LATER EOCENE (UINTAN) LIZARDS FROM THE
GREATER SAN DIEGO AREA, CALIFORNIA

A Thesis
Presented to the
Faculty of
San Diego State University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
in
Geology

by
Richard Allen Schatzinger
August 1975
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Approved by:

[Signatures and dates]
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INTRODUCTION

Later Eocene fossil vertebrate bearing terrestrial strata interdigitate with marine beds in the San Diego area allowing correlation of the marine sequence with part of the terrestrial record (see Lillegraven, 1973).

Only two published records of lower vertebrates from the San Diego Eocene have so far been described; a monitor lizard, *Saniwa brooksi* was described from the Old Mission locality LACM (CIT) 249 (Brattstrom, 1955) and a turtle was reported by Brattstrom (1958). The lack of published accounts reflects neither the diversity nor the importance of the San Diego Eocene fauna.

San Diego and Sespe area later Eocene vertebrate faunas are widely separated geographically from other vertebrate bearing localities of the same age (see Black and Dawson, 1966).

This study considers in detail only the lizards and amphisbaenids. The San Diego later Eocene
lizard fauna represents the most speciose lizard fauna presently known from the North American Paleogene. A middle Paleocene fauna from the Tongue River Formation of southeastern Montana contains eight lizards (Estes, 1976, in press). The Bridgerian Tabernacle Butte lizard fauna of Wyoming (Hecht, 1959) contains ten species and the early Oligocene Cypress Hills local fauna of Saskatchewan (Holman, 1972) contains six forms. San Diego later Eocene sediments have so far yielded twelve lizards and one amphisbaenid.

Unfortunately, most of the fossils used in this study were very fragmentary. Therefore, estimates of minimum numbers of individuals recovered from various localities (used to aid faunal analysis) could not be profitably made.

Abbreviations

Abbreviations used in the report include:

AMNH--Department of Vertebrate Paleontology, American Museum of Natural History.

LACM--Natural History Museum of Los Angeles County.
LACM (CIT)--specimens originally in the California Institute of Technology now housed in the Natural History Museum of Los Angeles County.

loc.--locality

locs.--localities

no.--number

nos.--numbers

UCMP--University of California Museum of Paleontology, Berkeley.

USNM--United States National Museum, Smithsonian Institution.

YPM--Peabody Museum, Yale University.
Figure 1. *Palaeoxantusia kyrentos* sp. n. Skull of holotype, UCMP 106000. Dorsal view, anterior toward top of page. Scale in millimeters.
Figure 2. *Palaeoxantusia kyrentos* sp. n. Skull of holotype, UCMP 106000. Ventral view, anterior toward top of page. Scale in millimeters.
Figure 3. Index map of the greater San Diego and Los Angeles regions, southern California. UCMP loc. V-72088 is indicated by "x." Other localities are indicated on the inset.
SYSTEMATICS

In general, the form used throughout this section follows that of Estes (1964). All of the lizards are considered to belong to the Order Sauria, a commonly used taxonomic framework. I choose, however, to follow Berman (1973) in placing the amphisbaenians within a separate Order Amphisbaenia.

CLASS REPTILIA

ORDER SAURIA

FAMILY ?GEKKONIDAE

Referred specimens.—Dentary fragments, UCMP nos. 104809, 113225, and 113226.

Localities.—UCMP locs. V-71211, V-72157, and V-72179.

Description.—UCMP 104809 (Figure 4), the best preserved of the three specimens, is the anterior tip of a right dentary missing the symphyseal region and bearing 13 teeth and tooth spaces (Figure 4). The comparatively tall, delicate teeth project only about
one-fifth of their height above the jaw parapet; all preserved teeth have a slight posterior cant and there is slight anteriorly convex curvature to the teeth. Owing to close spacing of the teeth adjacent shafts are in contact at a point slightly below the jaw parapet. Dorsally the simple but rather pointed crowns are inflected medially. There is no evidence of accessory cusps or other complications of the crowns. Directly beneath the base of the first preserved tooth lies a tiny replacement tooth. Beneath the tooth bases is a wide, well developed but shallow dental gutter. Its medial edge is marked by a definite bony ridge which becomes less obvious beneath the base of the third preserved tooth so that there is only a flattened shelf anterior to this. Meckel's groove is closed and fused along the entire length of the specimen. The ventral margin of the dentary is concave, although if more of the dentary were preserved this curvature might not be so conspicuous. Aside from the curvature seen in lateral view, there is also a weak lingual convexity when the specimen is viewed dorsally. Externally there are the remains of
two widely spaced anteroposteriorly elongate external mental foramina placed about midway between the dorsal and ventral margins.

UCMP 113225 and 113226 are essentially like UCMP 104809 with the exception that no external mental foramina are visible on UCMP 113226; UCMP 113225 shows several irregularly placed foramina near the external symphyseal region. No complete teeth are preserved on UCMP 113226, also the distance between the ventral dentary margin and subdental gutter decreases anteriorly. The crista dentalis appears somewhat taller on UCMP 113225 than 104809.

