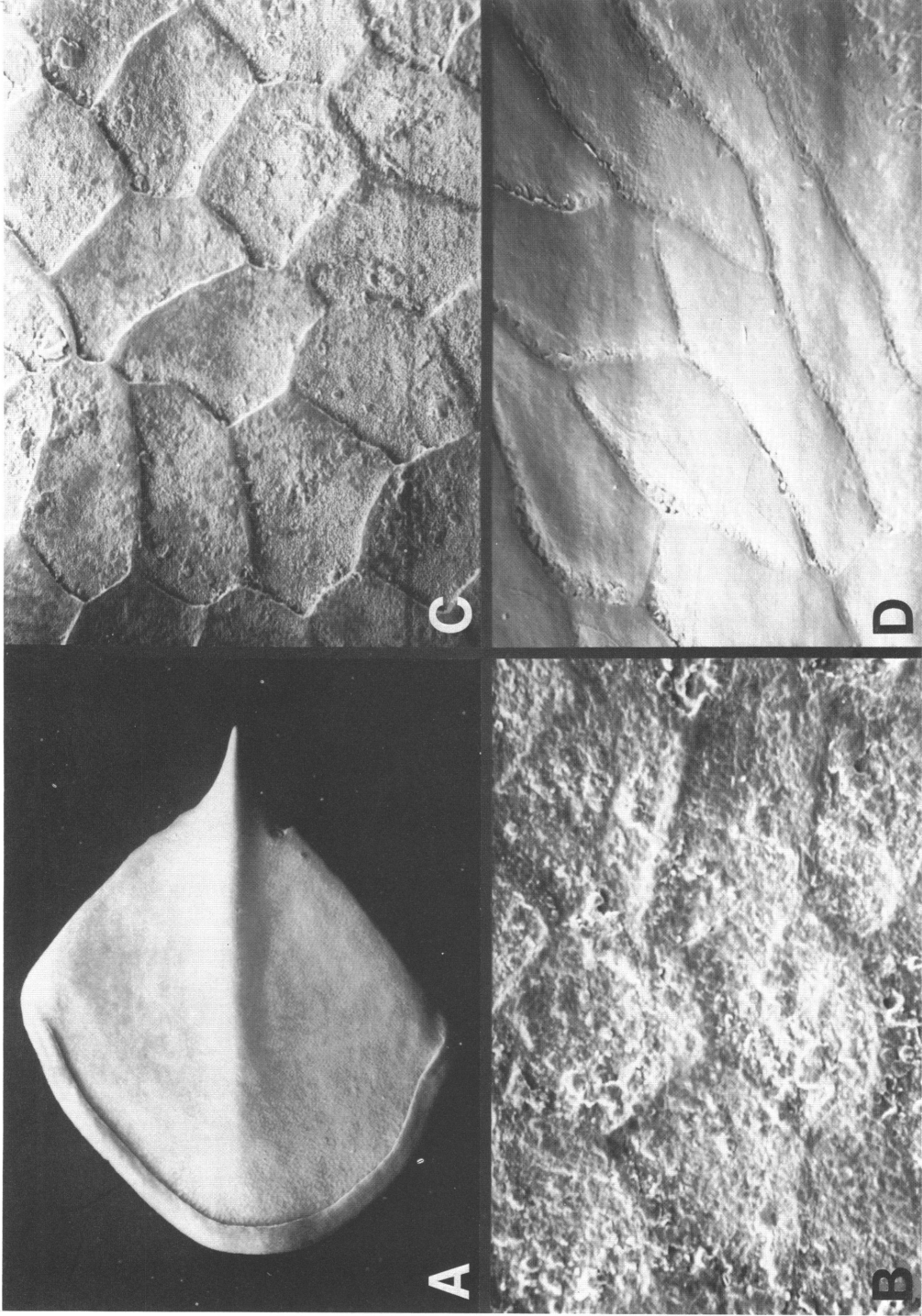


FIG. 10. Dorsal scale of *Sceloporus occidentalis*, adult female, AMNH 107495. A. Entire scale, no angle, $\times 24$. B. Region 1, no angle, $\times 1200$. C. Region 2, no angle, $\times 600$. D. Region 3, 45° angle, $\times 1200$.

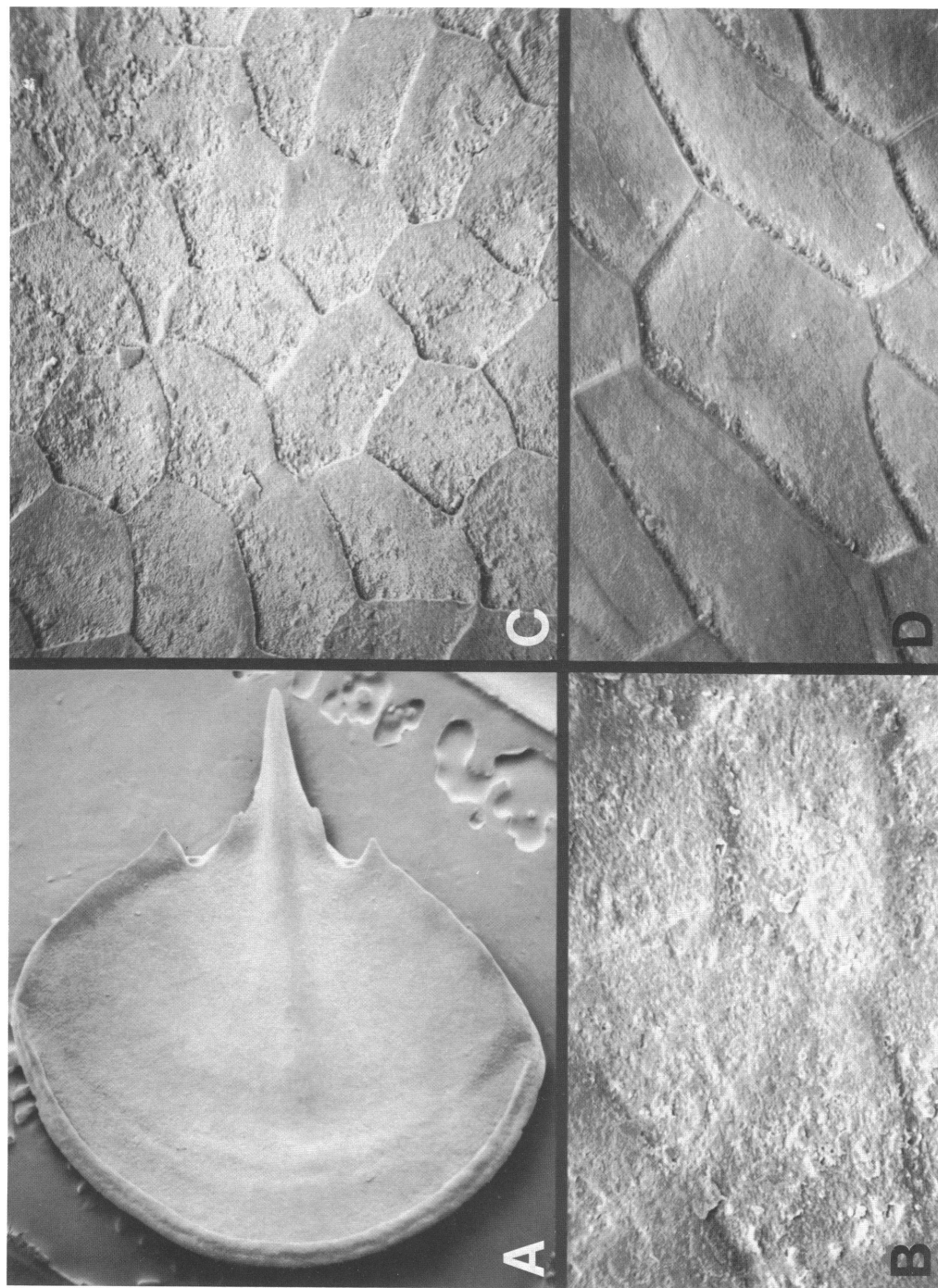


FIG. 11. Dorsal scale of *Sceloporus occidentalis*, adult male, AMNH 108047. A. Entire scale, no angle, $\times 24$. B. Region 1, no angle, $\times 1200$. C. Region 2, no angle, $\times 600$. D. Region 3, no angle, $\times 1200$.

distribution of spinules on a newly exposed scale surface (e.g., fig. 14D) as compared with those on a somewhat older scale surface (e.g., fig. 5D) suggests that the spinules may break off in places during exposure, thus revealing more clearly the generally inconspicuous ridge reticulum below. In addition, newly exposed cell surfaces in Region 3 may (or may not) have scattered spinules in addition to the numerous pits, particularly near their anterior boundaries (fig. 15B).

Clearly, the extreme variation in scale surface structure of *S. occidentalis* described above is a reflection of extensive changes that occur between molts. After shedding, the newly exposed scale surfaces are highly ornamented; they deteriorate drastically in time, however, and the ornamentation is replaced when the animal casts its skin again. The surface deterioration appears to be a process of erosion and sedimentation, including deposition of a film of variable thickness over the surface of the scale (fig. 13). These conclusions are supported by similar observations on scales from a molting *S. olivaceus* (not illustrated here) and *S. undulatus* (see below).

In addition, we tore pieces from the anterior edges of several scales (both cast and newly exposed scale surfaces) from the same shedding male (AMNH 111140) to determine that not only the extreme outermost few layers of cells are cast off. Indeed, the cast scale and the newly exposed keratinized scale surface are of approximately the same thickness (fig. 16).

Sceloporus undulatus

We examined a total of 10 dorsal scales from four individuals of *S. undulatus*. Scales of specimens that were preserved soon after capture were similar to those of the females of *S. occidentalis* with deteriorated surfaces (i.e., shortly prior to molting). Thus, as with *S. occidentalis*, we maintained some living *S. undulatus* in captivity in order to investigate the effects of the shedding cycle on surface structure of the scales. Upon noticing a lizard molting for the first time (fig. 12), we obtained concurrent samples of the scale surfaces that were cast off as well as the newly exposed scale surfaces from beneath the cast scales of the same individual (AMNH 111141).

Surface details of a cast scale are unclear and include low, bluntly rounded cell boundaries (indiscernible in places) and blunt spinules which in many areas are so obscured as to be indiscernible (fig. 17); nevertheless, cell surfaces in Region 3 may be clearly pitted (fig. 18). These conditions are similar to those on scale surfaces of *S. occidentalis* prior to shedding (compare with figs. 10, 11, 13). All details of the newly exposed scale surfaces, however, are clean and distinct, including the spinules on the surfaces of the cells and sometimes on the cell boundaries (fig. 19); cell surfaces in Region 3 (fig. 20) are pitted more distinctly than those on cast scales, and occasionally they have some scattered spinules, particularly near their anterior edges.

We also examined samples of cast scales and newly exposed scale surfaces obtained concurrently from a young (*ca.* seven months old) female (AMNH 111136) that we had hatched and raised in the laboratory. Essentially no deterioration had occurred on the surface of the cast scale prior to molting. Indeed, in this instance the details on the cast and on the newly exposed scale surfaces were most similar to one another (figs. 21, 22), being clean and distinct, including the cell boundaries and spinules. Failure of the surfaces of the cast scales to deteriorate prior to shedding on this laboratory-reared animal may be attributed to the shorter duration between molts in this young lizard as compared with adults and to the lack of exposure to conditions of living in the field.

The material we examined does not indicate that there are any significant differences in the

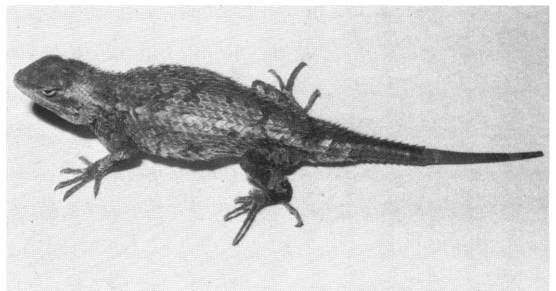


FIG. 12. Molting *Sceloporus undulatus*, AMNH 111141, adult female, snout-vent length, 60 mm.

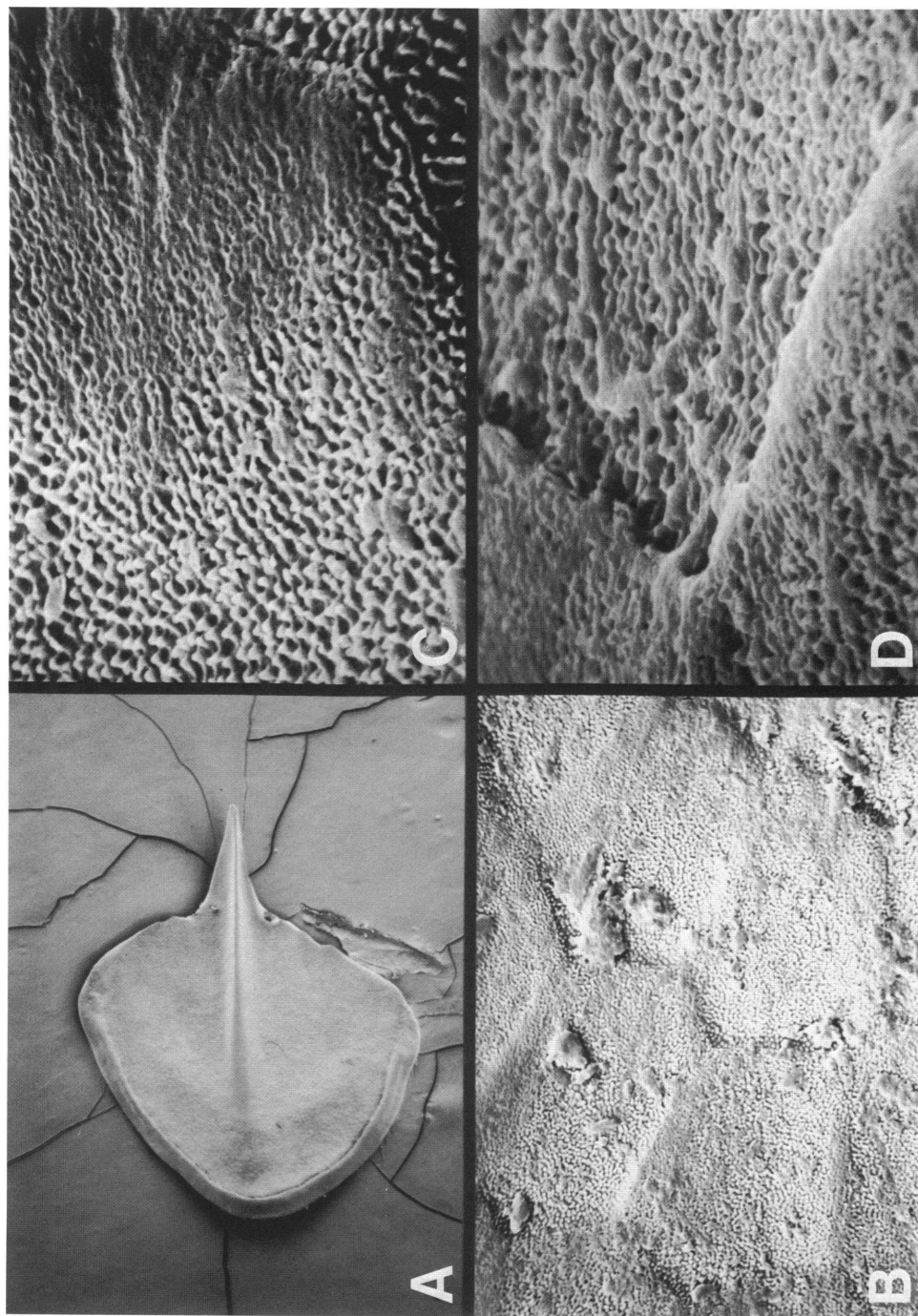


FIG. 13. Cast (shed) dorsal scale of *Sceloporus occidentalis*, adult male, AMNH 111140. A. Entire scale, no angle, $\times 24$. B. Region 1, no angle, $\times 1200$. C. Region 1, 45° angle, $\times 6000$. D. Region 2, 45° angle, $\times 6000$.

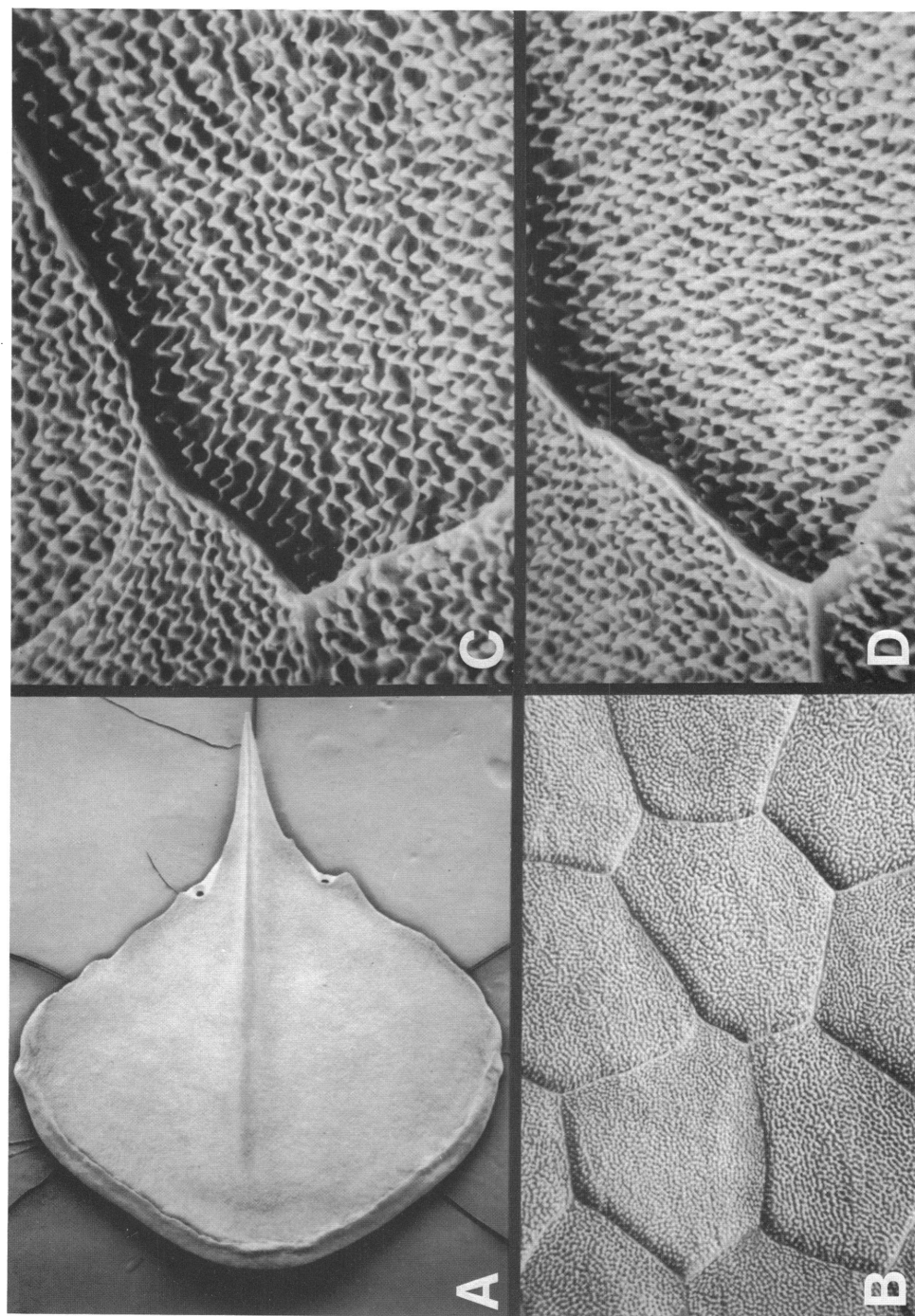


FIG. 14. Newly exposed dorsal scale surface following molting of *Sceloporus occidentalis*, adult male, AMNH 111140 (same lizard as fig. 13). A. Entire scale, no angle, $\times 24$. B. Region 2, 35° angle, $\times 6000$. C. Region 1, no angle, $\times 1200$. D. Region 1, 45° angle, $\times 6000$.

surface micro-ornamentation of dorsal scales from *S. occidentalis* and *S. undulatus*. Gross features of the scales of these species are similar also (see below).

Sceloporus graciosus

We examined two dorsal scales (fig. 23A, B) from an adult male (AMNH 109109); the scales are similar to each other. Each has a pore in a notch in its posterior edge and the following characteristics of micro-ornamentation: Region 1 with cells having conspicuous boundaries and surfaces covered with spinules distributed densely on an inconspicuous ridge reticulum (fig. 23C); Region 2 similar, but with cleaner, larger cells having somewhat fewer spinules (some probably broken off); Region 3 with transversely elongate cells whose surfaces are covered with pits. In Regions 1 and 2, cell boundaries may (or may not) bear some spinules, and in Region 3, scattered spinules occasionally are present, particularly near the anterior edges of the cells. We did not detect any features of the surface micro-ornamentation that clearly distinguishes *S. graciosus* from *S. occidentalis* and *S. undulatus*. However, the largest scales of *S. graciosus* are

distinctly smaller and usually have fewer pores than those on similar regions of the body of *S. occidentalis* and *S. undulatus* (see below).

Sceloporus jarrovi

We examined two dorsal scales from an adult male (AMNH 109117); the scales are similar to each other. Each one has a pore in a conspicuous notch on each side of the spine (fig. 24A). Large scales from large adults often have more notches and pores than occur in the species considered above. Micro-ornamentation was observed as follows: Region 1 with cell boundaries partly obscured by the extremely dense distribution of particularly tall spinules on the ridge reticulum of the cell surfaces (fig. 25A, B), the spinules also occurring on the partitions comprising the cell boundaries; Region 2 similar, but with larger cells having generally higher and more distinct boundaries (fig. 25C, D); Region 3 with transversely elongate cells whose surfaces are covered with pits, spinules of various heights, and tubercles (fig. 24B). The extreme tallness and abundance of the spinules in Regions 1 and 2 and the conspicuous abundance of spinules and tubercles on the cell surfaces in Region 3 on *S.*

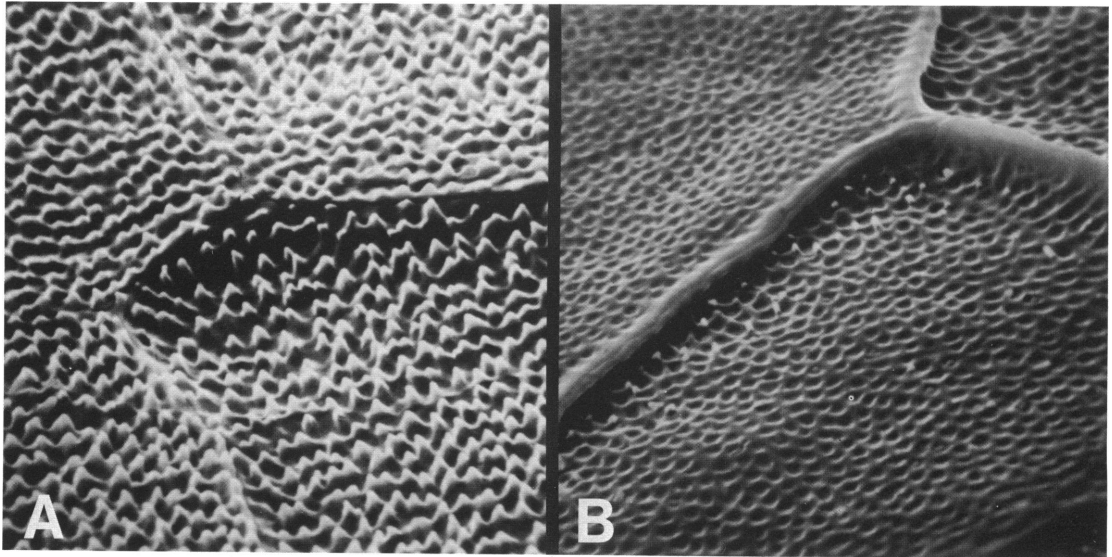


FIG. 15. Same scale of *Sceloporus occidentalis* as in figure 14. A. Region 1, 35° angle, $\times 6000$. B. Region 3, 35° angle, $\times 6000$.

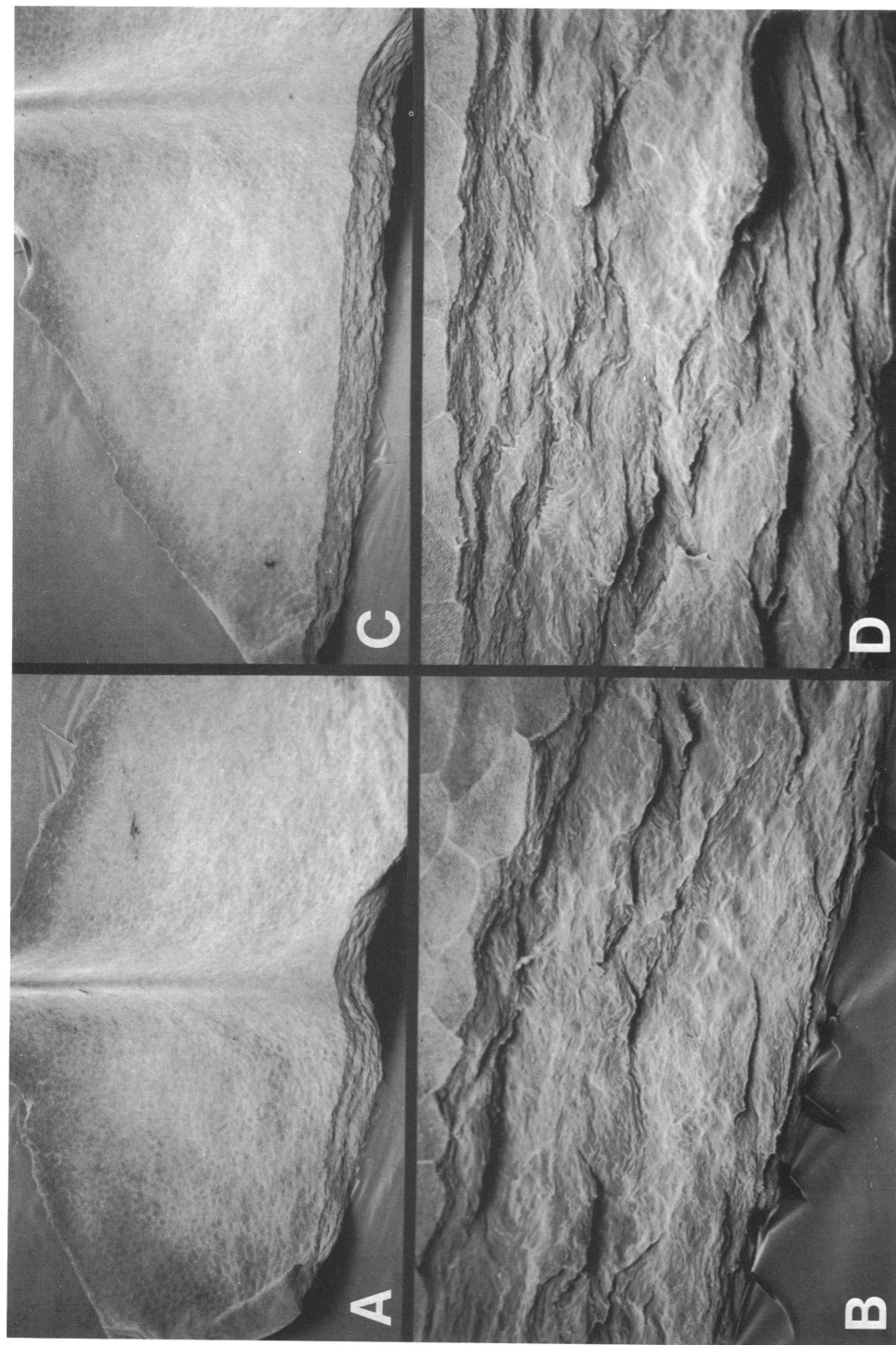


FIG. 16. Edges of two torn dorsal scales of molting *Sceloporus occidentalis*, adult male, AMNH 111140. A. Cast scale, 45° angle, ×60. B. Cast scale, 45° angle, ×600. C. Newly exposed scale surface, 45° angle, ×60. D. Newly exposed scale surface, 45° angle, ×600.

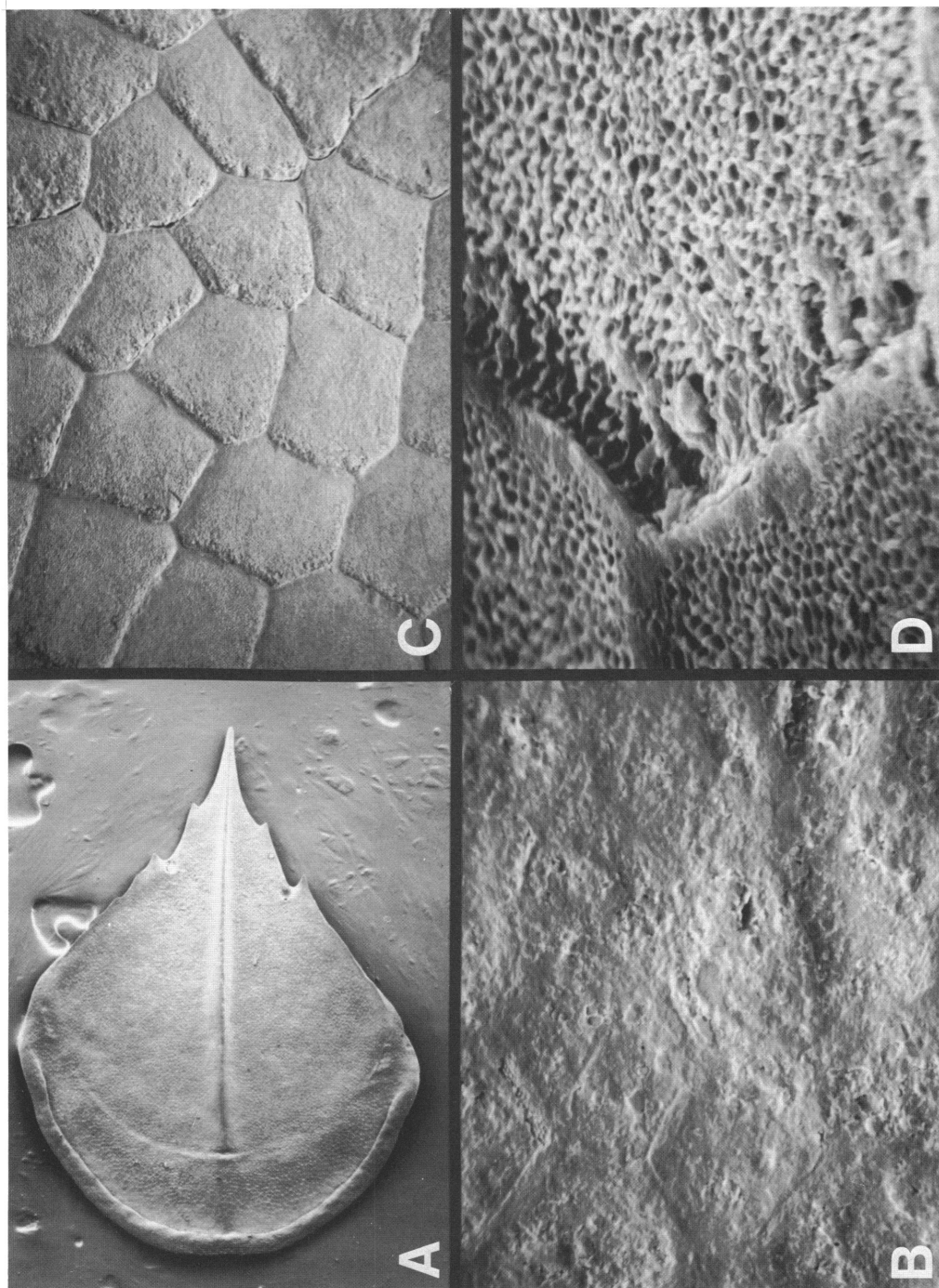


FIG. 17. Cast (shed) dorsal scale of *Sceloporus undulatus*, adult female, AMNH 111141. A. Entire scale, no angle, $\times 24$. B. Region 1, no angle, $\times 1200$. C. Region 2, no angle, $\times 600$. D. Region 2, 45° angle, $\times 6000$.

jarrovii differ from the *S. occidentalis*, *S. undulatus*, and *S. graciosus* we examined. Some gross features of the scales of *S. jarrovii* are distinctive among these species also (see below).

Sceloporus orcutti

We examined two dorsal scales from an adult male (AMNH 75597); the scales are similar to each other. While each scale has a serrated posterior edge, pores occur only in the most conspicuous notches on each side of the spine (fig. 26A). Micro-ornamentation was observed as follows: Region 1 with cells having low, bluntly rounded, nearly completely obscured boundaries and with no conspicuous surface micro-ornamentation (fig. 26B); Region 2 similar but with cleaner, larger cells having numerous spinules (obscure in places); Region 3 with transversely elongate cells whose surfaces are covered with pits. In Region 1 cell boundaries often bear spinules, and in Region 3 scattered spinules occasionally are present, particularly near the anterior edges of the cells. The appearance of these scales is consistent with our observations on deteriorated scales of *S. occidentalis* and *S. undulatus* (prior

to molting), and we did not detect any features of surface micro-ornamentation that clearly are distinctive to *S. orcutti*. However, we have yet to see a newly exposed, undeteriorated scale surface of *S. orcutti*. The observations of Burstein, Larsen, and Smith (1974) apparently were on a newer scale surface and suggest that the micro-ornamentation of *S. orcutti* may be rather similar to that of *S. jarrovii*. Scales from large adults of *S. orcutti* often are larger and in many cases have more notches and pores than those on similar regions of the body of *S. occidentalis*, *S. undulatus*, and *S. graciosus*.

Sceloporus clarkii

We examined three dorsal scales from two adult males (AMNH 84602 and 111138); all the scales are similar to one another. The large scales from large adults may have a high number of notches and pores in their posterior edges (fig. 27), but often they do not. One of the pores contained a plug of material whose surface was covered with ridges that appeared to be cell boundaries (fig. 27B, C, D); this was also observed occasionally in other species. In

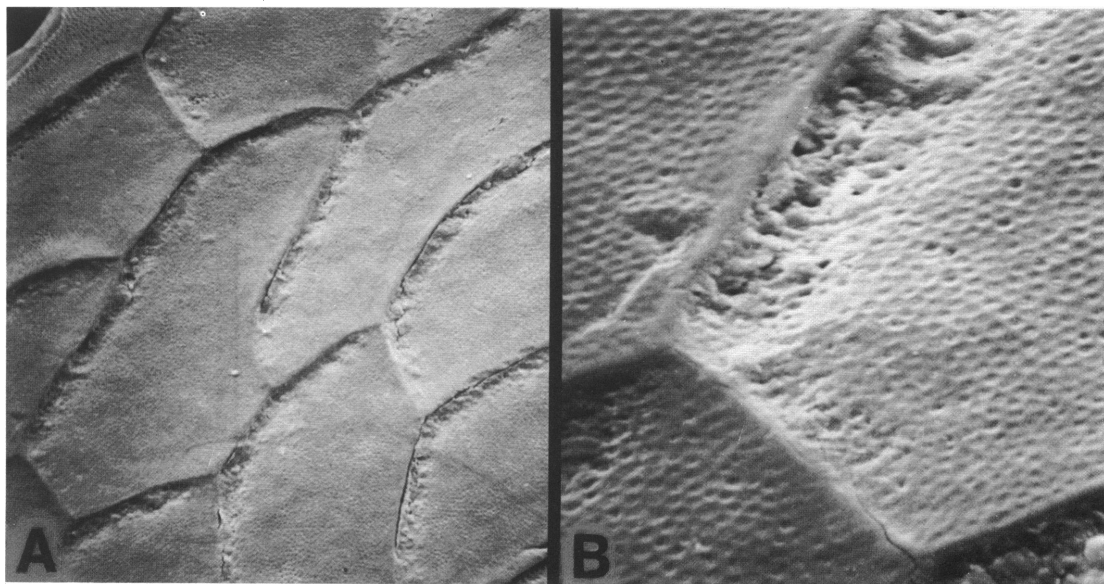


FIG. 18. Same cast scale of *Sceloporus undulatus* as in figure 17. A. Region 3, no angle, $\times 1200$. B. Region 3, 45° angle, $\times 6000$.

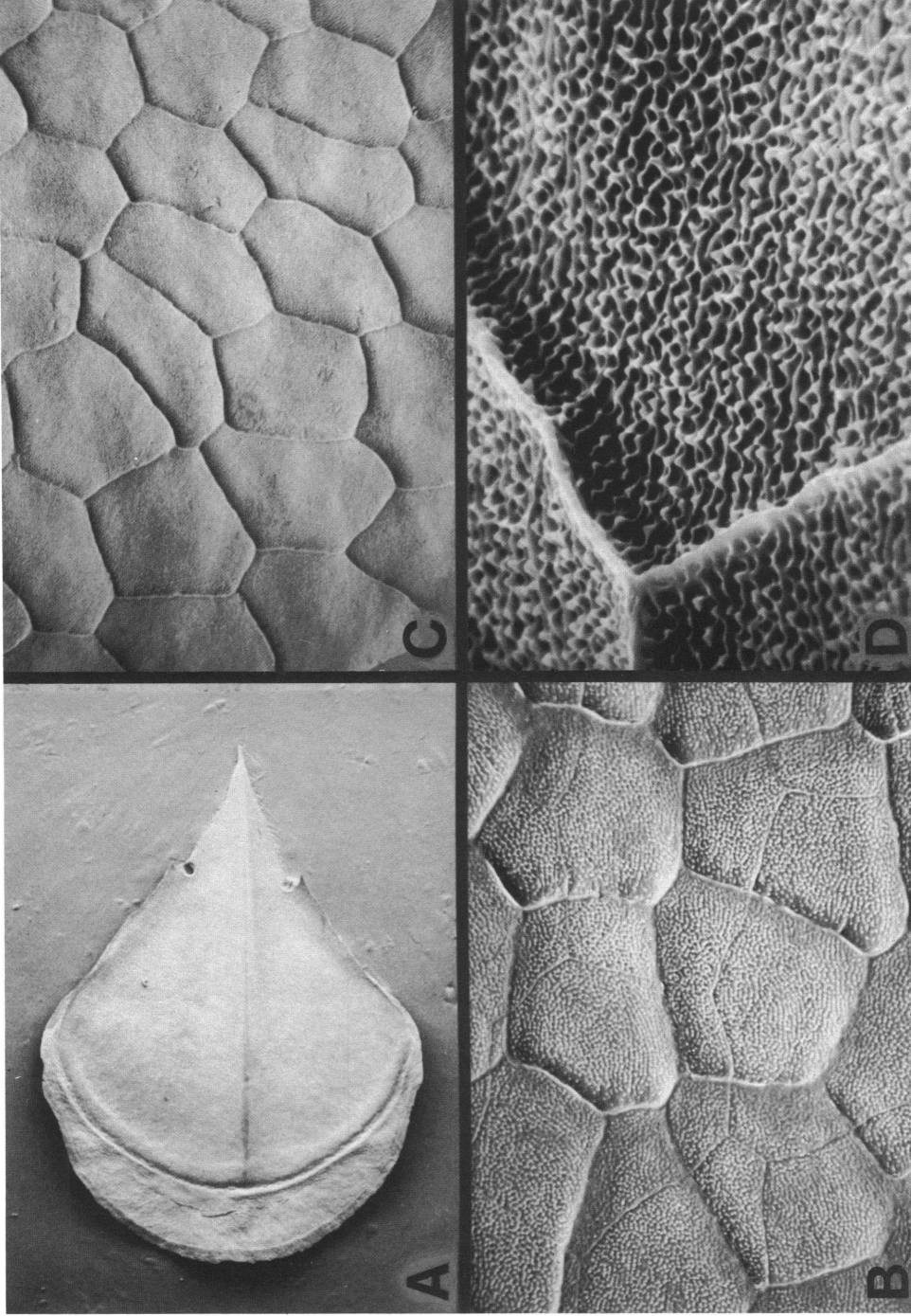


FIG. 19. Newly exposed dorsal scale surface following molting of *Sceloporus undulatus*, adult female, AMNH 111141 (same lizard as fig. 17). A. Entire scale, no angle, $\times 24$. B. Region 1, no angle, $\times 1200$. C. Region 2, no angle, $\times 600$. D. Region 2, 45° angle, $\times 6000$.

addition, on some scales, there is a second (weakly developed) troughlike depression on the surface approximately two-thirds of the distance from the anterior to the posterior edge. Micro-ornamentation was observed as follows: Region 1 with cells having low, bluntly rounded boundaries (fig. 28A), essentially completely obscured in places, and with surface details mostly obscured but in places clearly seen as deteriorated, blunt spinules and pits; Region 2 similar but in places clearly having much cleaner, more distinct, larger cells covered with spinules (fig. 28B), which sometimes also are seen on the cell boundaries; Region 3 with transversely elongate cells whose surfaces are covered with pits. The appearance of these scales is consistent with our observations on deteriorated scales of *S. occidentalis* and *S. undulatus* prior to molting, and we did not detect any features of surface micro-ornamentation that clearly are distinctive to *S. clarkii*. However, we have yet to see a newly exposed, undeteriorated scale surface of *S. clarkii*. The observations of Burstein, Larsen, and Smith (1974) apparently were on a newer scale surface of *S. clarkii* and suggest that its micro-ornamentation may be rather similar to that of *S.*

orcutti. Scales from large adults often are larger than those on similar regions of the body of *S. occidentalis*, *S. undulatus*, *S. graciosus*, *S. jarrovii*, and *S. orcutti* and may have more notches and pores than all of these excluding *S. jarrovii* and *S. orcutti*.

Sceloporus magister

We examined 12 dorsal scales from three adult males (AMNH 97781, 108053, 111139). In addition, we examined eight scales from various other parts of the body of two of these males for comparison with selected fossils (see below). The large dorsal scales from large adults often have a high number of notches and pores in their posterior edges, similar to those of *S. clarkii* (e.g., fig. 27A), but often they do not (e.g., fig. 29A).

Not all the dorsal scales are similar to one another in micro-ornamentation, but the differences observed are attributable to different lizards being at different stages in the shedding cycle, with some scale surfaces being more deteriorated than others. Micro-ornamentation of a presumably rather newly exposed scale surface was observed as follows: Region 1 with distinct

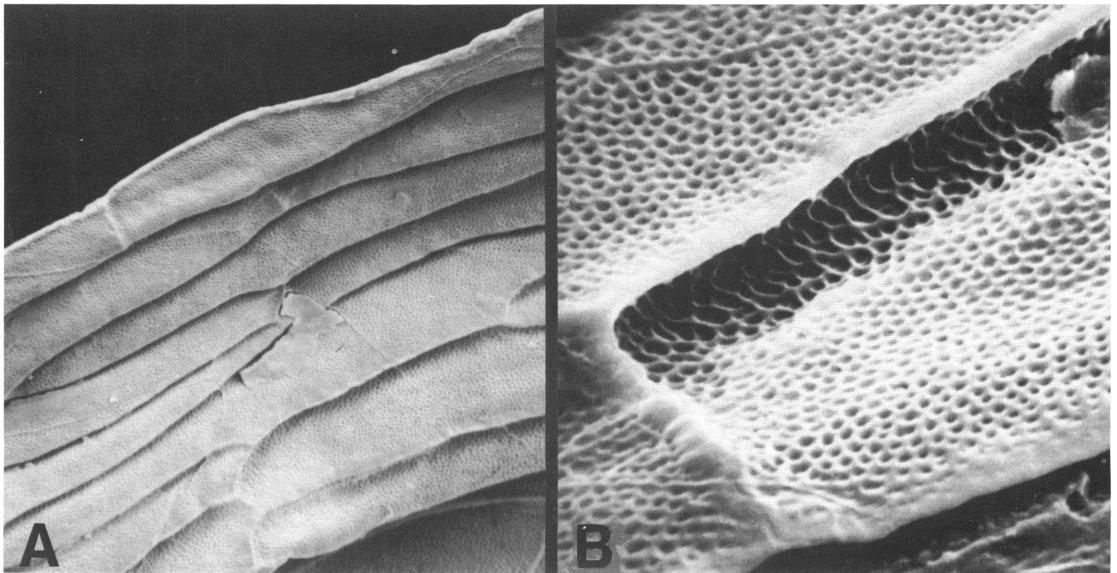


FIG. 20. Same newly exposed scale surface of *Sceloporus undulatus* as in figure 19. A. Region 3, no angle, $\times 1200$. B. Region 3, 45° angle, $\times 6000$.