Discussion.--This form is questionably referred to the family Gekkonidae on the basis of a combination of the following characters: direct tooth replacement, a wide, well developed dental gutter with medial bony ridge, fused Meckelian groove, numerous delicate, closely-spaced teeth, slightly posteriorly curved medially inflected crowns, and the conspicuous concavity of the ventral dentary margin.
As preserved, these specimens cannot be separated from the Pygopodidae, Sphaerodactylidae or Eublepharidae, but it would seem much more probable to suppose that a more primitive gekkonid would be represented as a lower Tertiary fossil than a member of such an advanced or aberrant gekkonoid family.

Modern gekkonids are found in South America, Central America and extreme southwestern North America, the West Indies, Africa, southern Asia, the East Indies, Australia, New Zealand, and numerous Pacific islands. Pygopodids are currently known to inhabit New Guinea, Tasmania, and Australia. Therefore geographic evidence would run counter to expecting a member of this group in the San Diego fauna. Sphaerodactylids are found in Central and South America as well as the West Indies so the same argument might hold for this group. Eublepharids are a widespread group with a disjunct distribution in southwestern North America to Central America, southern Asia, western Africa, and the Indo-Australian Archipelago. Although eublepharids have no known fossil record and their present geographic distribution suggests
(perhaps weakly) a southern origin, it is possible that the family could have arrived in southwestern North America early enough to have been preserved in sediments of Uintan age. A similar Paleogene south to north dispersal for the Iguanidae was suggested by Tihen (1964) and Estes and Price (1973).

Although gekkonid jaws superficially resemble those of prosirenid salamanders (Estes, 1969b) they may be distinguished from them by lack of the complex interdigitating symphysis seen in the latter.

The overall preserved length of specimens UCMP 104809, 113226, and 113225 are 2.23, 2.67 and 2.90 mm., respectively. The height of the jaw measured at the level of the next to last preserved tooth in UCMP 104809 (from dorsal tip of crown to ventral edge of dentary) is 1.14 mm; the same measurement is 1.22 mm at the level of the last preserved tooth in specimen UCMP 113225; no teeth are preserved in UCMP 113226.
Figure 4. Unidentified gekko, dentary fragment UCMP 104809, a, lingual view; b, dentary of Parasauromalus olseni, UCMP 104356, lingual view; c, enlargement of posterior teeth of UCMP 104356, lingual view.
Figure 5. Iguanid lizards: a, dentary fragment of iguanid, Form A, UCMP 104326, lingual view; b, enlargement of replacement tooth from UCMP 104326; c, iguanid, Form B, dentary UCMP 99965, lingual view.
FAMILY IGUANIDAE

Introduction to the Family

Living iguanids are primarily distributed across North, Central, and South America, but are also known from the Galapagos Islands, Fiji and the Tonga Islands, and Madagascar.

Etheridge (1964) informally grouped iguanids into the following subgroups: sceloporines, tropidurines, iguanines, and Crotaphytus.

The earliest record of the Iguanidae is Pristiguana brasiliensis (Estes and Price, 1973) from the Upper Cretaceous Baurú Formation of Brazil. Estes (1970) also reported that there are at least eight species of iguanid lizards in the Paleocene of Brazil. The oldest described North American iguanid is Parasauromalus olseni, which was previously known only from the early to middle Eocene of Wyoming. The description of P. olseni below considerably extends its known geographic and geologic range.

Both Tihen (1964) and Estes (1970) have suggested that the late occurrence of iguanids in
North America may be explained by assuming that much of early iguanid evolution took place in South America and that they reached North America relatively late (late Paleocene or early Eocene) by waif dispersal.

**Parasauromalalus** Gilmore, 1928

**Revised diagnosis.**—Distinguished from species of all other iguanid genera by the following combination of characters. Teeth pleurodont, laterally compressed, with vertical lingual striations giving a serrate effect to the spoon-shaped crowns in lateral view; teeth closely spaced with flaring crowns, tricuspid on the posterior half of the tooth row; lateral cusps comparatively small, poorly developed; on the average, teeth projecting a little more than a third of their height above the parapet of the jaw; maximum number of teeth on a complete dentary 25-27; Meckelian groove closed but not fused for the space of several teeth anterior to the splenial, then reopening and remaining narrowly open to the symphysis; splenial large, underlying more than half of the dentary tooth row; no lateral coronoid overlap of dentary along
posterior edge of dentary; posterior border of dentary extending posterior to posterolateral limit of coronoid.

**Parasauromalus olseni** Gilmore, 1928

**Referred specimens.**—Dentaries, UCMP nos. 104212, 104356, 104625, 104677; maxillary fragments, nos. 104232, 104352, 104377, 104638, and unnumbered specimens; teeth, nos. 104236, 104241, 104331, 104625, 109855, 109858, and unnumbered specimens; premaxilla, no. 104365, LACM nos. 55924, an anterior maxilla; 55926, a dentary fragment.