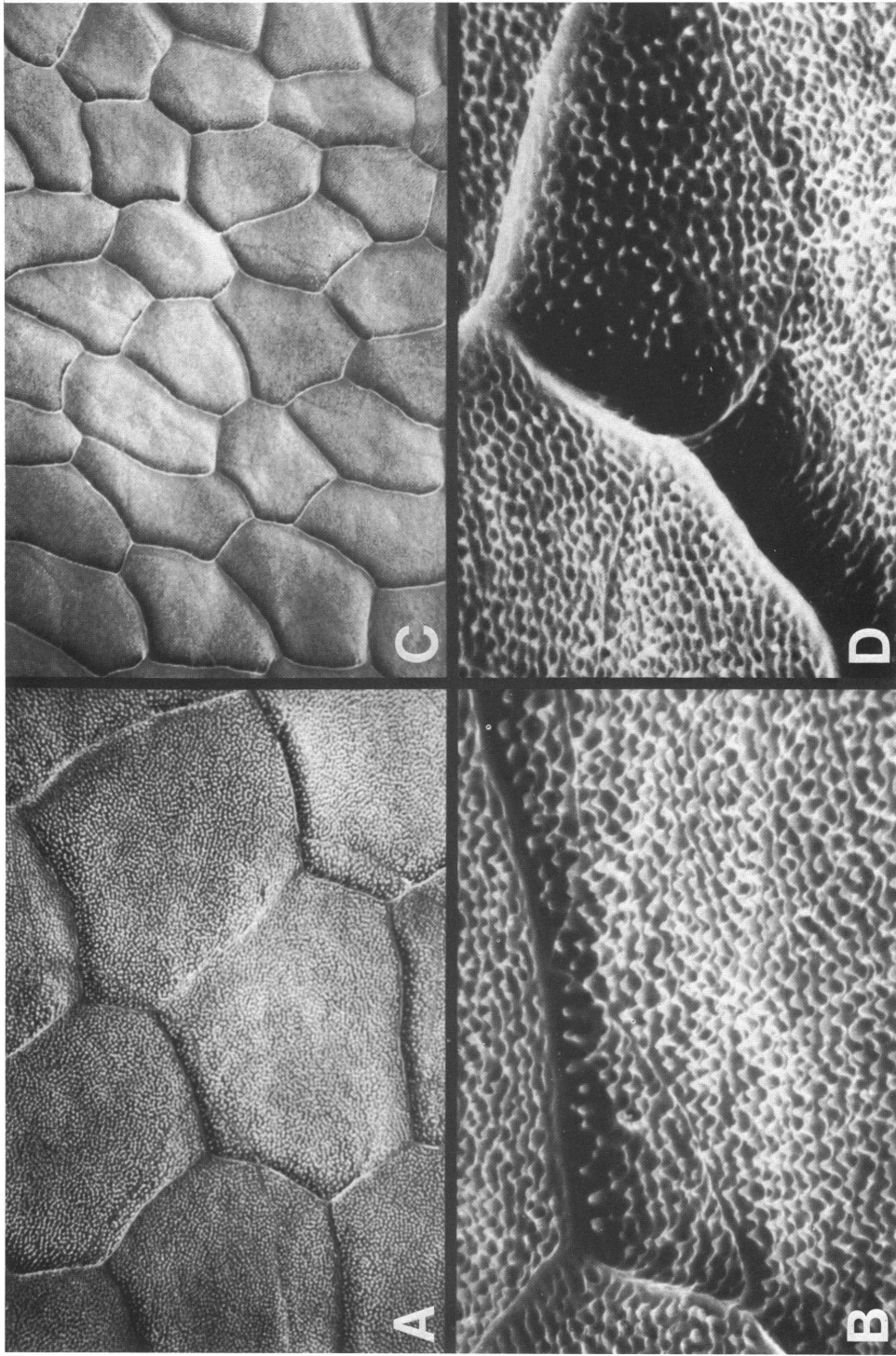


FIG. 21. Cast (shed) dorsal scale of *Sceloporus undulatus*, immature, laboratory-reared female, AMNH 111136. A. Region 1, no angle, $\times 1200$. B. Region 1, 45° angle, $\times 6000$. C. Region 2, no angle, $\times 600$. D. Region 2, 45° angle, $\times 6000$.

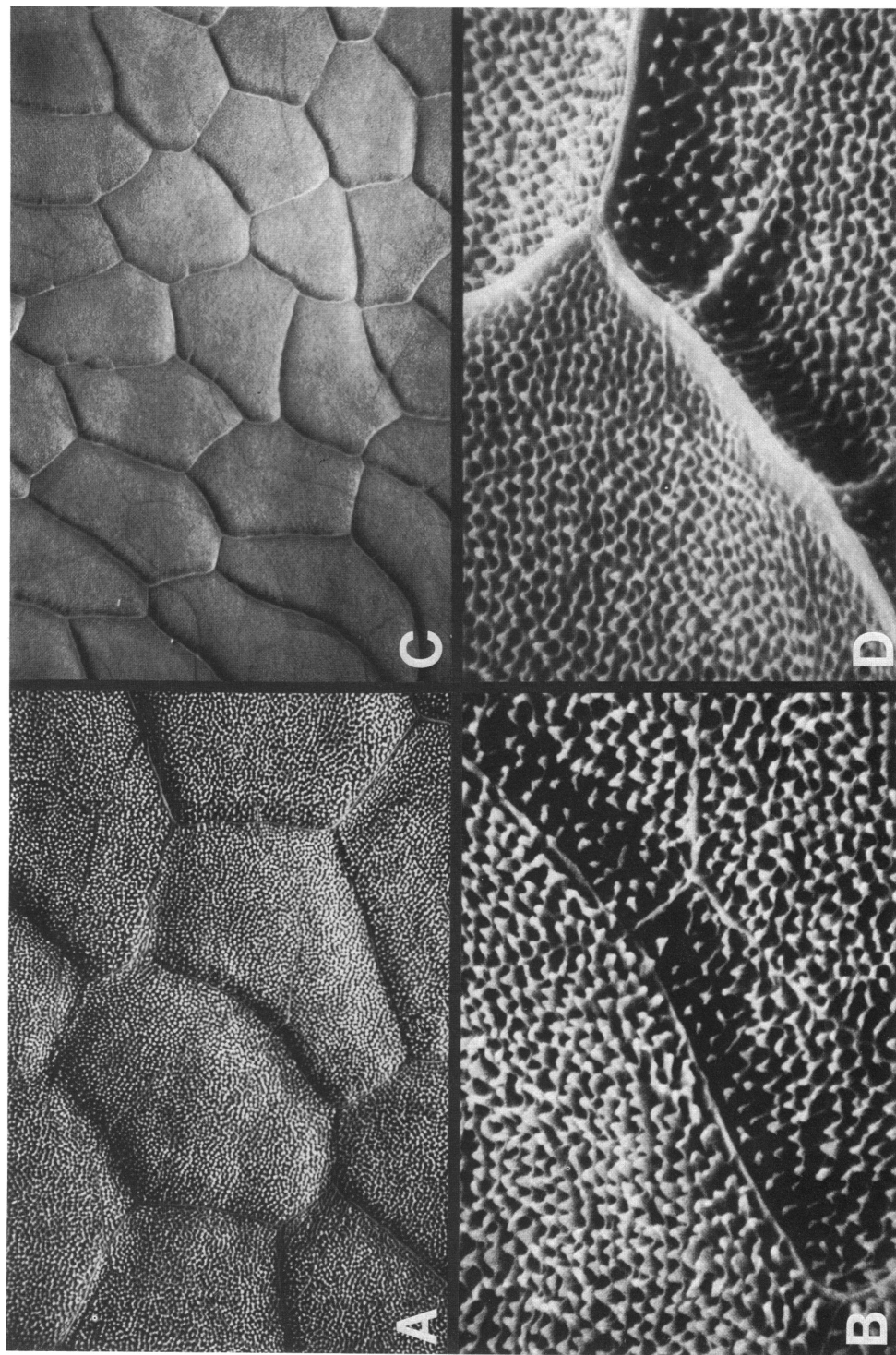


FIG. 22. Newly exposed dorsal scale surface following molting of *Sceloporus undulatus*, immature, laboratory-reared female, AMNH 111136 (same lizard as fig. 21). A. Region 1, no angle, $\times 1200$. B. Region 1, 45° angle, $\times 6000$. C. Region 2, no angle, $\times 600$. D. Region 2, 45° angle, $\times 6000$.

although somewhat deteriorated cell boundaries (fig. 29B), with surface details rather obscure but in places clearly seen as somewhat deteriorated, blunt spinules and pits among a ridge reticulum; Region 2 similar but with cleaner, larger cells (fig. 29C) whose surfaces are covered with tall spinules, which also are distributed densely on the partitions comprising the cell boundaries (fig. 29D); Region 3 with transversely elongate cells (fig. 30A), whose surfaces are covered with pits and also some scattered spinules of various heights (fig. 30B). The appearance of this scale is consistent with our expectations for a somewhat used scale of *S. jarrovii*, and we did not detect any features of surface micro-ornamentation that clearly are distinctive to *S. magister*. Scales from large adults often are larger than those on similar regions of the body of *S. occidentalis*, *S. undulatus*, *S. graciosus*, *S. jarrovii*, *S. orcutti*, and *S. clarkii*, and they may have more notches and pores than all of these excluding *S. jarrovii*, *S. orcutti*, and *S. clarkii*.

Micro-ornamentation of scales from various parts of the body (head, neck, tail, abdomen) is rather similar to that of middorsal scales. The

most conspicuous difference is that in some cephalic scutes (e.g., the frontal illustrated in fig. 39A), the cell boundaries in Region 2 consist of very high partitions, so that the cells themselves at low magnifications appear as large pits. Pores in most cephalic plates (e.g., the frontal and supraocular illustrated in figs. 39A and 40A, respectively) are in depressions on the scale surfaces rather than in notches. Also, pores usually are at the bases of the conspicuous notches in the posterior edges of the ventral scales (e.g., fig. 38).

FOSSILS

We examined 30 fossil scales from 10 different deposits. These included many scales that appeared to have been from the middorsal part of the body of a *Sceloporus* and many that were selected because they were from other areas of the body (e.g., tail, head; see below). In addition, we photographed several scales of *Sauromalus obesus* (see below). Not all the fossil *Sceloporus* scales are similar in micro-ornamentation. The differences observed are attributable to different lizards being at different stages in the shedding

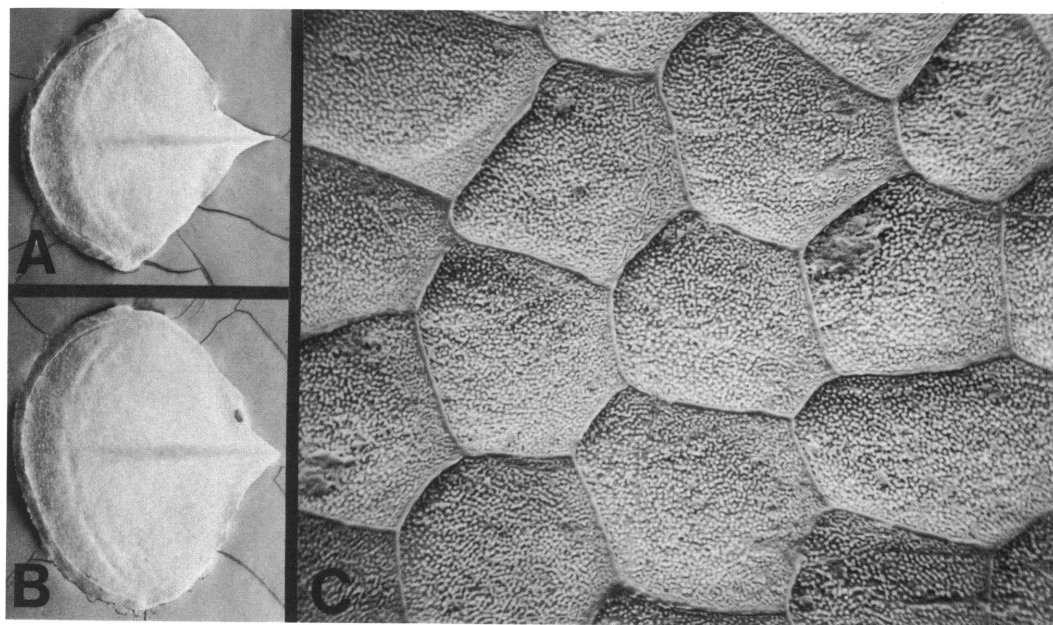


FIG. 23. Two dorsal scales of *Sceloporus graciosus*, adult male, AMNH 109109. A. Entire scale, no angle, $\times 24$. B. Entire scale, no angle, $\times 24$. C. Region 1 of scale in B, no angle, $\times 1200$.

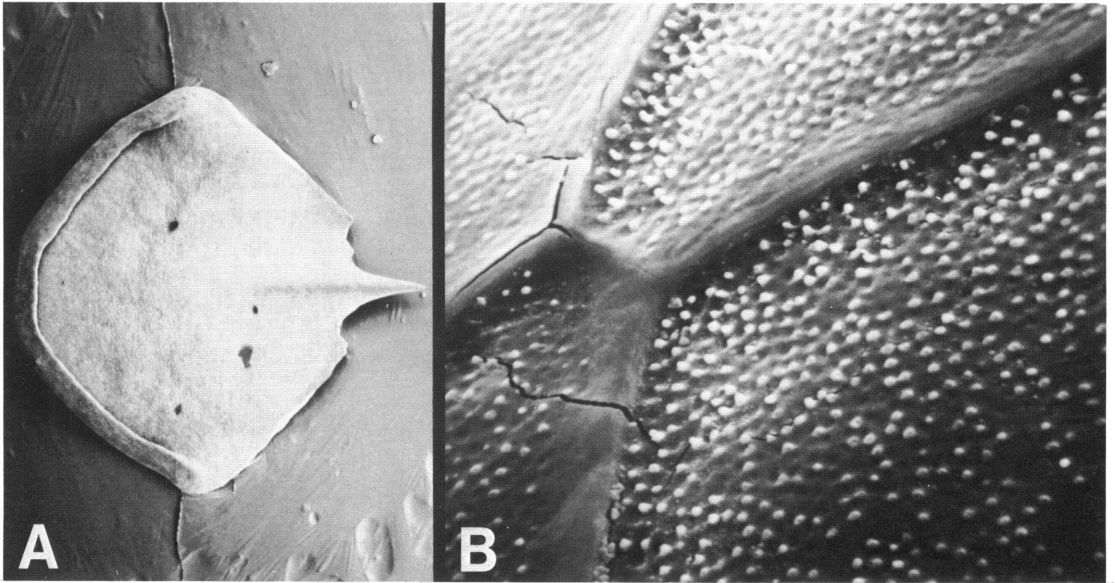


FIG. 24. Dorsal scale of *Sceloporus jarrovii*, adult male, AMNH 109117. A. Entire scale, no angle, $\times 24$. B. Region 3, no angle, $\times 6000$.

cycle. Most of the fossils are preserved excellently.

Some of the large fossil scales have a high number of notches and pores in their posterior edges (e.g., fig. 32A). Micro-ornamentation of the dorsal scales was observed as follows: Region 1 with cells of various degrees of clarity, depending on the scale (figs. 31B, 32B), being completely obscured on some scales, and on other scales having surface details usually obscured but in places clearly seen as spinules and pits among a fine reticulum of ridges; Region 2 similar but with larger cells (figs. 31C, 32C) and in places on some scales clearly seen as having much cleaner, more distinct cells covered with spinules and pits among a fine reticulum of ridges, sometimes including spinules on the cell boundaries (fig. 32D); Region 3 with transversely elongate cells (long axes approximately paralleling the anterior edge of the scale), whose surfaces are covered with pits (fig. 31D, 33A). One fossil scale clearly has some spinules in addition to the numerous pits on the scale surfaces in Region 3 (fig. 33B).

Many of the fossils are incomplete scales or fragments. Examination of damaged edges reveals that some of the scales apparently have been torn

(fig. 34A, B; compare with fig. 16), whereas others have a completely different appearance, suggesting that they have been gnawed on, possibly by insects (fig. 34C, D).

Appearance of the surface micro-ornamentation of the fossil scales is consistent with that of the Recent scales, including indications of deterioration of scale surfaces between molts. We did not detect any feature of surface micro-ornamentation that clearly is distinctive to the fossils, or that could be used unequivocally to identify them to species.

SUMMARY OF SURFACE DETAILS

The scales of the seven species of *Sceloporus* we have examined have basically similar surface micro-ornamentation. Differences observed are in two minor details: (1) spinules on the cell surfaces of *S. jarrovii* and *S. magister* are taller and more abundant than those observed on *S. occidentalis*, *S. undulatus*, and *S. graciosus*; and (2) in *S. jarrovii* tubercles and spinules appeared on cell surfaces in Region 3 considerably more densely than in *S. occidentalis*, *S. undulatus*, *S. graciosus*, and *S. magister*. We could not deter-

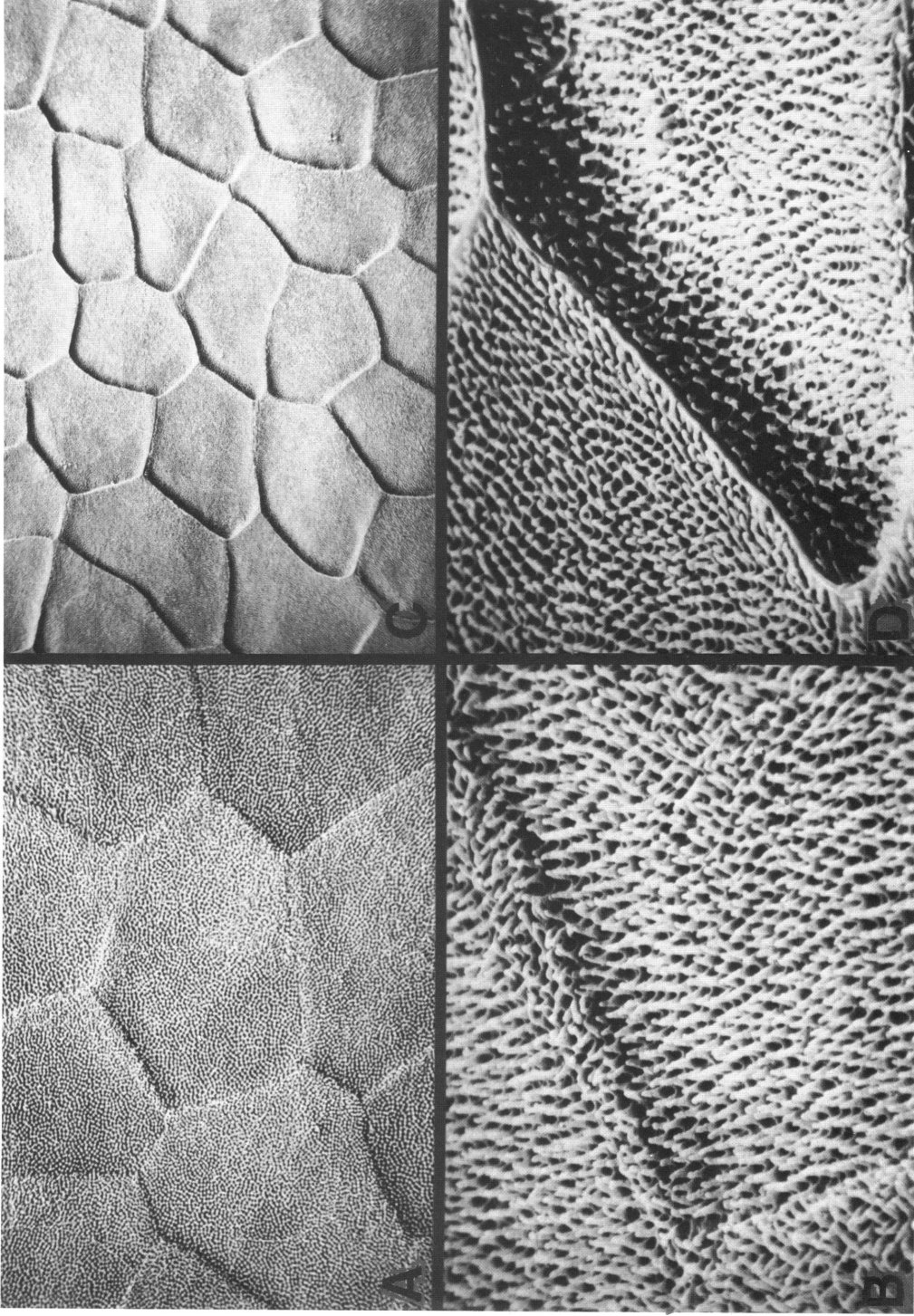


FIG. 25. Ornamentation of same scale of *Sceloporus jarrovi* as in figure 24. A. Region 1, no angle, $\times 1200$. B. Region 1, 45° angle, $\times 6000$. C. Region 2, no angle, $\times 600$. D. Region 2, 45° angle, $\times 6000$.

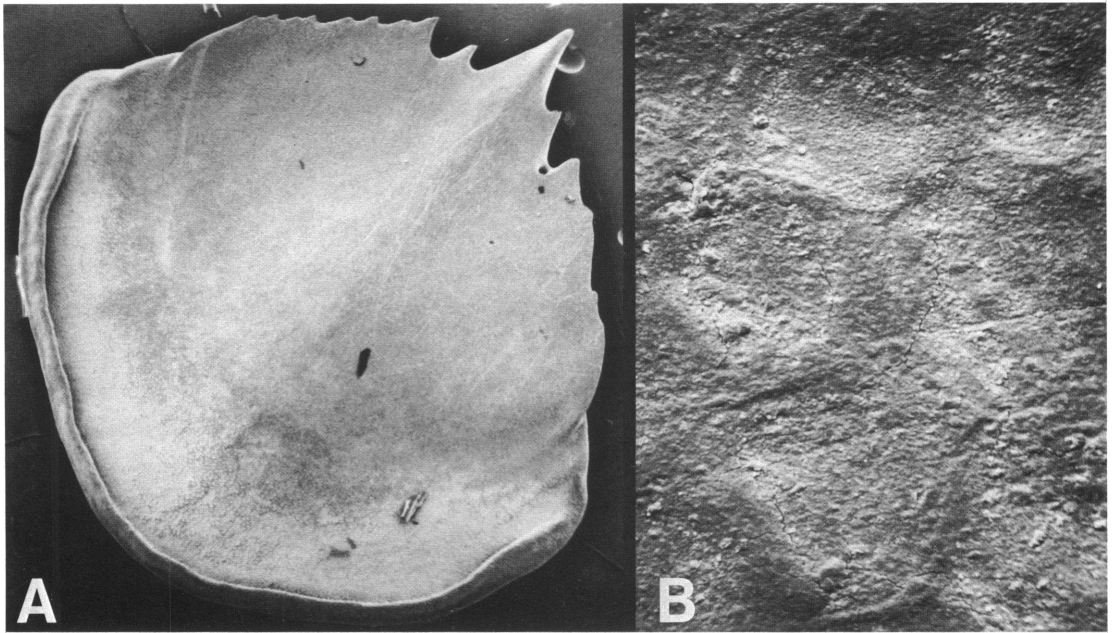


FIG. 26. Dorsal scale of *Sceloporus orcutti*, adult male, AMNH 75597. A. Entire scale, no angle, $\times 19$. B. Region 1, no angle, $\times 1200$.

mine the nature of these characteristics in *S. orcutti* and *S. clarkii* because we did not see relatively newly exposed scale surfaces of these species.

It is not possible to understand the significance or the reliability of the minor differences observed without examining considerably more specimens than we have examined. In addition, the extensive variation in surface details that we found to be correlated with shedding in *S. occidentalis* and *S. undulatus* suggests that the most reliable method for studying surface micro-

ornamentation is to work with living captives of each species and to examine their newly exposed scale surfaces immediately following molting. We could not accomplish this with the fossil forms, of course, and our observations suggested it was not practical to examine in excess of 2000 fossil scales with the SEM in hopes of finding reliable characteristics for specific identifications. Therefore, we turned our attention to other characteristics of *Sceloporus* scales that casual observations suggested may be helpful in identifying the fossils: absolute size and shape.

GROSS FEATURES OF *SCELOPORUS* SCALES

RECENT SCALES

Casual observations on specimens of the seven Recent species discussed above indicated that within each species, the largest individuals had some scales that were larger than those on smaller individuals. Also, large specimens of the larger species appeared to have

some scales distinctly larger than the largest scales on the largest specimens of the smaller species. In addition, larger scales often, although not always, had more notches and pores than smaller scales. Although it seemed that scales of the smaller species become similar to those of the larger species during growth, it appeared that

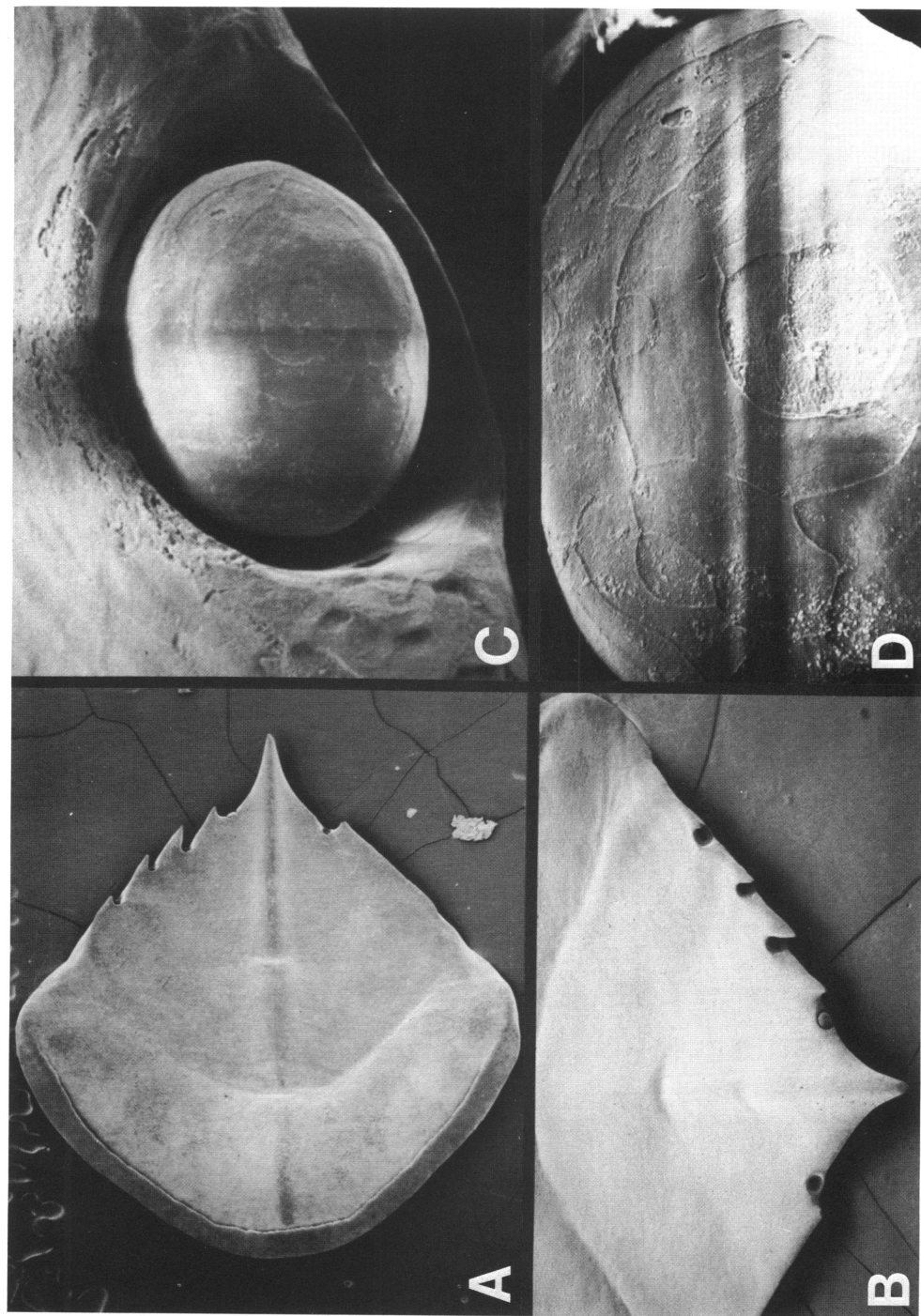


FIG. 27. Dorsal scale of *Sceloporus clarkii*, adult male, AMNH 111138. A. Entire scale, no angle, $\times 17$. B. Notches and pores in posterior edge, 45° angle, $\times 24$. C. Plugged pore (first to right of spine in B), 45° angle, $\times 600$. D. Surface of plug in C, 60° angle, $\times 1200$.

some of the largest scales on the larger species were distinctive because they exceeded the maximum dimensions that occur even on the largest individuals of the smaller species. Thus, it seemed that in examining fossil scales, certain large and distinctive ones would be significant in ruling out the possibility that they had been deposited by individuals of the smaller species.

For each of the seven species under investigation, we selected the largest specimens in the herpetological collection at the AMNH, using samples from geographically relevant localities. We examined and measured distinctive, recognizable scales on series of large specimens of all of them, using a dissecting microscope and ocular micrometer. When possible, we examined large representatives of both sexes, but in two instances large females were not available. It was necessary to examine series of large specimens for each species because variation in scutellation is such that the largest scale of a particular type may not necessarily be on the largest individual. The largest specimen we examined for each species is identified in table 1, along with the maximum known length reported by Smith (1946). Most of the specimens we used are close to the maximum sizes known, and two may exceed them.

TABLE 1
Body (Snout-Vent) Lengths (in Millimeters) of
Seven Species of *Sceloporus*

| Species | AMNH Number | Length of Specimen | Maximum Length (<i>fide</i> Smith, 1946) |
|------------------------|----------------|-----------------------|----------------------------------------------------|
| <i>S. graciosus</i> | 22953 | 62 | 65 |
| <i>S. undulatus</i> | 111131 | 86 | 82 |
| <i>S. occidentalis</i> | 107495 | 85 | 94 |
| <i>S. jarrovi</i> | 84626 | 98 | 90 |
| <i>S. orcutti</i> | 20479 | 100 | 109 |
| <i>S. clarkii</i> | 2556 | 119 | 130 |
| <i>S. magister</i> | 27641 | 135 | 140 |

DORSAL SCALES, EXCLUDING CEPHALIC
SCUTES

The largest dorsal scales on all species occur dorsally or laterally on the base of the tail or dorsally on the sacral region (table 2). The greatest number of notches and pores in dorsal scales occurs in the same areas (table 2), but the notches generally (not always) are considerably less conspicuous on caudal than on body scales. Notch counts include only notches having pores;

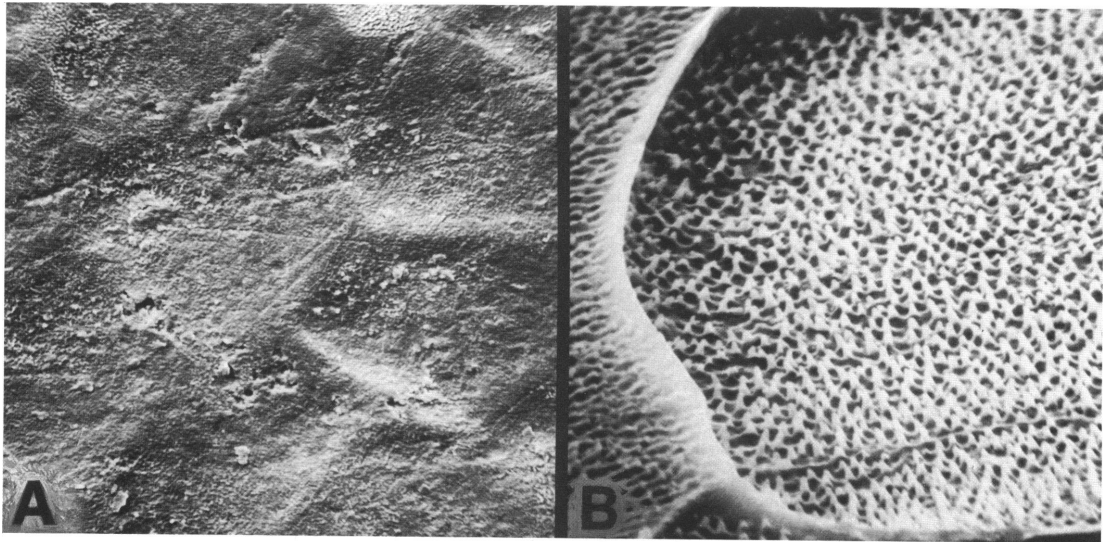


FIG. 28. Surface of same scale of *Sceloporus clarkii* as in figure 27. A. Region 1, no angle, $\times 1200$. B. Region 2, 45° angle, $\times 6000$.

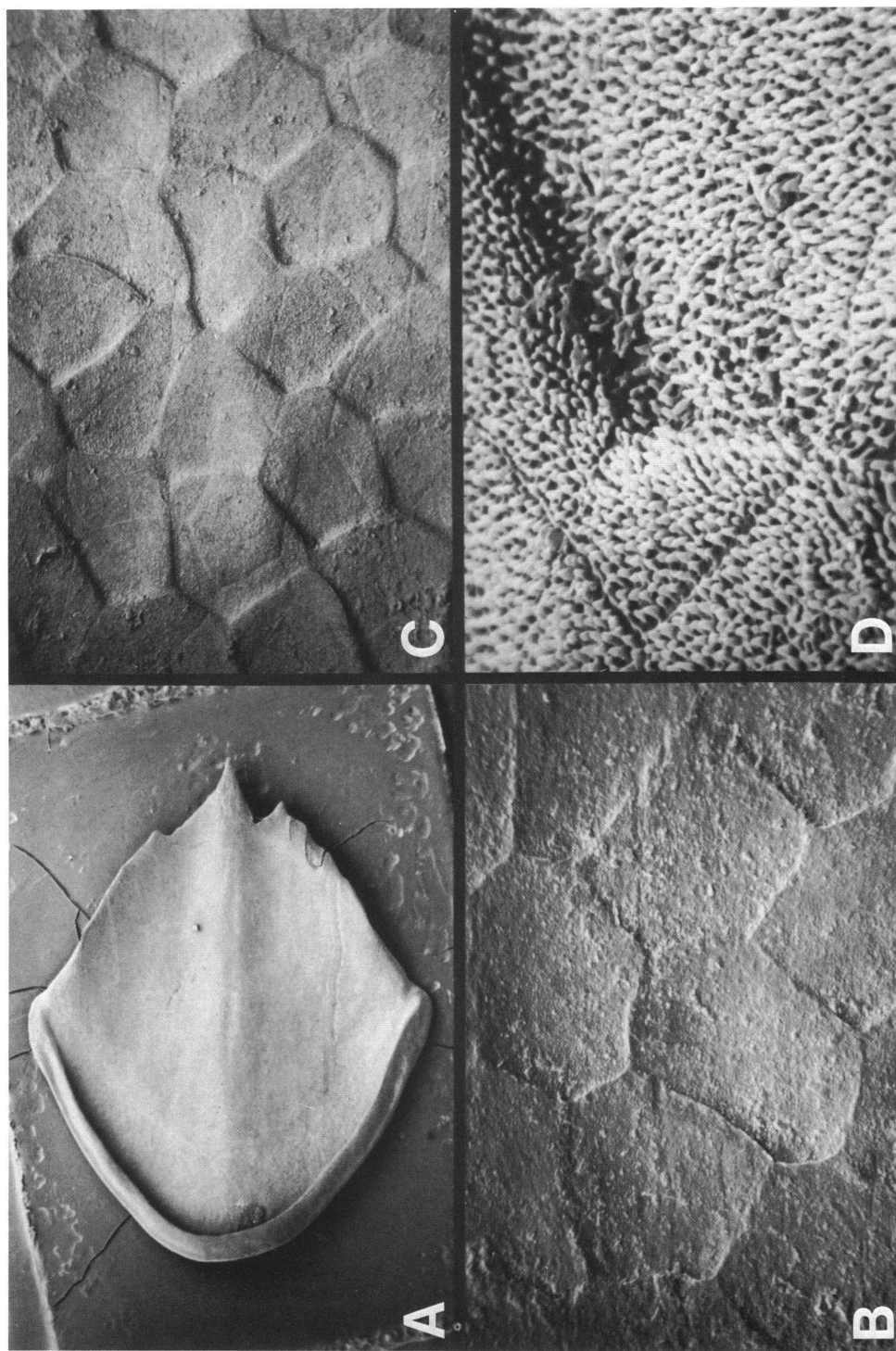


FIG. 29. Dorsal scale of *Sceloporus magister*, adult male, AMNH 97781. A. Entire scale, no angle, $\times 14$. B. Region 1, no angle, $\times 1200$. C. Region 2, no angle, $\times 600$. D. Region 2, 35° angle, $\times 6000$.

TABLE 2
Maximum Dimensions (in Millimeters) and Notch Counts for Dorsal Scales
of Seven Species of *Sceloporus*

| Species | Broadest, 1-keeled, on Neck Width | Posterior Body ^a | | | Basal Caudal ^a | | | Medial Caudal ^b | |
|------------------------|-----------------------------------------|-----------------------------|-------|---------|---------------------------|-------|---------|----------------------------|-------|
| | | Length | Width | Notches | Length | Width | Notches | Length | Width |
| <i>S. graciosus</i> | 1.4 | 2.1 | 2.1 | 3 | 2.2 | 2.2 | 4 | 2.2 | 1.8 |
| <i>S. undulatus</i> | 2.0 | 3.4 | 3.4 | 4 | 3.4 | 3.9 | 6 | 2.8 | 2.2 |
| <i>S. occidentalis</i> | 2.1 | 3.2 | 3.4 | 3 | 3.5 | 3.4 | 6 | 3.2 | 2.2 |
| <i>S. jarrovi</i> | 3.5 | 3.5 | 3.6 | 7 | 4.9 | 4.6 | 14 | 4.6 | 3.2 |
| <i>S. orcutti</i> | 4.1 | 5.0 | 5.9 | 7 | 4.8 | 4.6 | 9 | 4.5 | 3.1 |
| <i>S. clarkii</i> | 3.8 | 7.0 | 6.6 | 7 | 6.7 | 6.4 | 10 | 5.0 | 3.8 |
| <i>S. magister</i> | 5.0 | 7.4 | 7.8 | 9 | 7.6 | 7.3 | 10 | 5.5 | 4.3 |

^aNot all traits necessarily from one scale.

^bDimensions apply to both dorsal and lateral caudals near midtail.

some large scales have scalloped or serrated posterior edges (e.g., fig. 26A), on which small notches were not included in the count unless they contained pores. The notch counts presented are the total number per scale, including those to each side of the keel. Scales from mid-dorsal surfaces generally are symmetrical in shape with a medial keel; lateral scales have an unsymmetrical shape characteristic to their side of the body and usually have their keel situated dorsal to the midline. Lateral body scales and those on the arms and legs generally are similar to the other dorsals, but they are smaller and usually have fewer notches and pores.

Only two species had distinctive traits to note in addition to absolute size and notch counts. On many scales of *S. jarrovi*, particularly on laterals and caudals, keels usually are exceptionally prominent, being relatively high and sharp-edged and having an elongate, upturned spine; the posterior edges of the scales are relatively thick also, and their ventral envelopes, which contain deeper layers of the scale *in situ*, are relatively short. On scales of *S. orcutti* also, particularly on laterals and caudals, keels and spines usually are very prominent, but not so much so as on *S. jarrovi*.

VENTRAL SCALES

The largest ventrals on all the species are on either the abdomen (often ventrolaterally) or

tail, near its base (table 3). These scales lack the keel and spine that characterize dorsals, and they appear smooth at very low magnifications (e.g., fig. 38), although frequently certain scales on the ventral surface of the chest region are distinctive due to their unusually broad width relative to their length (table 3). Whereas many ventrals lack posterior notches and pores, most have one or two.

CEPHALIC SCUTES

Many scales from different parts of the head have distinctive morphology (e.g., frontals, supraoculars; Smith, 1939, p. 23; our fig. 1B, p. 456). We measured only those kinds that were found among the fossils (table 4).

FOSSIL SCALES

The 35 middens in which a total of more than 2100 fossil scales were found are listed in table 5 along with their available radiocarbon dates. The localities are plotted in figure 35. We examined each fossil scale from each deposit and compared its characteristics with those of the Recent species examined. The scales of each midden are discussed below, and measurements for selected ones are presented (length × width).

Burro Canyon, Number 1 (samples from levels 1, 3, and 6), Kofa Mountains, Yuma County, Arizona: There is a total of 30 *Sceloporus* scales

TABLE 3
Maximum Dimensions (in Millimeters) for Ventral Scales of Seven Species of *Sceloporus*

| Species | 1-notched Abdominal ^a | | 2-notched Abdominal ^a | | Basal Caudal ^{a,b} | | Broadest on Chest | |
|------------------------|----------------------------------|-------|----------------------------------|-------|-----------------------------|-------|-------------------|-------|
| | Length | Width | Length | Width | Length | Width | Length | Width |
| <i>S. graciosus</i> | 1.4 | 1.5 | 1.4 | 1.4 | 2.0 | 2.1 | 1.4 | 1.8 |
| <i>S. undulatus</i> | 2.2 | 2.1 | 2.1 | 2.2 | 2.5 | 2.2 | 2.1 | 2.2 |
| <i>S. occidentalis</i> | 2.2 | 2.1 | 2.5 | 2.1 | 2.8 | 2.2 | 2.1 | 2.4 |
| <i>S. jarrovi</i> | 2.7 | 2.8 | 2.2 | 2.2 | 3.5 | 3.5 | 2.2 | 2.9 |
| <i>S. orcutti</i> | 2.5 | 2.8 | 3.6 | 3.5 | 3.6 | 3.9 | 2.9 | 3.9 |
| <i>S. clarkii</i> | 4.6 | 3.8 | 4.1 | 3.5 | 4.1 | 4.5 | 4.3 | 5.0 |
| <i>S. magister</i> | 5.3 | 4.5 | 4.8 | 4.6 | 4.8 | 5.2 | 4.5 | 5.0 |

^aBoth dimensions not necessarily from one scale.