**Localities.**—UCMP locs. V-6893, V-68116, V-71175, V-71183, V-72088, V-72157, V-72158, V-73138; CIT loc. 249.

**Diagnosis.**—As for the genus.

**Description.**—In lateral view the gently tapering dentary has a very slightly convex ventral margin with no flattened or sculptured areas. Four mental foramina are present, beneath the fourth, fifth, eighth, and eleventh teeth from the front of the tooth row in UCMP 104356 (Figure 4). The first, third, and
fourth foramina are at the same level and form a nearly straight line; the second, however, lies higher—immediately beneath the base of the fifth tooth. Three mental foramina are preserved on UCMP 104212, the broken anterior end of a right dentary, beneath the fourth, tenth, and sixteenth teeth from the front. All foramina on this specimen are located midway between the dorsal and ventral margins of the dentary. The posterior and posterodorsal margins of UCMP 104356 are broken although probably not much bone is missing. There is no evidence that a labial coronoid overlap ever existed despite this minor breakage. Dorsal orientation shows that posterior to the seventh tooth from the front the dentary is nearly straight. There is a slight swelling and related lingual thickening centered about the fifteenth tooth, beyond this the margins of the bone are smooth and parallel.

The medial borders of the dentary are separated by a large splenial notch reaching forward to the thirteenth tooth from the front. The borders of the Meckelian groove close anterior to the splenial but do
not fuse. The groove opens again at the level of the
ninth tooth from the front and remains narrowly open
and ventrally placed as it continues to the symphysis.
Directly beneath the twentieth tooth from the symphysis
the internal mental canal opens. The maximum length
of the dentary as preserved on UCMP 104356 is 24.15 mm.
Four posterior teeth occupy 3.79 mm. There are 27
tooth spaces from which 16 completely or nearly com-
pletely preserved pleurodont teeth project. Teeth
making up the posterior half of the tooth row are
broadly and bluntly tricuspid with small side cusps
lower than the central cusp and set off from it by a
broad, shallow vertical groove. The subequal accessory
cusps are sloping and protruding "shoulders." The
closely spaced tooth shafts are tall and nearly
straight in lateral view but slightly antero-
posteriorly compressed so that cross-sections of the
shafts are oval with the long axis at right angles to
the axis of the dentary. All preserved crowns are
slightly lingually inflected. In anterior or posterior
view the teeth are widest at their bases and slope
regularly upward to the lingually inflected tips. Teeth lack basal expansions.

Tooth crowns are laterally compressed and crudely spoon-shaped. The lingual surface is marked with coarse vertical striations but the crowns are smooth labially (UCMP 104356 and most other specimens); crown flare is generally lacking so that tooth bases are approximately the same width as the crowns in lateral view.

Depending upon the location, 30-45 percent of individual teeth project above the jaw parapet. The bases of the fifth, tenth, eighteenth, twenty-first, and questionably the twenty-fourth teeth (UCMP 104356) are excavated or were being replaced. The sulcus dentalis is only moderately developed.

The premaxilla, UCMP 104365, bears five procumbent teeth and indications are that at least two more were originally present. The teeth are moderately thick but in all respects like anterior dentary teeth. The broad base of the nasal process rises smoothly from the rostral portion at an angle indicating that the snout was not highly domed and
that the premaxillary teeth were protrusive even when the premaxilla is oriented as it would have been when articulated with the skull. Both broken bases of the lobes of the incisive process are rather widely spaced, the distance equal to the diameter of one tooth separating them. A groove is present dorsally on either side of the base of the nasal process.

**Discussion.**—Parasauromalus olseni is based on AMNH 1620, a partial right mandible including part of the dentary, splenial, and three complete teeth. The holotype is from the lower Eocene Wind River Formation of Wyoming. Five other specimens of the species are also known from the Eocene of Wyoming.

The San Diego specimens may be referred to *P. olseni* on the basis of similarity of the Meckelian groove (closed but not fused for a space anterior to the splenial but reopening anteriorly), tooth count, form and cross sectional shape, the fact that about half of tooth row is tricuspid, and the presence of a large splenial, and the apparent lack of a lateral coronoid overlap onto the dentary.
The splenial underlies 52 percent of the tooth row in UCMP 104356. YPM 3947, an almost complete skull and mandibles from the lower Eocene Willwood Formation of Wyoming, has a splenial underlying 60 percent of the tooth row. Twenty-seven teeth are present in UCMP 104356, the most complete San Diego specimen. There were probably no other teeth present originally. YPM 3947 had an estimated dentary tooth count of 25 (Estes and Etheridge, ms.). The condition of the Meckelian groove (closing for a space anterior to the splenial) is essentially the same in the San Diego and Wyoming specimens. However, the anteriormost portion of YPM 3947 is missing. There is only a slight development of crown flare in the Wyoming specimens, including the type (AMNH 1620). Crown flare is extremely poorly developed or absent in the San Diego specimens; tooth shafts are sub-parallel. Three to four mental foramina and a moderately developed sulcus dentalis are present in the local material while two to three mental foramina and a poorly developed sulcus dentalis are found on the Wyoming specimens.
The minor differences listed here are insufficient to describe a new species based on the San Diego specimens.

Gilmore (1928) compared the teeth of *Parasauromalus olseni* to those of *Sauromalus ater*, but this is unjustified. The teeth of *S. ater*, as is characteristic of all iguanine iguanids, show highly compressed, spatulate crowns with very strong accessory cusps separated from one another by distinct and deep valleys. The teeth of *Parasauromalus olseni*, in contrast, are simply tricuspid and little if at all flared—the accessory cusps more in the form of enlarged shoulders with vertical striations giving the impression of a serrate edge. I believe that the condition of the teeth of *Parasauromalus* may be said only to approach what was probably an early iguanid style that was later highly developed in *Iguana, Ctenosaura, Dipsosaurus, Sauromalus* and others, but does not imply close relationship to these modern forms.

The condition of the Meckelian canal is a feature often used when discussing iguanid
intrafamilial relationships. *Pristiguana brasiliensis*, *Paradipsosaurus mexicanus*, and living morunasaurines have a Meckelian canal which is wide open between the splenial and the symphysis. A slightly more advanced condition, groove closed but unfused for the space of a few teeth anterior to the splenial, but reopening anteriorly, is typical of basiliscines, oplurines, *Crotaphytus*, and the Oligocene genera *Cypressaurus* and *Aciprion*. A Meckelian groove in this condition probably represents merely a small advance over the morunasaurine condition, not close affinity of groups. Sceloporines and some tropidurines exhibit a slightly more specialized condition in which the groove is characteristically closed but unfused anterior to the splenial. The condition of *Parasauromalus* may lie between the "sceloporine" and "basiliscine-oplurine" conditions, but closer to the latter state since the groove remains closed for the distance of at least seven teeth in YPM 3947 and remains closed but not fused beneath only four teeth in UCMP 104356. Iguanines, most tropidurines, and anoles show what is
probably the most advanced condition, the canal being closed and fused anterior to the splenial.

The large splenial of *Parasauromalus* is clearly primitive (it underlies 52-60 percent of the tooth row on various specimens examined) but is not as primitive as the very large splenial that extends well forward of the middle of the tooth row in morunasaurines. A somewhat smaller splenial, extending nearly to the middle of the tooth row, but still smaller than that possessed by *Parasauromalus*, occurs in *Aciprion, Crotaphytus*, oplurines, and basiliscines. The splenial is comparatively smaller in all other iguanids.

There is no lateral coronoid lappet at the posterior edge of the dentary in *Parasauromalus*, most tropidurines, all sceloporines, oplurines and basiliscines. There is usually no coronoid overlap in *Crotaphytus* (Etheridge, 1964). A strong coronoid lappet is present in all iguanines, some tropidurines, all morunasaurines, and all anoles except *Anolis agazzii*. 
Taking all characters of the dentary together it appears that *Parasauromalus* has no close relation to any living group. Morunasaurines and *Pristiguana brasiliensis* are slightly more primitive while the other iguanids are slightly to considerably more advanced. Characters of the dentary of *Parasauromalus* present a mosaic of resemblances. A comparison of the features of the entire skull and mandibles of *Parasauromalus* with other iguanids is currently being undertaken by Estes and Etheridge (ms.). Estes (1970) believes that *Parasauromalus* has no close relationship to living groups and that agrees with the discussion above based upon the dentary alone.

Fossils referable to *Parasauromalus olseni* from the San Diego area extend the range of the species upward in time to include the Uintan (later Eocene).

Unidentified iguanid, Form A

**Referred specimens.**--Dentary fragments, UCMP nos. 104326, 104359, and 106279; maxillary fragment, UCMP no. 113243.
Localities.--UCMP locs. V-71211, V-72157, and V-72158.

Description.--The description is based on UCMP 104326, a fragmentary right dentary (Figure 5). Although the specimen is broken anteriorly, posteriorly and ventrally it appears quite distinct from the other iguanids in the fauna. The smoothly curving lateral surface flattens anteriorly so that a marked "mid-lateral angle" separates the dorsolateral flattened portion from an inflected ventrolateral portion. The upper flattened portion of the lateral surface is pierced by the first three of six preserved regularly spaced mental foramina.

High up on the posterolateral edge of the bone lies a very shallow elongate depression which does not deepen as it extends posteriorly to the broken rear edge of the dentary. This depression is the anterior portion of a somewhat larger groove developed to retain the anterolateral process of the coronoid.

Because most of the medial surface of the dentary is broken it is impossible to say how large the splenial was or how far forward it extended.
Anteriorly the Meckelian groove is closed and fused, failing to reopen as far forward as the dentary is preserved.

There are 22 teeth and spaces. Although the medial surface is badly broken it appears that the posterior edge of the specimen was near the rear of the tooth row with probably no more than two to three teeth posterior to the last preserved space. Judging from the medial curvature of the anterior tip of the specimen there were, likewise, no more than two to three additional teeth at the anterior end of the jaw. The total tooth count then probably was between 26 and 28.