^bThese may be unnotched, 1-notched, or 2-notched.

or fragments in the three samples (AMNH 111970-111972). A medial caudal (incomplete, but at least 3.9 mm. long and with six posterior notches and pores) exceeds the maximum length for those of *S. occidentalis* (table 2). A right supraocular (fig. 40B; 3.4 × 1.8 mm.) exceeds the maximum size for *S. jarrovi* (table 4). A frontoparietal (fig. 39D; 2.4 × 1.8 mm.) also is consistent with those occurring on larger species (e.g., *S. orcutti*, table 4). These large scales are among those from level 1. The remaining scales or fragments are not particularly useful for identification. The fossil scales could have been deposited by *Sceloporus magister*, which occurs in the immediate vicinity of this locality today. None of the other Recent species of *Sceloporus*

occurs within approximately 150 km. of the fossil locality. Two radiocarbon dates are associated with the fossil scales: 14,400±330 YBP (level 1), and 13,400±250 YBP (level 6).

Emery Falls, Number 1, N side of the lower Grand Canyon, mile 275 below Lee's Ferry (Coconino County), Mohave County, Arizona: The single scale in this sample (AMNH 111973) is an incomplete *Sceloporus* dorsal (3.2+ × 3.1+ mm.) that is too large for *S. graciosus* (table 2). A radiocarbon date of 10,100±200 YBP is associated with this scale. The following middens labeled as Emery Falls are from the same canyon.

Emery Falls, Number 4: The sample (AMNH 111974) contains two *Sceloporus* scales. The largest is a single-notched ventral (3.1 × 2.8

TABLE 4
Maximum Dimensions (in Millimeters) for Selected Cephalic Scutes of Seven Species of *Sceloporus*

| Species | Anterior Frontal | | Frontonasal ^a | | Supraocular ^a | | Frontoparietal ^a | | Parietal ^a | |
|------------------------|------------------|-------|--------------------------|-------|--------------------------|-------|-----------------------------|------------------|-----------------------|-------|
| | Length | Width | Length | Width | Length | Width | Length | Width | Length | Width |
| <i>S. graciosus</i> | 2.5 | 2.5 | 2.1 | 1.5 | 2.5 | 1.7 | 2.2 | 1.5 | 1.5 | 2.0 |
| <i>S. undulatus</i> | 3.4 | 3.5 | 2.5 | 2.2 | 2.9 | 2.0 | 2.7 | 1.5 | 3.8 | 2.7 |
| <i>S. occidentalis</i> | 3.4 | 3.5 | 2.9 | 2.0 | 3.2 | 2.0 | 2.4 | 1.5 | 2.8 | 3.1 |
| <i>S. jarrovi</i> | 3.6 | 4.2 | 3.5 | 2.2 | 3.2 | 1.8 | 2.7 | 2.1 | 3.9 | 2.8 |
| <i>S. orcutti</i> | 3.6 | 3.6 | 3.4 | 2.7 | 4.8 | 2.4 | 2.4 | 1.8 | 3.6 | 3.9 |
| <i>S. clarkii</i> | 4.5 | 5.2 | 3.8 | 3.6 | 4.9 | 2.4 | 3.1 ^b | 2.4 ^b | 4.3 | 4.6 |
| <i>S. magister</i> | 4.9 | 7.1 | 4.1 | 3.2 | 5.7 | 2.8 | 2.8 ^b | 2.5 ^b | 4.6 | 5.9 |

^aBoth dimensions not necessarily from one scale.

^bLarger, distinctively shaped, irregular scales not included because they were not found among the fossils.

TABLE 5
Fossil Packrat Middens that Contained Fossil Lizard Scales

| Midden | Elevation (m.) | C ¹⁴ Date YBP ^a | Laboratory Number ^b | Area | County | State |
|----------------------------------|-------------------|---------------------------------------|-----------------------------------|------------------|----------------|------------|
| Burro Canyon No. 1, Level 1 | 862 | 14,400±330 | A-1315J | Kofa Mts. | Yuma | Arizona |
| Burro Canyon No. 1, Level 3 | 862 | None | — | Kofa Mts. | Yuma | Arizona |
| Burro Canyon No. 1, Level 6 | 862 | 13,400±250 | A-1357J | Kofa Mts. | Yuma | Arizona |
| Emery Falls No. 1 | 520 | 10,100±200 | A-1380Nm | Grand Canyon | Mohave | Arizona |
| Emery Falls No. 4 | 550 | 11,990±490 | A-1423J | Grand Canyon | Mohave | Arizona |
| Emery Falls No. 6 | 550 | 10,910±450 | A-1427FNm | Grand Canyon | Mohave | Arizona |
| Falling Arches No. 1 | 325 | 11,650±190 | A-1548J | Whipple Mts. | San Bernardino | California |
| Muav Gate No. 1 | 440 | 12,430±550 | A-1455J | Grand Canyon | Mohave | Arizona |
| New Water Mts. No. 7 | 603 | 11,000±505 | A-1295J | New Water Mts. | Yuma | Arizona |
| Peach Springs Wash No. 1 | 855 | 12,040±400 | A-1454J | Grand Canyon | Mohave | Arizona |
| Rampart Cave Roof Crack | 530 | 13,510±190 | A-1421J | Grand Canyon | Mohave | Arizona |
| Rampart Cave Stake 0+35 | 530 | 12,230±350 | A-1535F | Grand Canyon | Mohave | Arizona |
| Rampart Cave Stake 45 | 530 | 13,170±310 | A-1325J | Grand Canyon | Mohave | Arizona |
| Rampart Cave Stake 0+50 | 530 | 9,770±160 | A-1450J | Grand Canyon | Mohave | Arizona |
| Rampart Cave Pit B, Front | 530 | 16,330±270 | A-1569J | Grand Canyon | Mohave | Arizona |
| Rampart Cave Pit B, Left Wall | 530 | None | — | Grand Canyon | Mohave | Arizona |
| Redtail Peaks No. 1 | 525 | 8,910±380 | A-1580J | Whipple Mts. | San Bernardino | California |
| Shinumo Creek No. 1 | 730 | 13,660±160 | A-1321J | Grand Canyon | Coconino | Arizona |
| South Crest, Level 4B | 2030 | 21,700±500 | LJ-2840P | Sheep Range | Clark | Nevada |
| Tucson Mts. No. 2 | 708 | 2,720±100 | A-1235D | Tucson Mts. | Pima | Arizona |
| Tunnel Ridge No. 2 | 370 | 10,330±300 | A-1470J | Whipple Mts. | San Bernardino | California |
| Vulture Canyon No. 2B | 410 | 10,210±290 | A-1567J | Grand Canyon | Mohave | Arizona |
| Vulture Canyon No. 3B | 465 | None | — | Grand Canyon | Mohave | Arizona |
| Vulture Canyon No. 4 | 465 | 10,610±320 | A-1566J | Grand Canyon | Mohave | Arizona |
| Vulture Canyon No. 6 | 595 | 17,610±290 | A-1603J | Grand Canyon | Mohave | Arizona |
| Vulture Canyon No. 8 | 595 | 13,820±220 | A-1564J | Grand Canyon | Mohave | Arizona |
| Vulture Canyon No. 9 | 595 | None | — | Grand Canyon | Mohave | Arizona |
| Vulture Canyon No. 10 | 595 | None | — | Grand Canyon | Mohave | Arizona |
| Vulture Canyon No. 11 | 630 | None | — | Grand Canyon | Mohave | Arizona |
| Vulture Canyon No. 12 | 630 | 8,540±180 | A-1568F | Grand Canyon | Mohave | Arizona |
| Wellton Hills No. 1 | 162 | 10,750±400 | A-1406E | Wellton Hills | Yuma | Arizona |
| Wellton Hills No. 1 | 162 | 10,580±550 | A-1407L | Wellton Hills | Yuma | Arizona |
| Whipple Mts. No. 2 | 525 | 9,980±180 | A-1538J | Whipple Mts. | San Bernardino | California |
| Whipple Mts. No. 3 | 525 | 9,920±130 | A-1551Nb | Whipple Mts. | San Bernardino | California |
| Window Rock No. 1 | 465 | 11,310±380 | A-1314J | Grand Canyon | Mohave | Arizona |
| Window Rock No. 2 | 525 | 10,250±220 | A-1352J | Grand Canyon | Mohave | Arizona |
| Wolcott Peak No. 2 | 862 | 14,550±800 | A-1286J | Silver Bell Mts. | Pima | Arizona |
| Wolcott Peak No. 5 | 862 | 12,130±500 | A-1287J | Silver Bell Mts. | Pima | Arizona |

^aRadiocarbon years before present.

^bSpecimens dated.

Abbreviations: A, laboratory number, Radiocarbon Laboratory, University of Arizona; D, midden debris; E, *Ephedra nevadensis*; F, *Fraxinus anomala*; J, *Juniperus*; L, *Larrea divaricata*; LJ, laboratory number, La Jolla Radiocarbon Laboratory, Scripps Institute of Oceanography, University of California at San Diego; Nb, *Nolina bigelovii*; Nm, *Nolina microcarpa*; P, *Pinus*.

mm.), which is from a lizard that exceeded the size of the largest *S. occidentalis* (table 3). Among the four candidate species, only *S. magister* lives at the fossil locality today. The nearest record for *S. clarkii* is approximately 80 km. south of this locality (at Valentine, Mohave County, Arizona; UAZ 20191), and neither of the other two large species occurs within 150 km. of the fossil locality today. A radiocarbon date of $11,990 \pm 490$ YBP is associated with this sample.

Emery Falls, Number 6: There are 646 *Sceloporus* scales or fragments in the sample (AMNH 111975). Twenty-three are dorsal scales from the base of the tail with notch counts varying from 0 to 9; the largest (4.2×4.1 mm.) is from a lizard that exceeded the size of *S. occidentalis* (table 2). The largest (3.1×2.5 mm.) of eight medial caudals (e.g., fig. 37D) is from a lizard whose minimum body length was approximately as large as the largest *S. occidentalis* (table 2). Notch counts of the numerous dorsal scales (from the body, limbs, or basal caudal region) varied from 1 to 7; the largest (4.5×4.1 mm.) has five conspicuous notches and came from a lizard that was considerably larger than the largest *S. occidentalis* (table 2). Indeed, an average-sized dorsal (3.4×3.1 mm.) from this

sample is approximately as large as the largest occurring on *S. occidentalis* (table 2). Among the 257 ventral scales, the largest (3.5×3.5 mm.) is double-notched, and this, as well as an average-sized one (2.8×2.5 mm.), exceeds the largest occurring on *S. occidentalis* (table 3). The largest (3.1×3.1 mm.) single-notched ventral and an average-sized one (2.8×2.5 mm.) also exceed the largest occurring on *S. occidentalis* (table 3), as does the largest (3.1×3.1 mm.) unnotched ventral. An incomplete left supraocular (2.1 mm. wide) slightly exceeds the widest measured on *S. occidentalis* (table 4). The largest (2.9×2.2 mm.) of two frontonasals (fig. 34C, D) is approximately as large as the maximum size attained by those of *S. occidentalis* (table 4). A complete anterior frontal scale (2.9×3.1 mm.; fig. 39B), however, is well within the size range for *S. undulatus*, and a smaller anterior frontal (2.4×2.5 mm.) probably came from a smaller lizard (table 4). The combined data from the dorsal, ventral, and cephalic scales suggest that at least three lizards of two distinctly different sizes contributed to the sample. Of the four species we studied that become larger than *S. occidentalis*, and at least one of which presumably is represented by the largest scales in this sample, only *S. magister* occurs at the fossil locality today. The

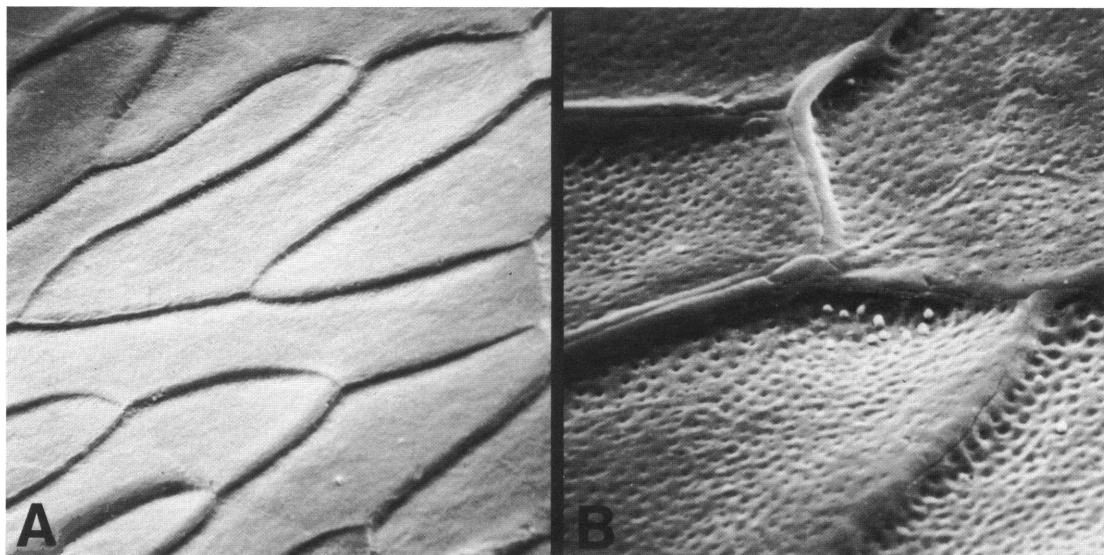


FIG. 30. Surface of same scale of *Sceloporus magister* as in figure 29. A. Region 3, no angle, $\times 1200$. B. Region 3, 25° angle, $\times 6000$.

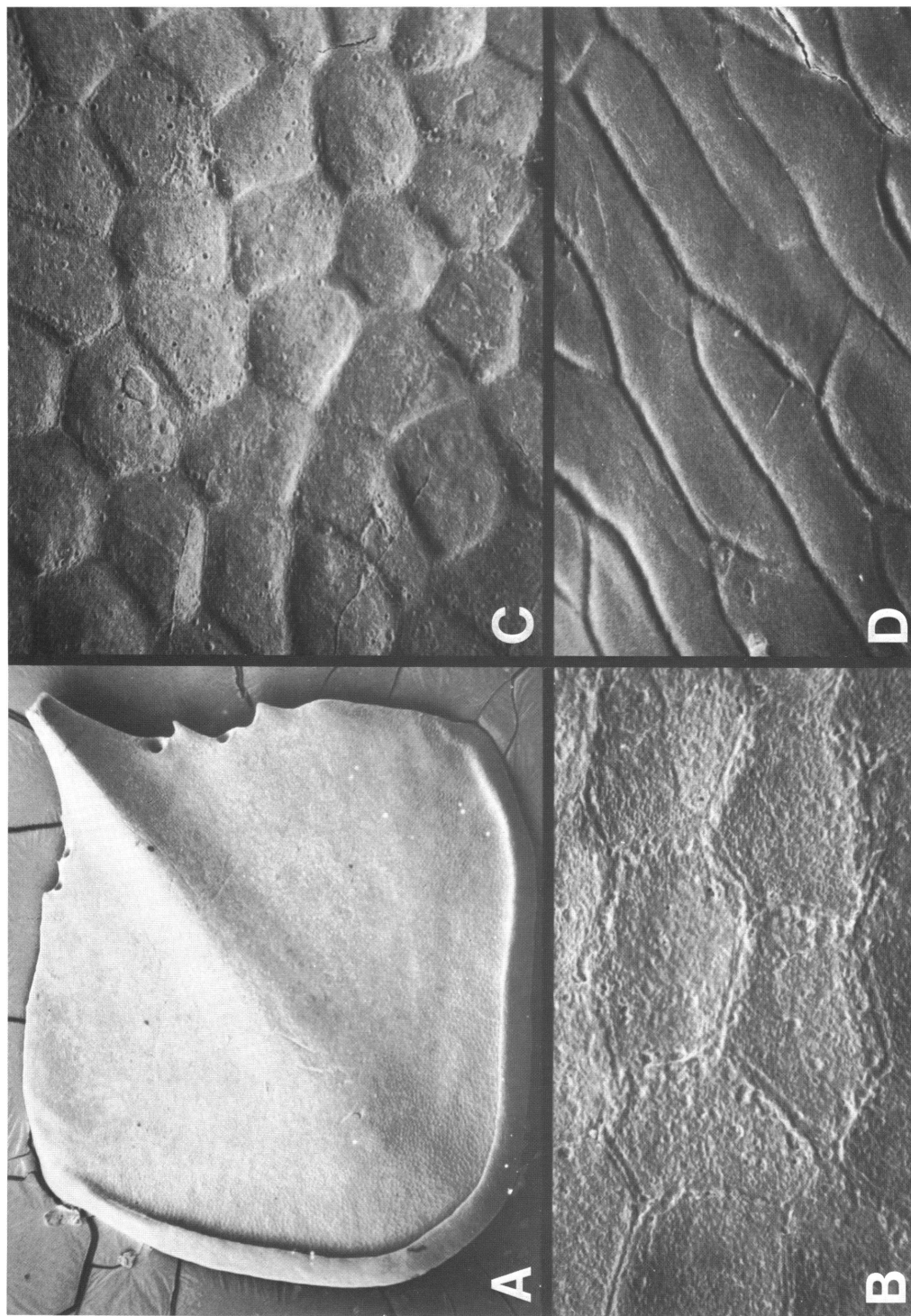


FIG. 31. Fossil basal caudal scale, cf. *Sceloporus magister*, AMNH 112010. A. Entire scale, no angle, $\times 24$. B. Region 1, no angle, $\times 1200$. C. Region 2, no angle, $\times 600$. D. Region 3, no angle, $\times 1200$.

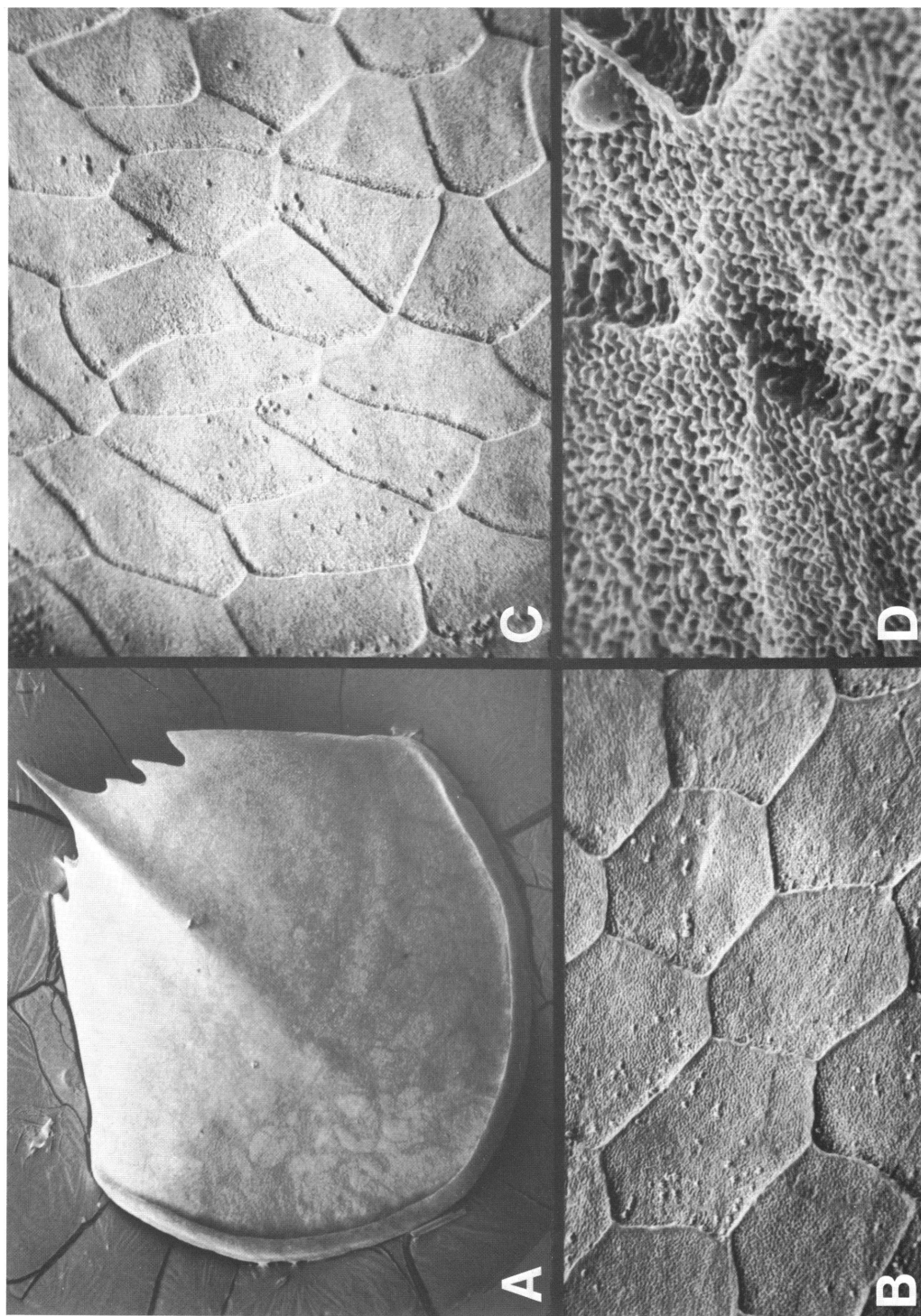


FIG. 32. Fossil dorsal scale, cf. *Sceloporus magister*, AMNH 112011. A. Entire scale, no angle, $\times 24$. B. Region 1, no angle, $\times 1200$. C. Region 2, no angle, $\times 600$. D. Region 2, 35° angle, $\times 6000$.