The teeth themselves are pleurodont, moderately high crowned, and with anteroposteriorly compressed shafts that give an oval shape in cross section. In lateral view the shafts have generally subparallel borders with a slight enlargement at the level of contact with the dentary. Unbroken teeth show a marked medially expanded basal "belly" so that in anterior view the bases are much wider than the crowns toward which they rapidly taper.
The crowns are laterally compressed, medially curved and tricuspid on all unbroken teeth. Lateral cusplets of equal height are well developed and separated from the broader middle cusp by a vertical groove on both labial and lingual tooth surfaces. Crown flare is lacking. Striations are also absent on all teeth—including a completely unworn and unerupted replacement tooth preserved in place posterior to the fourth unbroken tooth. Teeth of this sort are very common among iguanids.

UCMP 104326 is broken into two comparatively poorly articulating portions so that measurement of its length would be virtually meaningless.

Discussion.—The closed and fused Meckelian groove of this form is not uncommon among many iguanines, most tropidurines and anoles. A lateral coronoid lappet onto the dentary is known in all morunasaurines, iguanines, all anoles except Anolis agazzii, some tropidurines, Paradipsosaurus and occasionally Crotaphytus (Etheridge, 1964, p. 628). Teeth of iguanines contrast strongly with the form
represented by UCMP 104326 in possessing strongly compressed and deeply cuspate as well as multicuspate, flaring crowns; UCMP 104326, on the other hand, possesses typical "sceloporine" tooth crowns.

Among oplurine iguanids there is no lateral coronoid lappet. The condition of Meckel's groove anterior to the splenial varies between open to the symphysis, closed but not fused for a space of about five teeth to closed and fused anterior to the splenial but reopening anteriorly. There seems to be no resemblance of these Madagascan forms to UCMP 104326.

There is no lateral coronoid lappet among basiliscines. Among basiliscines the condition of Meckel's groove anterior to the splenial ranges from closed and fused to closed but not fused, and is occasionally open to the symphysis. There is probably no close relationship between fossils and basiliscine iguanids.

Although poorly preserved, UCMP 104326 appears equally close to anoles and some tropidurines. Anoles generally show rather unspecialized teeth, closed and
fused Meckelian groove, and a strong coronoid lappet in most forms—as in UCMP 104326. It also resembles some tropidurines, especially *Leiocephalus* and *Stenocercus* in the same features listed for anoles except that the tropidurines often show slightly anteroposteriorly flared crowns. *Stenocercus* approaches *Leiocephalus* so much that Etheridge (1966: 87) questioned whether all the continental species of *Leiocephalus* are distinguishable from those of *Stenocercus*.

Although the specimens are fragmentary, their relationships appear to be with either the tropidurines or the anoles.

The form appears distinct from all known fossil iguanid lizards. I prefer not to name it, however, owing to poor preservation and fragmentary nature of all specimens. Nevertheless two interesting possibilities are suggested if these specimens are in fact either anoline or tropidurine. First, the suggestion (Estes and Price, 1973) of a relatively late (late Paleocene to early Eocene) invasion of iguanids into North America from a southern source may
be strengthened by the possible relationships of the Uintan iguanid represented by UCMP 104326. Secondly, the fossil could represent part of an anoline, tropidurine or intermediate (preanoline, pre­tropidurine) stock which independently invaded North America in the early Tertiary and left no known descendants.

Unidentified iguanid, Form B

Referred specimens--Dentaries, UCMP nos. 99965, 104233, 104363, 104378, 104820; 113241, 113242, and LACM (CIT) 37912.

Localities.--UCMP locs. V-6893, V-72088, V-71175, V-72157, V-72158; LACM (CIT) 220.

Description.--UCMP 99965 (Figure 5), a partial left dentary, is the best preserved specimen and thus the description will be based on it. The anterior portion of the splenial is preserved on UCMP 99965. The dentary is broken anteriorly and posteriorly. It tapers anteriorly with a very slightly convex ventral surface. A single mental foramen is preserved near
the anterior end of the lateral surface about midway between dorsal and ventral edges. The lateral surface is gently curving and smooth except for the posterodorsal coronoid insertion. This groove is elongate and oriented subparallel with the dorsal edge of the bone; it is well marked by sharp borders. The posterodorsal edge is overhanging and lateral to the deepest portion of the groove. The depressed surface of the groove rises anteriorly where it connects with and runs forward as a very shallow sulcus which reaches forward almost to the level of the mental foramen.

The posterior border of the dentary is broken in an irregular, convex manner. There is no evidence of a large anterior-reaching surangular. The angular is not evident on the specimen as preserved.

Medially the borders of the dentary are separated by a wide splenial notch which closes at the level of the eleventh tooth from the rear. I would estimate that two or three more teeth were present posteriorly in the unbroken state. If this is the case the splenial notch would close about 13 to 14 teeth
from the rear of the tooth row. The internal mental canal opens beneath the fourth tooth posterior to where the splenial notch closes. The Meckelian groove is closed anterior to the splenial notch but not fused in specimens UCMP 99965 and 104233. In UCMP 113241 Meckel's groove is narrowly open anterior to the splenial, however, the specimen is badly worn. UCMP 113242 agrees with specimens UCMP 99965 and UCMP 104233 in having a closed but unfused Meckel's groove. In UCMP 99965 the Meckelian groove reopens again further anterior at the level of the third most anterior preserved tooth. Noting the curvature of the bone and nature of the anterior preserved teeth in UCMP 99965 I would estimate that there were five to six more anterior teeth in a complete dentary. This would bring the estimated total tooth count to a probable 30 to 32 as there are 23 spaces preserved in UCMP 99965.