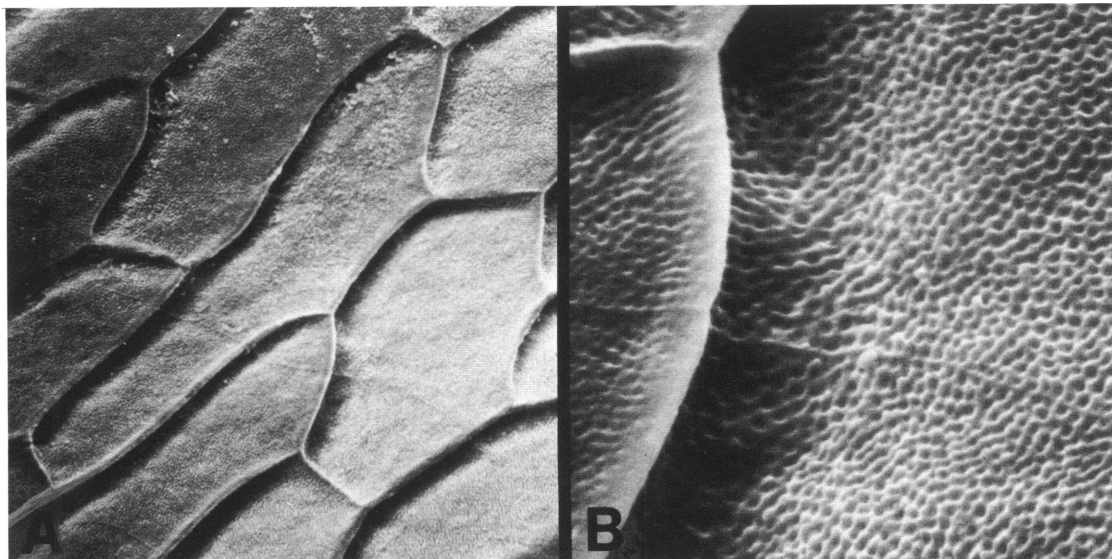


FIG. 33. Surface of a fossil dorsal scale, cf. *Sceloporus magister* or cf. *Sceloporus clarkii*, AMNH 112013. A. Region 3, no angle, $\times 1200$. B. Region 3, 10° angle, $\times 6000$.

nearest record for *S. clarkii* is approximately 80 km. south of this locality (at Valentine, Mohave County, Arizona; UAZ 20191), and neither of the other two large species occurs within 150 km. of the fossil locality today. Furthermore, none of the scales in this large sample has the distinctive morphology that characterizes certain dorsals, laterals, and caudals of *S. jarrovi* and *S. orcutti*. A radiocarbon date of $10,910 \pm 450$ YBP is associated with this sample.

Falling Arches, Number 1, Whipple Mountains, San Bernardino County, California: The single scale in this sample (AMNH 111976) is a complete single-notched ventral (2.0×2.1 mm.) from a *Sceloporus* that was so small that it cannot be identified (table 3). A radiocarbon date of $11,650 \pm 190$ YBP is associated with this scale.

Muav Gate, Number 1, N side of the lower Grand Canyon, mile 274.5 below Lee's Ferry (Coconino County), Mohave County, Arizona: This site is slightly upstream from Emery Falls Canyon. There are 13 scales or fragments in the samples (AMNH 111977, 111978). Eight (AMNH 111977) are from *Sceloporus*, and the largest, most distinctive one is a dorsal (3.4×3.4 mm.) that came from a lizard that exceeded the

maximum body length of *S. graciosus* (table 2). In addition, there are five scales (AMNH 111978) that are not recognizable as any of those on a *Sceloporus*. Comparisons with scales of all other lizards occurring in the Southwest today revealed that these fossils are most similar to caudal scales ($N = 4$ fossils; e.g., fig. 36B) and cephalic scales ($N = 1$ fossil; fig. 36D) of *Sauromalus obesus*, primarily a desert and chaparral species, which occurs at the fossil locality today. A radiocarbon date of $12,430 \pm 550$ YBP is associated with these samples.

New Water Mountains, Number 7, Yuma County, Arizona: There are only four *Sceloporus* scales or fragments in the sample (AMNH 111979). The largest, most distinctive scale is a single-notched ventral (3.1×2.8 mm.), which came from a lizard that exceeded the length of a large *S. occidentalis* (table 3). Of the four species in this category, only *S. magister* occurs at or near the fossil locality today; none of the others occurs within 120 km. A radiocarbon date of $11,000 \pm 505$ YBP is associated with this sample.

Peach Springs Wash, Number 1, S side of the Grand Canyon, above Diamond Creek, mile 225 below Lee's Ferry (Coconino County), Mohave County, Arizona: There are 11 *Sceloporus* scales

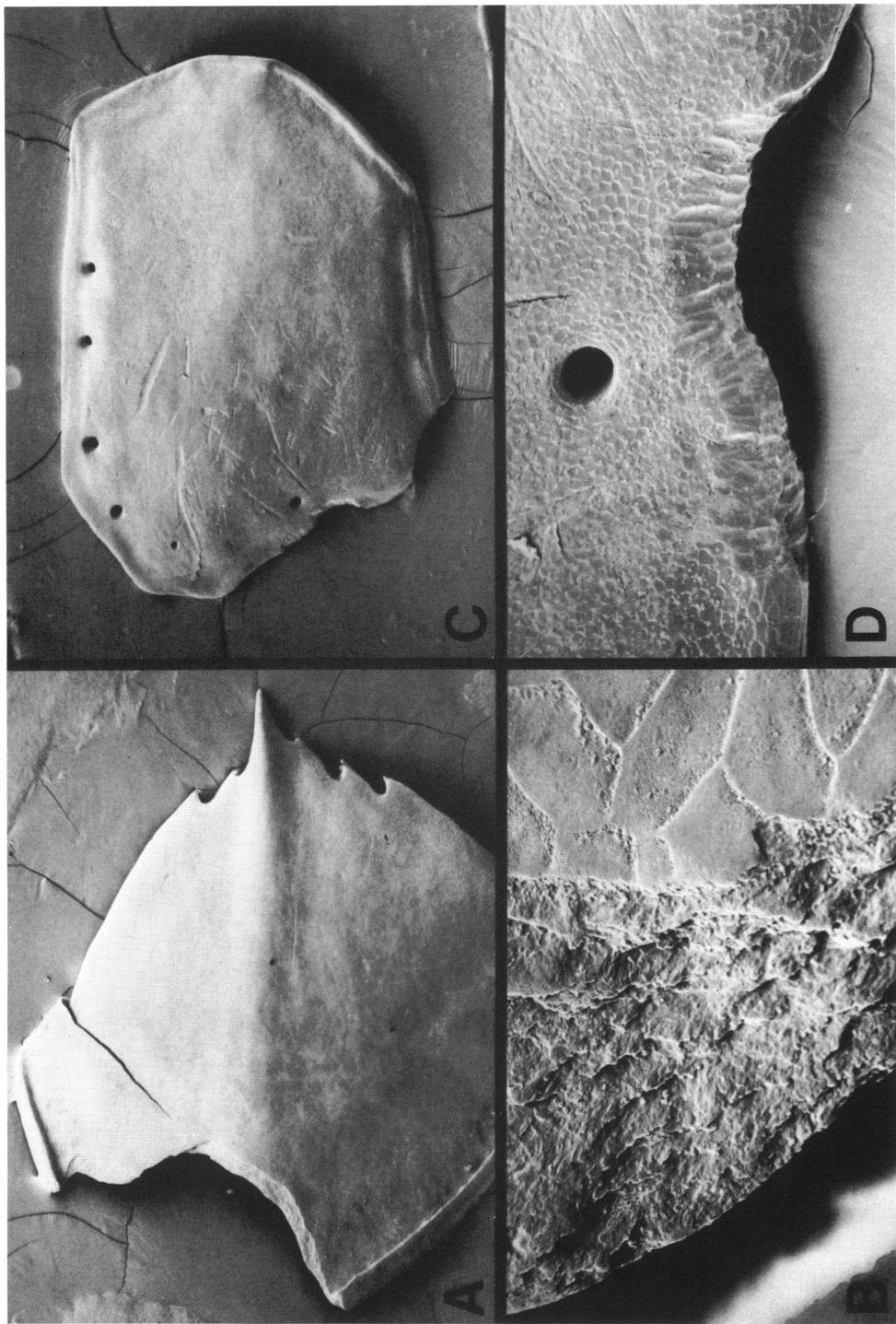


FIG. 34. Two incomplete fossil scales of *Scoloporus*. A. Dorsal from same deposit as scale in figure 32, $\times 24$. B. Torn edge of scale in A, 45° angle, $\times 600$. C. Frontonasal from AMNH 111975, $\times 24$. D. Gnawed edge of scale in C, 35° angle, $\times 120$.

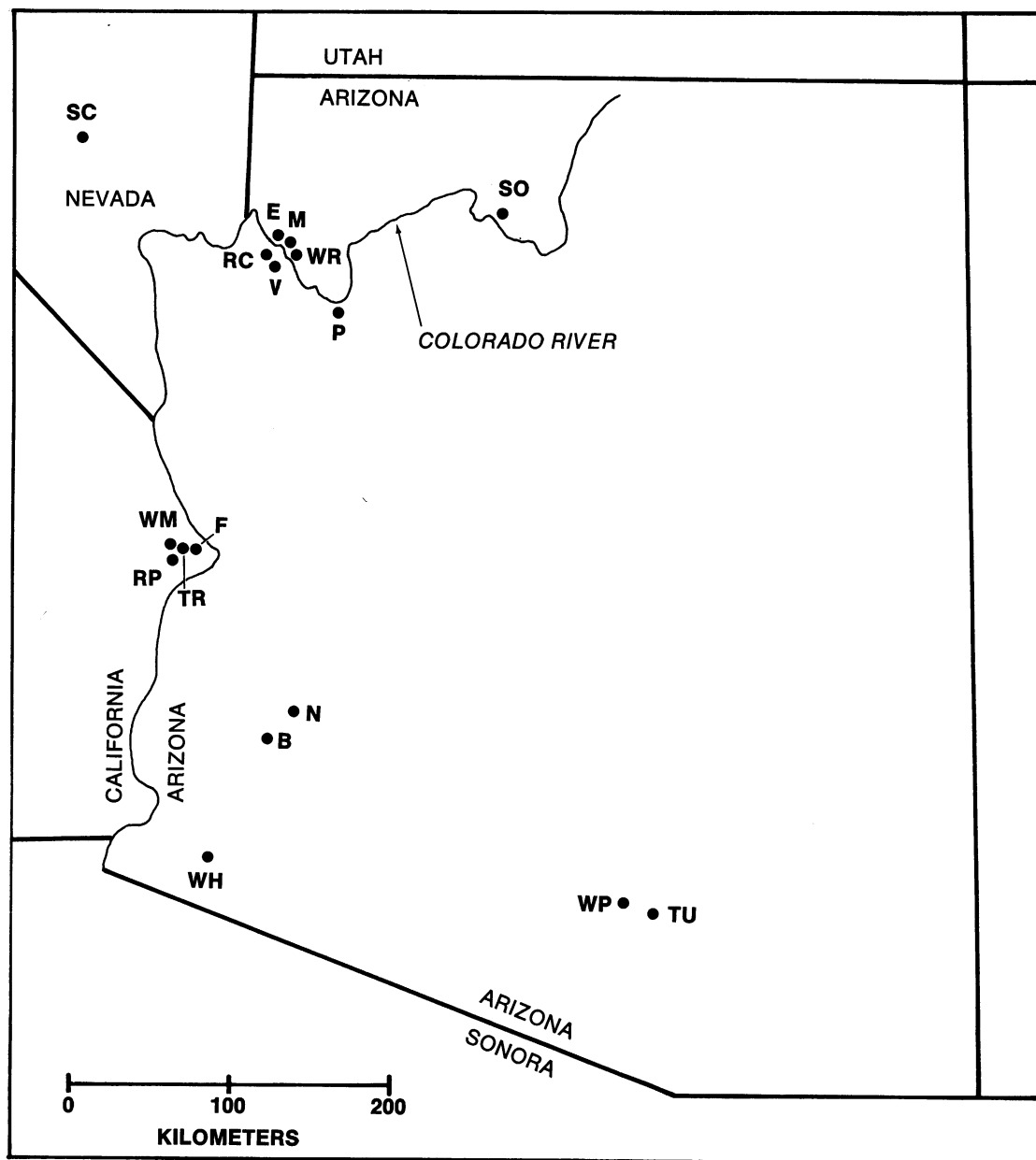


FIG. 35. Map of the localities where fossil middens (table 5) were found.

Abbreviations: B, Burro Canyon; E, Emery Falls; F, Falling Arches; M, Muav Gate; N, New Water Mountains; P, Peach Springs Wash; RC, Rampart Cave; RP, Redtail Peaks; SC, South Crest; SO, Shinumo Creek; TR, Tunnel Ridge; TU, Tucson Mountains; V, Vulture Canyon; WH, Wellton Hills; WM, Whipple Mountains; WP, Wolcott Peak; WR, Window Rock.

or fragments in the sample (AMNH 111980). Of the five complete or essentially complete scales,

two are dorsals (a five-notched one, $4.2 \times 3.5+$ mm.; and a three-notched one, 4.9×3.6 mm.),

one is a double-notched ventrolateral (3.8×3.2 mm.), and one is a double-notched ventral (2.7×2.7 mm.), all of which probably came from a lizard larger than the largest *S. occidentalis* (tables 2, 3). Of the four species in this category, only *S. magister* is known to occur at the fossil locality today. The nearest record for *S. clarkii* is approximately 45 km. southwest of this locality (at Valentine, Mohave County, Arizona; UAZ 20191) and eventually *S. clarkii* may be found at higher elevations in Peach Springs Wash. Neither of the other two large species occurs within 150 km. of the fossil locality today. A radiocarbon date of $12,040 \pm 400$ YBP is associated with this sample.

Rampart Cave, Roof Crack Midden, S side of the lower Grand Canyon, mile 275 below Lee's Ferry (Coconino County), Mohave County,

Arizona: There are seven *Sceloporus* scales or fragments in the sample (AMNH 111981). The largest of three large dorsals (five-notched; 3.9×3.6 mm.) and the largest ventral (single-notched; 3.6×3.2 mm.) came from a lizard that exceeded the size of the largest *S. occidentalis* (tables 2, 3). Of the four species in this category, only *S. magister* occurs at the fossil locality today. The nearest record for *S. clarkii* is approximately 80 km. south of this locality (at Valentine, Mohave County, Arizona; UAZ 20191), and neither of the other two large species occurs within 150 km. of the fossil locality today. A radiocarbon date of $13,510 \pm 190$ YBP is associated with this sample. The following middens labeled as Rampart Cave are from the same limestone cave.

Rampart Cave, Stake 0+35 Midden: There are 51 scales or fragments in the samples (AMNH



FIG. 36. Scales of *Sauromalus obesus*. A. Recent caudal, AMNH 57724, $\times 36$. B. Fossil caudal, AMNH 111985, $\times 24$. C. Recent cephalic scale, AMNH 57724, $\times 24$. D. Fossil cephalic scale, AMNH 111978, $\times 24$.

111982, 111983). The largest (4.3×3.9 mm.) of 18 *Sceloporus* dorsals with notch counts varying from 1 to 6, the largest (3.1×3.1 mm.) double-notched ventral, and the two largest (2.8×2.8 mm.) single-notched ventrals all came from a lizard that exceeded the body length of the largest *S. occidentalis* (tables 2, 3). Of the four species in this category, only *S. magister* occurs at the fossil locality today (see above discussion for Rampart Cave, Roof Crack Midden). In addition, one of the fossil scales (AMNH 111983) was indistinguishable from a caudal of *Sauromalus obesus* (e.g., fig. 36A), which also occurs at the fossil locality today. A radiocarbon date of $12,230 \pm 350$ YBP is associated with these samples.

Rampart Cave, Stake 45: There are 67 scales or fragments in the samples (AMNH 111984, 111985). The largest (4.8×3.9 mm.) of 30 *Sceloporus* dorsals with notch counts varying from 2 to 6, the largest (3.5×2.9 mm.; single-notched) of 13 ventrals (e.g., fig. 38B, D), and the largest (3.6×2.9 mm.) of four medial caudals are all from a lizard that exceeded the body length of the largest *S. occidentalis* (tables 2, 3). Of the four species in this category, only *S. magister* occurs at the fossil locality today (see prior discussion for Rampart Cave, Roof Crack Midden). In addition, a wide (5.2 mm.), single-keeled dorsal from the neck was most similar to those of *S. magister* (table 2). Four other fossil scales (AMNH 111985) were indistinguishable from caudals of *Sauromalus obesus* (fig. 36A, B), which also occurs at the fossil locality today. A radiocarbon date of $13,170 \pm 310$ YBP is associated with these samples.

Rampart Cave, Stake 0+50: There are more than 350 *Sceloporus* scales and fragments in the sample (AMNH 111986). The largest ($4.8+ \times 4.5$ mm.) of 108 dorsals with notch counts varying from 2 to 7, an average-sized dorsal (3.9×3.1 mm.), the largest (3.5×3.4 mm.) unnotched ventral, the largest (3.1×2.8 mm.) single-notched ventral, and the largest (2.9×2.7 mm.) double-notched ventral, all clearly are from a lizard that exceeded the body length of the largest *S. occidentalis* (tables 2, 3). Two of the three cephalic plates are more suggestive: The sizes of the two supraoculars (4.1×1.8 mm.; and 3.9×2.0 mm.) indicate deposition from a

lizard that exceeded the body length of the largest *S. jarrovii* (table 4). Of the three species in this category, only *S. magister* occurs at the fossil locality today (see prior discussion for Rampart Cave, Roof Crack Midden). Furthermore, none of the scales in this large sample has the distinctive morphology that characterizes certain dorsals, laterals, and caudals of *S. jarrovii* and *S. orcutti*. A radiocarbon date of 9770 ± 160 YBP is associated with this sample.

Rampart Cave, Pit B, Front: There are 55 *Sceloporus* scales and fragments in the sample (AMNH 111987). The largest (4.2×4.8 mm.) dorsal scale and the largest (3.5×3.1 mm.) two ventrals (single-notched and double-notched) are from a lizard that exceeded the body length of the largest *S. occidentalis* (tables 2, 3). Of the four species in this category, only *S. magister* occurs at the fossil locality today (see prior discussion for Rampart Cave, Roof Crack Midden). A radiocarbon date of $16,330 \pm 270$ YBP is associated with this sample.

Rampart Cave, Pit B, Left Wall: There are more than 675 scales and fragments in the samples (AMNH 111988-111990). Twelve of the *Sceloporus* dorsals or dorsal basal caudals measured at least 5.0 mm. in length or width, and 105 of these scales measured at least 4.2 mm. in length. These scales, along with the largest ventral (4.2×4.1 mm.) indicate that the largest lizard involved was the size of a large *S. magister* or *S. clarkii* (tables 2, 3), of which only *S. magister* is known from the fossil locality today (see prior discussion for Rampart Cave, Roof Crack Midden). Furthermore, none of the scales in this large sample has the distinctive morphology that characterizes certain dorsals, laterals, and caudals of *S. jarrovii* and *S. orcutti*. The presence of three interparietals in the sample reveals that at least three individuals contributed to the sample of *Sceloporus* scales. Epidermal remains of two other genera of lizards are present in this deposit also. These include the following: Several large fragments of skin having numerous attached dorsal granules (including distinctively small granules in between larger ones) that are attached to larger smooth ventrals, which are indistinguishable from skin of *Crotaphytus* (AMNH 111990); and numerous fragments of skin and scales that are indistinguishable from

those of *Cnemidophorus*, including dorsal and lateral granules, thin, smooth, large, rectangular ventrals, thin, large, rectangular caudals with diagonal (rather than medial) keels (one each), and several cephalic scutes, including a rostral attached to a pair of nasals (AMNH 111989). In addition, there are more than 60 fragments of scales from hands, feet, fingers, and toes, including 34 claws, many of which are referable to *Sceloporus* and many to *Cnemidophorus*. Representatives of all these genera are found at or near the fossil locality today.

Redtail Peaks, Number 1, Whipple Mountains, San Bernardino County, California: There are only two scales in the sample (AMNH 111991), both of which are indistinguishable from caudals of *Sauromalus obesus*, which occurs at or near the fossil locality today. A radiocarbon date of 8910 ± 380 YBP is associated with this sample.

Shinumo Creek, Number 1, N side of the Grand Canyon, mile 108.5 below Lee's Ferry, Coconino County, Arizona: There are six *Sceloporus* scales or fragments in the sample (AMNH 111992). The largest (4.3×3.9 mm.) dorsal, the largest (3.6×2.8 mm.) medial caudal, and the longest (2.9 mm.; width incomplete) ventral all came from a lizard that exceeded the body length of the largest *S. occidentalis* (tables 2, 3). Of the four species in this category, only *S. magister* occurs at the fossil locality today; none of the others has been found within 150 km., although *S. clarkii* someday may be found within that distance (see prior discussion for Peach Springs Wash). A radiocarbon date of $13,660 \pm 160$ YBP is associated with this sample.

South Crest Midden, Level 5, Sheep Range, Clark County, Nevada: There are 29 *Sceloporus* scales or fragments in the sample (AMNH 111993). The largest (2.9×2.7 mm.; with 5 notches) dorsal scale, the largest (2.5×2.0 mm.) ventral, and the largest (2.8×2.2 mm.) medial caudal all came from a lizard that exceeded the size of the largest *S. graciosus* (tables 2, 3). Of the six species in this category, *S. occidentalis* and *S. magister* occur at or near the fossil locality today, whereas none of the others occurs within 130 km. A radiocarbon date of $21,700 \pm 500$ YBP is available for level 4B (table 5), which was higher in the midden (possibly somewhat younger than level 5) and contained a floral

assemblage similar to that of level 5, although the material dated in this instance was not in direct association with the scales.

Tucson Mountains, Number 2, Pima County, Arizona: The single scale in this sample (AMNH 111994) is an essentially complete *Sceloporus* dorsal (3.9×3.8 mm.) that came from a lizard that exceeded the size of the largest *S. occidentalis* (table 2). Of the four species in this category, *S. magister* and *S. clarkii* occur at the fossil locality today. *Sceloporus jarrovi* presently occurs nearby (e.g., in the Santa Rita Mountains, approximately 55 km. to the SSE). A radiocarbon date of 2720 ± 100 YBP associated with the scale suggests a Holocene age.

Tunnel Ridge, Number 2, Whipple Mountains, San Bernardino County, California: There are 33 *Sceloporus* scales or fragments (mostly the latter) in the sample (AMNH 111995). The most distinctive is a large (5.2×5.3 mm.) dorsal from an animal that was larger than the largest size attained by *S. orcutti* (table 2). Of the two species in this category, only *S. magister* occurs at or near the fossil locality today. The nearest locality for *S. clarkii* (UAZ 10854) is near Hillside, Yavapai County, Arizona, approximately 125 km. to the east. A radiocarbon date of $10,330 \pm 300$ YBP is associated with these scales.

Vulture Canyon, Number 2B, S side of the lower Grand Canyon, mile 274.5 below Lee's Ferry (Coconino County), Mohave County, Arizona: There are four scales in the samples (AMNH 111996, 111997). Two are ventrals from *Sceloporus* (AMNH 111996), the largest (2.9×2.7 mm.) of which is single-notched. This came from a lizard that exceeded the size of the largest *S. occidentalis* (table 3). Of the four species in this category, only *S. magister* occurs at the fossil locality today. The nearest record for *S. clarkii* is approximately 80 km. south of this locality (at Valentine, Mohave County, Arizona; UAZ 20191), and neither of the other two large species occurs within 150 km. of the fossil locality today. Two other fossil scales (AMNH 111997) are indistinguishable from those of *Sauromalus obesus*, which occurs at the fossil locality today. A radiocarbon date of $10,210 \pm 290$ YBP is associated with these scales. The following middens labeled as Vulture Canyon are from one and the same canyon.

Vulture Canyon, Number 3B: There are four scales in the samples (AMNH 111998, 111999). The most distinctive *Sceloporus* scale ($2.7+ \times 2.7$ mm.) is an incomplete single-notched ventral, which probably came from a lizard that exceeded the size of the largest *S. occidentalis* (table 3). Of the four species in this category, only *S. magister* occurs at the fossil locality today (see above discussion for Vulture Canyon Number 2B). Two fossil scales (AMNH 111999; one ventral, one cephalic) are indistinguishable from those of *Sauromalus obesus*, which occurs at the fossil locality today.

Vulture Canyon, Number 4: The single *Sceloporus* scale in the sample (AMNH 112000) is an incomplete dorsal ($2.8+ \times 2.7+$ mm.) that came from a lizard that exceeded the size of the largest *S. graciosus* (table 2). A radiocarbon date of $10,610 \pm 320$ YBP is associated with this scale.

Vulture Canyon, Number 6: There are eight *Sceloporus* scales in the sample (AMNH 112001). The most distinctive is a three-notched dorsal (4.2×3.9 mm.), which came from a lizard that exceeded the size of the largest *S. occidentalis* (table 2). Of the four species in this category, only *S. magister* occurs at the fossil locality today (see prior discussion for Vulture Canyon Number 2B). A radiocarbon date of $17,610 \pm 290$ YBP is associated with these scales. The next three samples (Numbers 8, 9, 10) are from the same cave.

Vulture Canyon, Number 8: There are 28 *Sceloporus* scales and fragments in the sample (AMNH 112002). The longest ($4.2+$ mm.) dorsal (incomplete) and the largest (3.1×2.8 mm.) ventral (single-notched) came from a lizard that exceeded the size of the largest *S. occidentalis* (tables 2, 3). Of the four species in this category, only *S. magister* occurs at the fossil locality today (see prior discussion for Vulture Canyon Number 2B). A radiocarbon date of $13,820 \pm 220$ YBP is associated with this sample.

Vulture Canyon, Number 9: There are 11 *Sceloporus* scales and fragments in the sample (AMNH 112003). The most distinctive is a double-notched ventral (2.5×2.7 mm.) that came from a lizard that exceeded the size of the largest *S. occidentalis* (table 3). Of the four species in this category, only *S. magister* occurs at the fossil locality today (see prior discussion for Vulture Canyon Number 2B).

Vulture Canyon, Number 10: There are 12 *Sceloporus* scales and fragments in the sample (AMNH 112004). The longest ($3.5+$ mm.) ventral (incomplete, single-notched) and the longest (4.6 mm.) dorsal (incomplete) came from a lizard that exceeded the size of the largest *S. occidentalis* (tables 2, 3). Of the four species in this category, only *S. magister* occurs at the fossil locality today (see prior discussion for Vulture Canyon Number 2B).

Vulture Canyon, Number 11: There are 10 *Sceloporus* scales and fragments in the sample (AMNH 112005). The largest (3.9×3.5 mm.) is a dorsal that came from a lizard that exceeded the size of the largest *S. occidentalis* (table 2). Of the four species in this category, only *S. magister* occurs at the fossil locality today (see prior discussion for Vulture Canyon Number 2B). The next sample (Number 12) is from the same shelter that housed this one.

Vulture Canyon, Number 12: The only scale in this sample (AMNH 112006) is an incomplete *Sceloporus* dorsal ($3.2+ \times 2.9$ mm.) that came from a lizard that exceeded the size of the largest *S. graciosus* (table 2). A radiocarbon date of 8540 ± 180 YBP is associated with this scale.

Wellton Hills, Number 1, Yuma County, Arizona: There are 12 *Sceloporus* scales or fragments in the sample (AMNH 112007). The most distinctive ones are a large ($4.2+ \times 4.6+$ mm.; incomplete) fragment of a lateral caudal and a wide (2.7 mm.; length incomplete) medial caudal, which came from a lizard that exceeded the size of the largest *S. occidentalis* (table 2). Of the four species in this category, only *S. magister* occurs at or near the fossil locality today; none of the others occurs within 150 km. Two radiocarbon dates are associated with these fossils: $10,580 \pm 550$ YBP (based on *Larrea divaricata*), and $10,750 \pm 400$ YBP (based on *Ephedra nevadensis*).

Whipple Mountains, Number 2, San Bernardino County, California: There are six *Sceloporus* scales in this sample (AMNH 112008). The two most distinctive ones are a large (2.9×2.9 mm.) unnotched ventral and a large (2.9×2.7 mm.) single-notched ventral, which came from a lizard that exceeded the size of the largest *S. occidentalis* (table 3). Of the four species in this category, only *S. magister* occurs at the fossil locality today. None of the other species occurs

within 130 km. A radiocarbon date of 9980 ± 180 YBP is associated with this sample; this is in the latest Pleistocene for this area. The following sample is from the same mountains.

Whipple Mountains, Number 3: The only *Sceloporus* scale in the sample (AMNH 112009) is from the side of the body or base of the tail (3.4×3.4 mm.). This came from a lizard that exceeded the size of the largest *S. graciosus* and was approximately as large as the largest *S. undulatus* (table 2). A radiocarbon date of 9920 ± 130 YBP is associated with this fossil.

Window Rock, Number 1, N side of the lower Grand Canyon, mile 274 below Lee's Ferry (Coconino County), Mohave County, Arizona: There are only two *Sceloporus* scales in the sample (AMNH 112010). The most distinctive is a large (4.1×3.8 mm.) dorsal from the base of the tail (fig. 31), which is from a lizard that exceeded the size of the largest *S. occidentalis* (table 2). Of the four species in this category, only *S. magister* occurs at or near the fossil locality today. The nearest record for *S. clarkii* is approximately 80 km. south of this locality (at Valentine, Mohave County, Arizona; UAZ 20191), and neither of the other two large species occurs within 150 km. of the fossil locality today. A radiocarbon date of $11,310 \pm 380$ YBP is associated with these fossils. The following sample is from another midden in the same small canyon.

Window Rock, Number 2: There are 27 *Sceloporus* scales and fragments in the sample (AMNH 112011). Of these, the largest (3.8×3.4 mm.) dorsal (fig. 32), the largest (2.7×2.5 mm.) single-notched ventral, and the largest (3.1×2.8

mm.) double-notched ventral all came from a lizard that exceeded the size of the largest *S. occidentalis* (tables 2, 3). Of the four species in this category, only *S. magister* occurs at or near the fossil locality today (see above discussion for Window Rock Number 1). A radiocarbon date of $10,250 \pm 220$ YBP is associated with these fossils.

Wolcott Peak, Number 2, Silver Bell Mountains, Pima County, Arizona: The only scale in this sample (AMNH 112012) is a nearly complete ($4.2 \times 3.8+$ mm.) *Sceloporus* dorsal, which came from a lizard that exceeded the size of the largest *S. occidentalis* (table 2). Of the four species in this category, both *S. clarkii* and *S. magister* occur in the Silver Bell Mountains today; the nearest records for *S. jarrovi* are approximately 50 km. away (in the Baboquivari Mountains to the S), and *S. orcutti* occurs in California. A radiocarbon date of $14,550 \pm 800$ YBP is associated with this scale. The following midden sample is from the same mountains.

Wolcott Peak, Number 5: There are 36 *Sceloporus* scales or fragments in the sample (AMNH 112013). Several scales (dorsals, caudals, ventrals) exceed the maximum sizes found on the largest *S. occidentalis*. Two distinctive scales are a broad chest scale (2.9×4.1 mm.) and a dorsal (5.0×4.8 mm.; fig. 33), which came from a lizard that was approximately the size of the largest *S. orcutti* (tables 2, 3). Of the three large species in this category, *S. clarkii* and *S. magister* occur in the Silver Bell Mountains today, and the nearest record for *S. orcutti* is in California. A radiocarbon date of $12,130 \pm 500$ YBP is associated with these fossils.

DISCUSSION

Examination of the seven Recent species of *Sceloporus* revealed that, when isolated, only certain scales with distinctive morphology are useful for distinguishing among these species, and even at best their utility is limited. The smaller fossils cannot be identified with certainty because most of the small scales on large lizards cannot be distinguished readily from the large scales on small lizards. However, certain large scales with distinctive morphology can be determined as not having been deposited by the

smaller species if their traits (dimensions, notch counts) clearly exceed the maximum conditions ever observed on the smaller species; this assumes that these species did not grow significantly larger in the past than they do today. Thus, gross morphology can be used to limit the number of candidate species represented by certain large scales in a sample of fossils.

Fossil packrat midden samples do not represent an instant in time. The period of accumulation of material may involve several hundred

years. The samples containing more than one fossil *Sceloporus* scale could contain scales from more than one individual. However, only two samples (Emery Falls Number 6; Rampart Cave, Pit B, Left Wall) contained scale samples with direct evidence that more than one individual of *Sceloporus* was involved in the deposit, and in both deposits there were remains of at least three individuals. In the sample from Emery Falls Number 6, lizards of at least two distinctly different sizes were involved. These could have been young and adult of a single large species or adults of two species in which the adults reach different sizes. In such instances we can reasonably estimate the identity of only the larger lizard.

In attempting to identify the larger fossils, we compared them with scales on all the Recent large species of *Sceloporus* that are known to occur anywhere within the boundaries of the states (Arizona, California, Nevada) where the middens were found. Although traits of most of the larger fossils are such that they cannot be distinguished among the four larger species (*S. jarrovi*, *S. orcutti*, *S. clarkii*, *S. magister*), the present ranges of these species are sufficiently different to permit geographical distributions to influence identification of the fossils, using the null hypothesis that the fossil scales are not significantly different from those of a species that occurs at or near the fossil locality today. Among the possible sources for error in this procedure, perhaps the greatest potential source is that there is no way to determine whether the fossils represent an extinct species rather than one of the Recent species with which we have compared them. Bearing these thoughts in mind, we review the fossil scales below.

IDENTIFICATION OF THE FOSSIL SCALES

Among the 35 samples of fossils, including a total of more than 2100, in no instance did we find a scale having the distinctive traits of the keel, spine, and thick posterior margin of *S. jarrovi* and *S. orcutti*. Thus, there is no direct evidence suggesting the presence of scales of one of these species among the larger fossils, as compared with the other two larger species (*S. clarkii*, *S. magister*).

None of the samples contained only scales that were within the sizes for *S. graciosus*. Seven samples contained only scales that were too large to have been deposited by *S. graciosus* but were sufficiently small to have been deposited by any of the other six species of *Sceloporus*. We shall not consider these samples (listed immediately below) further in this paper, except to note that fossil scales of *Sauromalus obesus* were found in one of the same middens (Muav Gate Number 1), and this species occurs primarily in desert and chaparral habitats today.

FOSSIL SAMPLES CONTAINING ONLY SCALES LARGER THAN THOSE OF *SCELOPORUS GRACIOSUS* BUT WITHIN THE SIZE RANGE OF THE OTHER SIX SPECIES OF *SCELOPORUS* COMPARED

Emery Falls, No. 1, Grand Canyon, Mohave Co., Arizona
Falling Arches, No. 1, Whipple Mts., San Bernardino Co., California
Muav Gate, No. 1, Grand Canyon, Mohave Co., Arizona
South Crest Midden, Level 5, Sheep Range, Clark Co., Nevada
Vulture Canyon, No. 4, Grand Canyon, Mohave Co., Arizona
Vulture Canyon, No. 12, Grand Canyon, Mohave Co., Arizona
Whipple Mts., No. 3, San Bernardino Co., California

The sample from Wolcott Peak, Number 5, Silver Bell Mountains, Pima County, Arizona contained large scales that reasonably could have been from only *S. clarkii* or *S. magister*; we rule out *S. orcutti* since today it does not occur within 430 km. of this locality. Both *S. clarkii* and *S. magister* are found at the fossil locality today. The fossil plants in this sample indicate the presence of a relatively xeric woodland with juniper (*Juniperus* sp.), shrub live oak (*Quercus turbinella*), Emory oak (*Quercus* cf. *emoryi*), and single-needle pinyon (*Pinus monophylla*; see Lanner and Van Devender, 1974). Associated with these woodland species are fossils of desert species that presently occur at the site, including the following: Desert hackberry (*Celtis pallida*), barrel cacti (*Ferocactus wislizenii*, *Ferocactus acanthodes*), brittle-bush (*Encelia farinosa*), and prickly pears and chollas (four species of

Opuntia). Fossil bones of such desert-adapted amphibians and reptiles as the red-spotted toad (*Bufo punctatus*, UALP 6258), shovel-nosed snake (*Chionactis occipitalis*, UALP 6259), night snake (*Hypsiglena torquata*, UALP 5769, 6260), leaf-nosed snake (*Phyllorhynchus* sp., UALP 6261), and bull snake (*Pituophis melanoleucus*, UALP 6266) were identified from the same midden sample as the *Sceloporus* scales. The past biotic community represented by these fossils well could have supported both *S. clarkii* and *S. magister*, as does the present community.

Three samples from Pima County, Arizona (Tucson Mountains, Number 2; Wolcott Peak Number 2; Wolcott Peak Number 5) contain large scales that reasonably could have been from *S. jarrovi*, *S. clarkii*, or *S. magister*. We rule out *S. orcutti*, since it does not occur within 430 km. of these localities today. *Sceloporus clarkii* and *S. magister* both are found at the fossil localities today. *Sceloporus jarrovi* occurs in the Baboquivari Mountains and the Santa Rita Mountains nearby, to the southwest and southeast, respectively. Indicators of the past biotic community for Wolcott Peak Number 5 were discussed above. In addition, Wolcott Peak Number 2 contained the following species of reptiles: western whiptail lizard (*Cnemidophorus tigris*, UALP 6251), collared lizard (*Crotaphytus collaris*, UALP 5611), blind snake (*Leptotyphlops* sp., UALP 6252), whipsnake (*Masticophis* sp., UALP 5678), long-nosed snake (*Rhinocheilus lecontei*, UALP 5680), and chuckwalla (*Sauromalus obesus*, UALP 5612, 5767).

There are 24 samples that contain large scales that we suspect came from *S. magister*. We rule out two of the three other large species (*S. jarrovi*, *S. orcutti*) because neither occurs within at least 150 km. of any of these fossil sites, whereas *S. magister* occurs at or near each locality today. For one sample from San Bernardino County, California (Tunnel Ridge Number 2), one of the scales exceeds the largest size found on *S. orcutti*. *Sceloporus clarkii* recently has been collected as far northwest as Valentine, Mohave County, Arizona (UAZ 20191). This is approximately 45 km. southwest of the nearest midden locality, Peach Springs Wash. Thus, *S. clarkii* also is a reasonable candidate species for the large scales in this midden. Several other southerly spe-

cies of reptiles such as the western diamondback rattlesnake (*Crotalus atrox*) and black-tailed rattlesnake (*C. molossus*) have northern disjunct populations in Peach Springs Wash.

The Pleistocene packrat midden records for the Mohave Desert in the Grand Canyon of Arizona (Phillips and Van Devender, 1974), southern Nevada (Wells and Berger, 1967), and the Sonoran Desert of Arizona (Van Devender and King, 1971; Van Devender, 1973) have documented past occurrence of lower elevation woodland plant species and communities in areas that presently are occupied by desert communities. Single needle pinyon (*Pinus monophylla*) occurred generally as low as 725 m. elevation and occasionally as low as 525 m. (Lanner and Van Devender, 1974). One xerophilous woodland component (*Juniperus*) formerly grew at 325 m. elevation in the Whipple Mountains of California (Falling Arches Number 1; table 5). The concurrent Pleistocene biotic communities below these elevations presumably were desert. However, considering the remains of only the woodland plants in these ancient middens is misleading. The assemblages actually are mixtures of woodland and desert plant species. Remains of Joshua tree (*Yucca brevifolia*) were in Burro Canyon Number 1 and Brass Cap Point Number 1 (551 m. elevation; 11,450±400 YBP, based on *Y. brevifolia*, A-1328) in the Kofa Mountains, Yuma County, Arizona, and in Falling Arches Number 1 and Tunnel Ridge Number 5 (708 m. elevation; 12,670±260 YBP, based on *Y. brevifolia*, A-1550) in the Whipple Mountains, San Bernardino County, California (Van Devender, 1973, and unpublished data). This species presently is an important community dominant in medium-elevation Mohave Desert communities to the north. Mohave Desert species of plants apparently replaced many of the cold-sensitive Sonoran Desert species southward at low elevations during the last Ice Age, and this also is consistent with the occurrence of *S. magister* to the north of each fossil locality today. *Sceloporus magister* can be very abundant in Joshua tree forests today and also thrives in some plant communities at both higher and lower elevations; there is no reason to believe it was absent from the paleocommunities recorded in the fossil middens as well. For four of the samples (Ram-

part Cave Stake 0+35 midden; Rampart Cave Stake 45; Rampart Cave, Pit B, Left Wall; Vulture Canyon Number 3B), this conclusion is consistent with the occurrence of fossil scales of *Sauromalus obesus* in the samples also. The 24 samples that contain *Sceloporus* scales that probably represent *S. magister* are listed immediately below, and comparisons between selected fossil scales from some of these samples and scales from Recent specimens of *S. magister* are shown in figures 37 through 40.

FOSSIL SAMPLES CONTAINING SCALES
PRESUMABLY FROM
SCELOPORUS MAGISTER

Burro Canyon, No. 1, Kofa Mts., Yuma Co., Arizona
Emery Falls, No. 4, Grand Canyon, Mohave Co., Arizona
Emery Falls, No. 6, Grand Canyon, Mohave Co., Arizona
New Water Mts., No. 7, Yuma Co., Arizona
Peach Springs Wash, No. 1, Grand Canyon, Mohave Co., Arizona
Rampart Cave, Roof Crack Midden, Grand Canyon, Mohave Co., Arizona
Rampart Cave, Stake 0+35 Midden, Grand Canyon, Mohave Co., Arizona
Rampart Cave, Stake 45, Grand Canyon, Mohave Co., Arizona
Rampart Cave, Stake 0+50, Grand Canyon, Mohave Co., Arizona
Rampart Cave, Pit B, Front, Grand Canyon, Mohave Co., Arizona
Rampart Cave, Pit B, Left Wall, Grand Canyon, Mohave Co., Arizona
Shinumo Creek, No. 1, Grand Canyon, Coconino Co., Arizona
Tunnel Ridge, No. 2, Whipple Mts., San Bernardino Co., California
Vulture Canyon, No. 2B, Grand Canyon, Mohave Co., Arizona
Vulture Canyon, No. 3B, Grand Canyon, Mohave Co., Arizona
Vulture Canyon, No. 6, Grand Canyon, Mohave Co., Arizona
Vulture Canyon, No. 8, Grand Canyon, Mohave Co., Arizona
Vulture Canyon, No. 9, Grand Canyon, Mohave Co., Arizona
Vulture Canyon, No. 10, Grand Canyon, Mohave Co., Arizona
Vulture Canyon, No. 11, Grand Canyon, Mohave Co., Arizona

Wellton Hills, No. 1, Yuma Co., Arizona
Whipple Mts., No. 2, San Bernardino Co., California

Window Rock, No. 1, Grand Canyon, Mohave Co., Arizona

Window Rock, No. 2, Grand Canyon, Mohave Co., Arizona

In addition to fossil scales of *Sceloporus*, seven Pleistocene midden samples contained fossil scales representing three other lizard genera as follows: *Sauromalus obesus* (Muav Gate Number 1, Grand Canyon, Mohave County, Arizona; Rampart Cave Stake 0+35, Grand Canyon, Mohave County, Arizona; Rampart Cave Stake 45; Redtail Peaks Number 1, Whipple Mountains, San Bernardino County, California; Vulture Canyon, Numbers 2B and 3B, Grand Canyon, Mohave County, Arizona); and *Crotaphytus* and *Cnemidophorus* (Rampart Cave, Pit B, Left Wall, Grand Canyon, Mohave County, Arizona). Representatives of each of these forms occur at or near each of the respective fossil localities today.

SIGNIFICANCE OF THE FOSSIL SCALES

Most fossil packrat middens contain remains of from 15 to 30 identifiable plant taxa that provide good records of the Ice Age floras near the sites. Animal remains are much less common and many middens contain no vertebrate fossils whatsoever. When bones are present, lizards often are represented. However, epidermal scales of *Sceloporus* are more common than bones, and bones are lacking in many middens that contain scales. Approximately 50 percent of the middens investigated contained one or more lizard scales. It is to be hoped that investigators will save these tiny, irreplaceable and perishable organic fossils when conducting analyses of packrat middens in the future.