The sulcus dentalis is poorly developed. Anteriorly the subdental shoulder is rounded and slopes away from the tooth bases without a subdental ridge separating the bases from the sloping shoulder.
The maximum length of UCMP 99965 is 16.03 mm. as preserved.

All but three eroded tooth crowns are broken off of specimens UCMP 99965 and 104233. Several crowns are well preserved in UCMP 104368 so that when both specimens are considered together a description of the tooth row can be made. The teeth are closely set. Anteriorly the teeth are unicuspid; broad, bluntly pointed cusps are somewhat laterally compressed and incurring. The posterior teeth are broadly tricuspid with poorly developed lateral cusps. Secondary cusps are separated from the main cusp by a shallow vertical groove. There are no striations on either the labial or lingual surfaces of the crowns. On none of the teeth are the crowns wider than the tooth shafts. In lateral view the edges of the shafts are subparallel, however, the bases may be very slightly swollen. A lingually directed "belly" is commonly present just above the tooth bases. All tooth shafts are anteroposteriorly compressed and therefore oval in cross section. In anterior or posterior view the teeth taper from the widest portion
at the base of their rather pinched crowns. The "belly" at the tooth bases accounts for a rather minor bulge in tooth profile in this orientation.

Individual teeth project about 30 percent of their height above the jaw parapet.

Discussion.--UCMP 99965 (iguanid, Form B) is considerably larger than UCMP 104326 (iguanid, Form A), however, the size range of unidentified iguanid, Form B extends down nearly to the size of UCMP 104326. The two species cannot be distinguished by tooth morphology.

The most primitive state of Meckel's groove is open from splenial to symphysis. This condition is found in Pristiguana, morunasaurines, some basiliscines, some oplurines, Paradipsosaurus, and Crotaphytus. In some basiliscines, some oplurines, a Crotaphytus, and the Oligocene genera Cypressaurus and Aciprion the canal may close anterior to the splenial for the space of a few teeth and then reopen to the symphysis. More specialized is the Meckelian canal of sceloporines, some tropidurines, and the San Diego
unidentified iguanid, Form B. Here Meckel's groove is closed but not fused anterior to the splenial. The remaining tropidurines, all iguanines and anoles have a closed and fused canal.

Among iguanids the splenial is largest in Pristiguana, Paradipsosaurus and living morunasaurines. Among these groups the splenial extends well forward of the middle of the tooth row. A second, slightly more advanced group includes oplurines, basiliscines, the Oligocene genera Aciprion and Cypressaurus, living Crotaphytus, and San Diego unidentified iguanid, Form B. In all other iguanids the splenial underlies relatively much less of the dentary tooth row. The splenial is absent (or fused) in most species of Anolis.

A strong coronid lappet onto the dentary is present in all iguanines, morunasaurines, nearly all anoles, some tropidurines, Paradipsosaurus, and occasionally in Crotaphytus as well as the fossil iguanid (Form B). The lappet is always absent in sceloporines, oplurines, basiliscines, most tropidurines, and the fossil genera Cypressaurus, Aciprion,
Pristiguana; the lappet is usually absent in Crotaphytus.

Taking all observable character states together there appears to be no very close relationship of the fossil iguanid (Form B) with any of the iguanid subgroups or fossil genera. The only group that has more than one character state in common with the fossil is the tropidurine iguanids—but only those tropidurines with an unfused Meckelian groove and a coronoid lappet. Even among these few tropidurines, the size of the splenial is considerably advanced (smaller) than that of the fossil. Among those tropidurines exhibiting an unfused Meckelian groove and coronoid lappet only Stenocercus and South American Leiocephalus compare to the fossil in possessing non-flared crowns. Also, Leiocephalus has slightly anteroposteriorly compressed tooth shafts as in the local fossil. Among sceloporines nonflaring crowns and anteroposteriorly compressed shafts are the rule so that the teeth of sceloporines are comparable to the unidentified iguanid, Form B, except that teeth of
the fossil are, in general, slightly more robust than those of sceloporines.

The relatively large splenial, comparable in size to that in oplurines, basiliscines, *Crotaphytus*, and the Oligocene genera *Cypressaurus* and *Aciprion*, I believe is merely the result of retention of a primitive (large) splenial size in all of these groups and does not imply a close relationship between the fossil form and any of the groups mentioned.

The presence of a coronoid lappet alone is not sufficient to place the fossil among the following subgroups of iguanid lizards: iguanines, morunasaurines, anoles, *Paradipsosaurus* and *Crotaphytus*. Certain other important character-states are found among the informal iguanid subgroups which are absent (or not preserved) in the fossil. Such character-states include: specialized mandibular teeth, reduced splenial, and fused Meckelian canal among iguanines; a very large splenial and widely open Meckelian canal among morunasaurines; a fused Meckelian canal and reduced splenial among anoles; a large splenial and widely open Meckelian canal in *Paradipsosaurus*; in
Crotaphytus Meckel's groove is usually open, there is usually no coronoid lappet, it has less high crowned teeth, and the tooth shafts are more rounded in cross-section.