As developed in preceding sections, the vast majority of the fossil scales can be identified accurately to the genus *Sceloporus*. In some cases they can be identified as probably representing one of either one or two Recent species, based on size, notching, and present geographic distributions. The identification of *Sceloporus* dentary bones and maxillaries usually can be carried farther with somewhat more confidence, if they are present in a sample. There are a number of

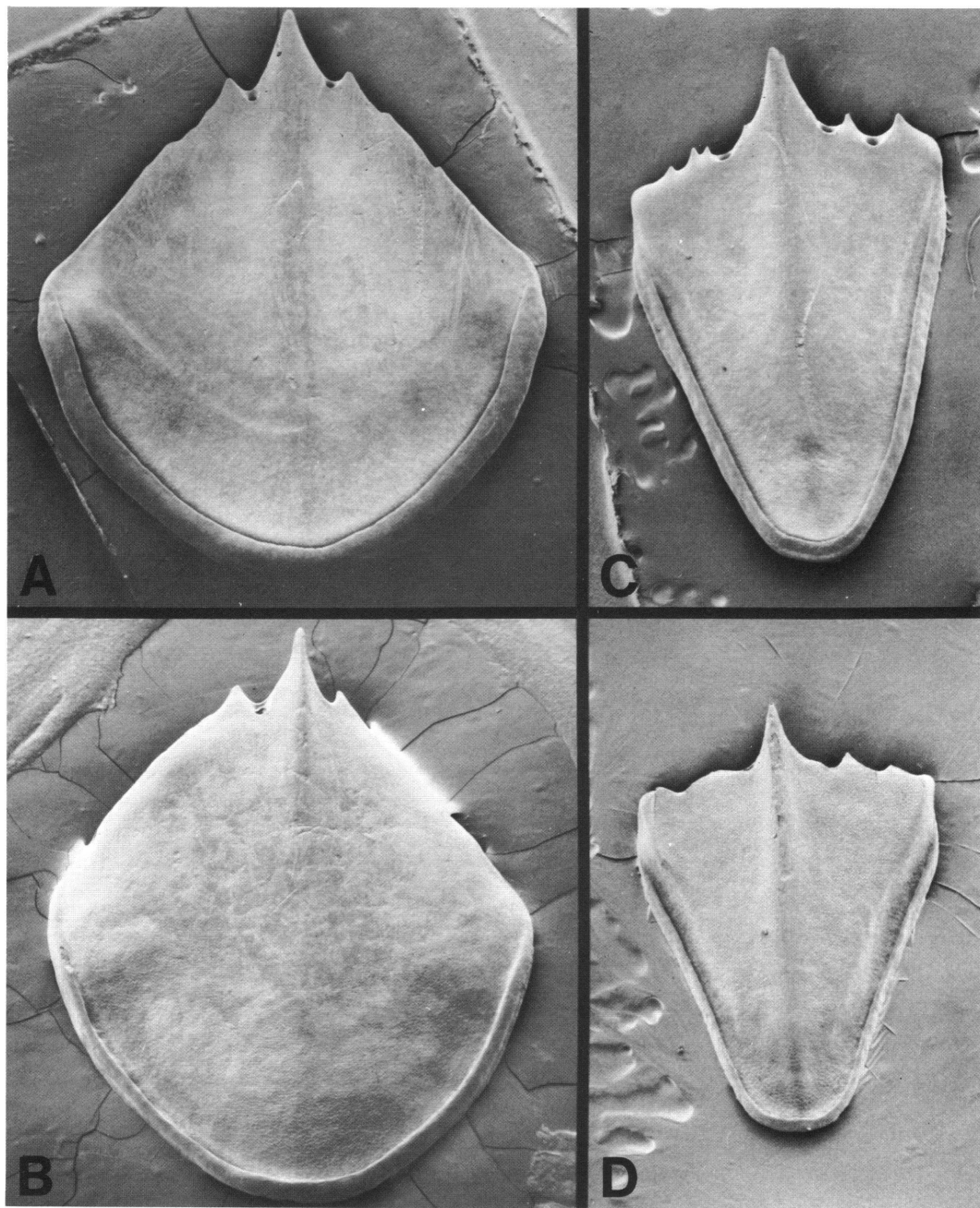


FIG. 37. Fossil and Recent scales of *Sceloporus*. A. Dorsal, Recent *S. magister*, AMNH 108053, $\times 12$. B. Fossil, AMNH 112011, $\times 24$. C. Left lateral medial caudal, Recent *S. magister*, AMNH 97781, $\times 12$. D. Fossil, AMNH 111975, $\times 24$.

characteristics of tooth and bone morphology that allow recognition of subgeneric groups. For

example, the *spinosus* group (e.g., *S. clarkii*, *S. magister*, *S. orcutti*), the *torquatus* group (e.g., *S.*

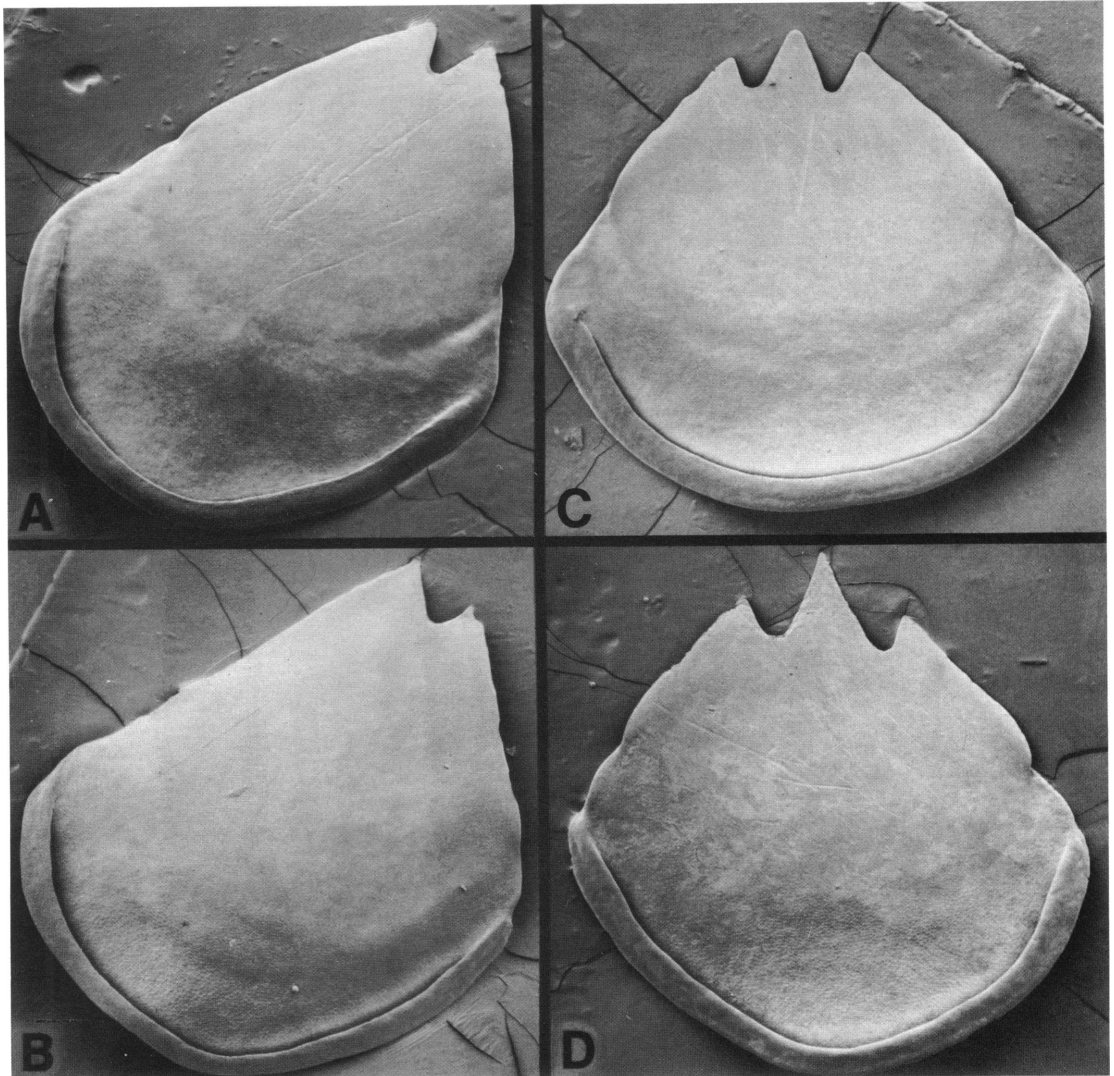


FIG. 38. Fossil and Recent scales of *Sceloporus*. A. Ventral, Recent *S. magister*, AMNH 108053, $\times 20$. B. Fossil, AMNH 111984, $\times 20$. C. Ventral, Recent *S. magister*, AMNH 108053, $\times 20$. D. Fossil, AMNH 111984, $\times 20$.

jarrovii), the *undulatus* group (e.g., *S. occidentalis*, *S. undulatus*), and the *graciosus* group (*S. graciosus*). With a large enough series of modern skeletons, certain well-preserved fossil bones can be assigned to a probable species. Details concerning the fossil *Sceloporus* bones found in these middens will be included in a later report on all the faunal remains.

One interesting aspect of fossil midden analy-

sis is the possibility of finding Pleistocene biotic communities that differ from communities of today. Midden fossils are from a small area and usually are well-associated. *Sceloporus magister* today is widespread in the lower deserts and less frequently occurs in chaparral and lower woodland habitats. The fossil scale record suggests that *S. magister* lived in woodlands more so in the late Pleistocene than at present. If so, this is an

example of a species that is able to adapt to changing climates and vegetations. The desert

tortoise (*Gopherus agassizi*) and chuckwalla (*Sauromalus obesus*) are additional desert species

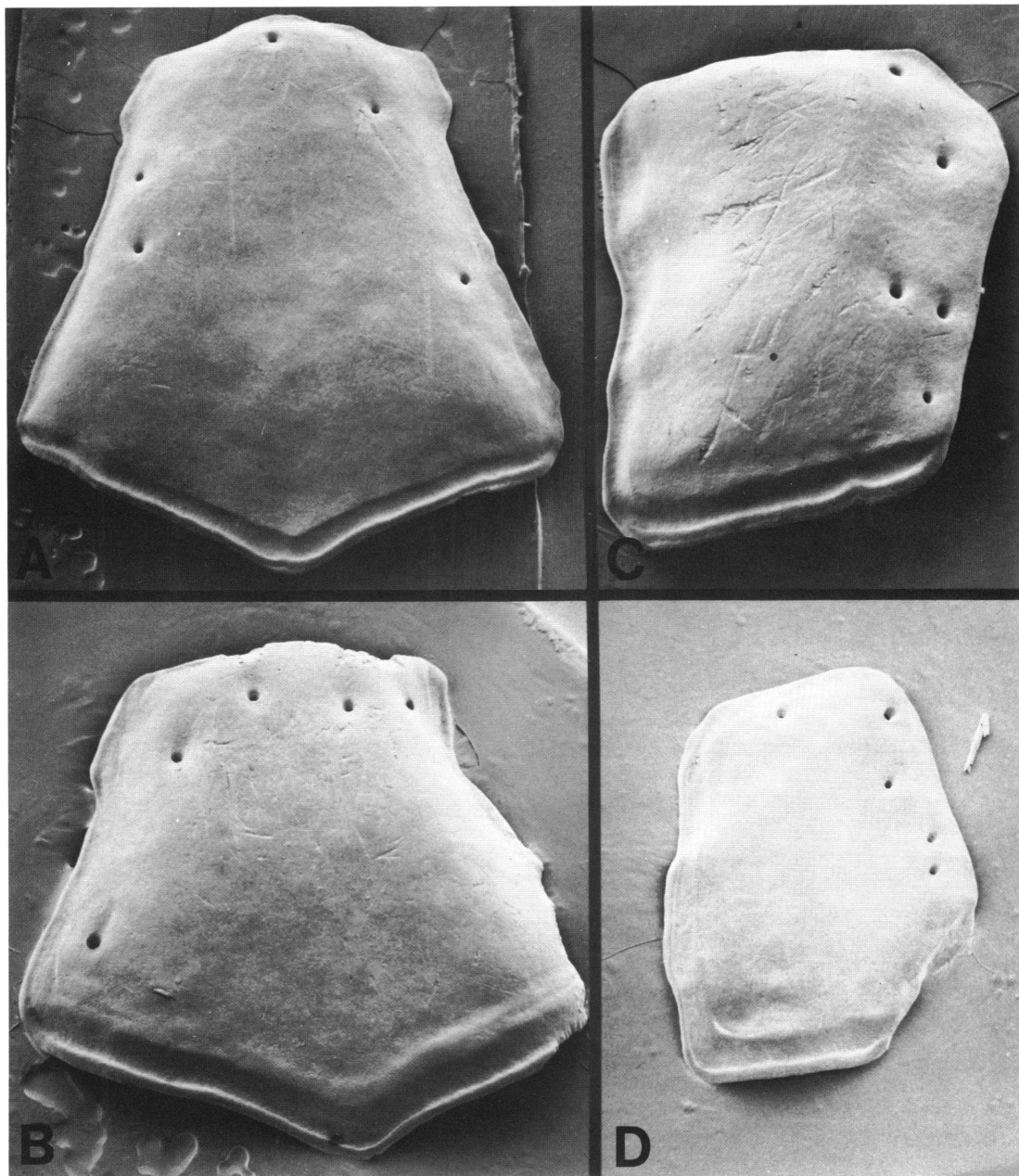


FIG. 39. Fossil and Recent scales of *Sceloporus*. A. Anterior frontal, Recent *S. magister*, AMNH 97781, $\times 12$. B. Fossil, AMNH 111975, $\times 24$. C. Right frontoparietal, Recent *S. magister*, AMNH 97781, $\times 24$. D. Fossil, AMNH 111970, $\times 24$.

whose remains have been recovered in some of the same fossil middens (Emery Falls Number 6; Rampart Cave Stake 0+35 and Stake 45; Vulture Canyon Number 2B and Number 3B; Whipple Mountains Number 2; and Window Rock Number 1). Combinations of desert animals and woodland plants together at these sites may indicate Ice Age climates with winter temperatures similar to or slightly milder than those at present and with the lowest extremes not sufficiently severe to exclude the desert species.

EVOLUTIONARY TRENDS IN SURFACE MICRO-ORNAMENTATION OF *SCELOPORUS* SCALES

None of the variation we observed in surface micro-ornamentation suggested the evolutionary trends that have occurred on *Sceloporus* scales. Indeed, by examining scales on living and preserved animals, we found that the surface micro-ornamentation is rather similar on the seven Recent species we examined, as long as scales at similar stages of the shedding cycle are compared. Our observations also indicate that the surface of a single scale varies considerably depending in part on the shedding cycle: when first exposed, the scale surface is clean and highly ornamented, but months later, following normal wear and prior to being cast, the surface ornamentation may be completely deteriorated.

Burstein, Larsen, and Smith (1974) examined the surface structure with an SEM on one area each of scales taken from preserved specimens of 51 species of *Sceloporus*. They considered the following characteristics as significant in comparing the species: pits and spinules on the cell surfaces (they recognized seven rather subjective character-states); height of the partitions comprising the cell boundaries (they recognized six rather subjective character-states); and extent of imbrication of the cell boundaries (they recognized six rather subjective character-states). Their conclusions included the following: "Dermatoglyphics are of no apparent diagnostic value at higher taxonomic levels in the genus *Sceloporus*, but may be very useful at the sub-species, species and species-group levels" (their p. 367); "Microornamentation of scale surfaces is seemingly unidirectional in evolution" (their p. 368); and "Dense spinulation, flat cell surfaces and lack of imbrication are primitive character-

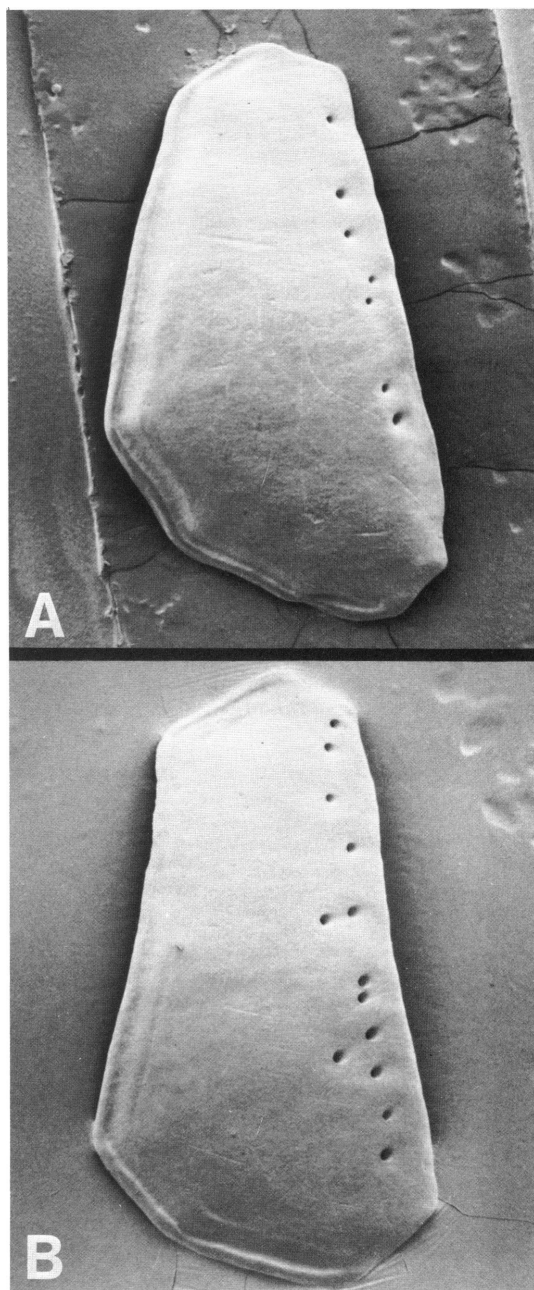


FIG. 40. Fossil and Recent scales of *Sceloporus*. A. Right supraocular, Recent *S. magister*, AMNH 97781, $\times 12$. B. Fossil, AMNH 111970, $\times 24$.

states in *Sceloporus*" (their p. 368). These authors, however, worked strictly with scales

from preserved specimens, and they did not properly account for variation. Comparison of their photographs with ours, including those of *S. occidentalis* and *S. undulatus* in particular, reveals that their conclusions are based in part on examination of lizards that were preserved at different stages of the shedding cycle, which influenced their results significantly. Our direct comparisons of shed scales with newly exposed scale surfaces obtained concurrently from living individuals demonstrate that most of the character-states utilized by Burstein, Larsen, and Smith (1974) are nothing more than differences that normally appear on a single scale surface at different periods in the shedding cycle.

SCALE FUNCTIONS

The possible functions of lizard scales and their surface ornamentation should be examined in the context of the functions of skin in general, attributes of members of the Reptilia and other higher taxonomic categories in general, and the special requirements and adaptations of individual species. Thus, the selective advantages resulting in the evolution of many of the structures illustrated here may be varied, numerous, and intricately interdependent. Lizard skin contributes to the following functions: support; defense and protection of the body from physical damage and invasion by micro-organisms (Bellairs, 1970); maintenance of the coloration and color patterns characteristic of the species (Monroe and Monroe, 1968; Bellairs, 1970); reception of stimuli from the environment (Miller and Kasahara, 1967; Düring, 1973); reflection, absorption, and transmission of certain wavelengths of solar radiation (Tercafs, 1963; Porter, 1967; Coleman and Livezey, 1968; Monroe and Monroe, 1968); thermoregulation and maintenance of water balance (Soulé, 1966; Soulé and Kerfoot, 1972; also see Licht and Bennett, 1972; Horton, "1972" [1973]; Soulé, "1972" [1973]); sound production (Hiller, 1974); secretion production (Darevsky, 1957; Gabe and Saint-Girons, 1965, 1967; Cole, 1966a, 1966b; Maderson, 1970); locomotion and providing the proper surface contact with the environment, particularly in regard to friction (Ruibal and Ernst, 1965; Ruibal, 1968; Bellairs, 1970; Maderson, 1970; Stewart and Daniel, 1973); and to repair, maintain, and replace itself periodically

(Maderson, 1970).¹

Consideration of the possible functions of the micro-ornamentation (e.g., exposed cell boundaries and spinules) should account for the observations of similar micro-ornamentation on epidermal cells of amphibians also (e.g., Stockem, 1970; Löfberg, 1974; Welsch, Storch, and Fuchs, 1974). Indeed, spinules similar to those on the surface of superficial epidermal cells of *Sceloporus* occur also on the surface of eggs of the painted frog, *Discoglossus pictus* (see Campanella, 1975, p. 442, fig. 8). Our observations demonstrating that the ornamentation on *Sceloporus* scales is developed best on newly exposed surfaces immediately following molting and that it may deteriorate drastically thereafter could be considered as evidence supporting Maderson's (1970) suggestion that it functions to facilitate skin shedding. One could also argue, however, that other possible functions are more important and the periodic skin shedding is important in part to replace these structures because they deteriorate between molts. We favor the proposal that the surface ornamentation functions to provide proper surface contact between the animal and its environment, with the greatest ornamentation providing the greatest friction and vice versa.

At a lower magnitude of resolution, the nature of *Sceloporus* scales probably performs a similar function, and they may be useful in locomotion and defense. We have observed evidence for this on a number of occasions with individual living lizards in gallon glass jars. Upon insertion of a hand into a jar, the lizard may scramble, standing vertically against the sides (supported by its hind legs and tail) but unable to make upward progress in its frenzy because the sides are too smooth. If the observer's hand or arm contacts the lizard's back, however, the lizard can progress upward due to the contact of its rough dorsal scales with the human skin. We suspect that this type of scutellation may be selectively advantageous on lizards seeking shelter from predators in deep crevices among rocks and vegetation, where their efficient entry into cover and their ability to cling there may be enhanced by the structure of their scales.

¹Also see the thoughtful work of Regal (1975), which we received as this manuscript was going to press.

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