I would therefore consider that although the fossil iguanid (Form B) has no close relation to modern subgroups it is probably nearest to the group of mainland South American tropidurines including Stenocercus and Leiocephalus. In this light unidentified iguanid, Form B, may be compared to unidentified iguanid, Form A, from the San Diego Eocene. Form B is very similar, if not conspecific with undescribed iguanid remains from the Green River Formation (early Eocene) of Utah. It may be that tropidurines or "near-tropidurines" were present in North America in the early Tertiary. Thus while Leiocephalus was well established in North America by the Miocene (Robinson and Van Devender, 1973; Estes, 1963; and possibly the unidentified iguanid, Form B, of Estes and Tihen, 1964), there is a chance that it may be related to the early Tertiary forms described in this paper. It is equally possible that the early
"near-tropidurine" stock described in this paper became extinct leaving no descendants. *Leiocephalus* might then have invaded North America from the West Indies as postulated by Etheridge (1966).

**FAMILY AGAMIDAE**

**Introduction to the Family**

Contemporary agamid lizards are a diverse Old World counterpart both ecologically and morphologically to the New World Iguanidae. Today agamids range across southern Asia, the Indo-Australian Archipelago, Australia, the Phillipines, southeastern Europe, and Africa. There is no current overlap between the geographic distribution of iguanids and agamids.

Among living Sauria, chamaeleons and agamids alone exhibit an acrodont dentition. The highly compressed body, structure of the feet, and great elongation of the temporal region of the skull owing to parietal expansion at once set chamaeleons apart from agamids. The single North American fossil agamid
Tinosaurus has been previously described only from the Bridgerian of Wyoming.

_Tinosaurus_ Marsh, 1872

**Revised diagnosis**.--Based on the San Diego fossils and those mentioned by Gilmore (1928) _Tinosaurus_ may be distinguished from all other forms by its relatively small teeth which are acrodont, short, laterally compressed and triangular in lateral view; tricuspid posteriorly, lateral cusps become less developed anteriorly on the tooth row so that anterior teeth lack lateral cuspulents completely; Meckelian groove open.

**Comment**.--At present _Tinosaurus_ may be a composite grouping. A comparison of all known specimens and hopefully any new material will one day be necessitated in order to clarify the position of this enigmatic taxon.
Tinosaurus cf. T. stenodon Marsh, 1872

Referred specimens.—UCMP nos. 104255, 104261, 104294, 104330, 104342, 104347, 104568, 104813, 105985, 106217, 106407, 106414, 109623, 109930, plus several unnumbered teeth.

Diagnosis.—Gilmore (1928, p. 31) diagnosed T. stenodon as "Typically larger than T. pristinus; teeth more swollen; dentary teeth with two, one, and no lateral denticles."


Description.—Most of the specimens consist of single teeth. The most complete specimens, UCMP 109930 and 106414, consist of no more than three teeth and fragments of jaw bone for each specimen. The reference to Tinosaurus, however, is made based on the acrodont nature and general form of the teeth. The teeth are laterally compressed, tricuspid and exhibit short crowns. The tips of the main cusp in specimens that do not appear to be abraded show fine
vertical wrinkles. Although in about half of the specimens the posterior lateral cusp is significantly higher than the anterior lateral cusp, neither lateral cusp ever approaches the height of the main cusp. All of the preserved teeth except for UCMP 104347 have three distinct cusps. UCMP 104347 consists of two teeth that appear to have come from the anterior portion of the jaw. There is not enough bone preserved to determine if this specimen is part of the maxilla or the dentary. The posterior tooth on this specimen has only a hint of a posterior lateral cusp. It is in contact with the anterior tooth to a greater degree than teeth originating farther back on the jaw. Modern agamids commonly have a closer packing of teeth anterior in the jaw. Another feature common in agamids is the presence of somewhat enlarged canine-like teeth near the front of the jaws. Perhaps the posterior tooth of UCMP 104347 is one of these "canines." The Meckelian groove is large and wide open in UCMP 109930 (Figure 6), which is the only specimen in which Meckel's groove is preserved. UCMP 104342 has a shallow vertical groove on the bone
Figure 6. *Tinosaurus* cf. *T. stenodon*, a, UCMP 109930, lingual view; b, *Palaeoxantusia allisoni*, dentary UCMP 110313, lingual view; c, a tooth from *Palaeoxantusia allisoni*, UCMP 104758; d, unidentified glyptosaurine anguid, dentary UCMP 104253, lingual view.
beneath and between the two teeth preserved. The
groove was undoubtedly worn by an opposing tooth of
the maxilla.

Discussion.—Vertical grooves of the sort seen
in UCMP 104342 are commonly found in Recent specimens
of the Agamidae and Chamaeleonidae. The San Diego
Uintan form generally has better developed lateral
cusps than those illustrated by Hecht (1959) although
this may be the result of wear in the Wyoming
specimens. In about half of the San Diego specimens
the main cusp rises steeper and comparatively higher
above the lateral cusps than in the illustration by
Gilmore (1928). Aside from these differences the
San Diego specimens compare favorably to the previous
photographs and drawings of T. stenodon.

The original description of Tinosaurus by
Marsh (1872) listed the space occupied by three lower
teeth as 4.5 mm. The material reported by Hecht
(1959) ranged between 3 and 6 mm. for the same
dimension. The two San Diego specimens with three
teeth give measurements of 2.2 and 3.5 mm.
The form at hand may represent a new species. I, however, prefer to defer judgment on this problem until more and better material is collected from the San Diego Eocene.

Both Camp (1923) and Gilmore (1928) placed the genus *Tinosaurus* within the Chamaeleonidae stating that *Tinosaurus* could equally well be placed in the Agamidae. Hecht (1959) listed *Tinosaurus* as an agamid without commenting on his placement. Incidentally, Hecht listed the form as *Thinosaurus* which is a synonym of *Saniwa*, a varanid lizard. The illustration and description on the other hand clearly imply that Hecht was discussing *Tinosaurus stenodon*.

I prefer to follow Hecht's designation of *Tinosaurus* as an agamid for two reasons. First, as Camp (1923) noted, there are no unquestioned New World fossil chamaeleons. Second, consideration of the present geographic distribution of the Chamaeleonidae gives me no reason to expect an early Tertiary representative of the family in North America. About half of the modern chamaeleons are found in Madagascar and neighboring islands in the Indian Ocean. Most of
the other half are native to North Africa (excluding the Sahara Desert) while a few forms are known from southern Spain, southern Arabia, India and Ceylon. None of the peculiarly expanded and ornamental chamaeleon parietals have been found in the San Diego material. Although this is negative evidence it does not go against inclusion of *Tinosaurus* within the Agamidae. It would seem best to place *Tinosaurus* in the more primitive group, the Agamidae.

**FAMILY XANTUSIIDAE**

*Introduction to the Family*

The xantusiids are a compact group of more or less crepuscular New World lizards. Living xantusiids have a rather restricted, disjunct distribution. One group is found in the southwestern United States, Baja California and the extreme northwestern portion of Sonora, Mexico. A second group is restricted to the Channel Islands off the coast of southern California. The third group ranges from central Mexico to Panama
and a rare genus is known only from the Cabo Cruz region of Cuba (Savage, 1963, 1964).

Two genera of xantusiids are known as fossils. The first, *Lepidophyma*, is a Pleistocene occurrence from Yucatan, Mexico. *Palaeoxantusia* is known from two previously described species. It ranges from the Middle Paleocene (Estes, unpublished manuscript) to Early Oligocene (Holman, 1972) of northwestern North America.

Hecht (1956) showed that all other lizard families are distinguished from the xantusiidae by a combination of the following characters: (1) absence of a posterior projecting external postcoronoid process of the dentary, (2) absence of a lingual shelf, (3) presence of distinct splenial and dentary, (4) presence of a Meckelian groove, (5) absence of a strong coronoid process of the dentary, and (6) higher number of teeth on the dentary, exceeding 18 in number.

*Palaeoxantusia* Hecht, 1956

Hecht (1956) characterized this genus as a moderately large, robust xantusiid with a distinct
splenio-dentary depression and a distinct groove along the posterolateral margin of the splenio-dentary for the adductor musculature plus the lack of lateral cusps on the teeth.

Revised generic diagnosis.--The material at hand shows a variable splenio-dentary depression, well developed lateral cusps on the teeth, quite a range in size between species, and a well developed posterolateral depression. The following characters should be relegated to infra-generic significance; (1) degree to which lateral cusps are developed, and (2) presence of a distinct splenio-dentary depression. Reasons for such changes include the presence of faint lateral crests in Hecht's specimen although not illustrated (Estes, unpublished manuscript), presence of well developed lateral cusps in the San Diego fossil forms, and the apparent variability of the "spleniodentary depression" which appears more as a flattened somewhat indented area with groove between the two splenio-dentary foramina rather than a general depression throughout the genus. The illustration of P. borealis (Holman, 1972) has no apparent depression
in this area. A slight depression in this area is clearly seen in *Klauberina*, *Xantusia*, and *Lepidophyema*. Dentaries of *Cricosaura* were not available.

*Palaeoxantusia allisoni* sp. nov.

**Etymology.**—This species is named in honor of the late Dr. Edwin C. Allison whose enthusiasm instilled in me an interest in paleontology.

**Type.**—UCMP no. 110313, a broken left splenio-dentary.

**Type locality.**—UCMP V-72157.

**Referred specimens.**—Splenio-dentaries: UCMP nos. 104388, 104534, 104559, 104686, 104717, 104756, 104758, 104772, 104778, 104824, 104854, 105975, 106717, 106752, 106770, 106772, 106773, 110311, 110312, 110317, and unnumbered specimens; maxillary fragments: 104499, 104741, 104827, plus unnumbered specimens.


**Diagnosis.**—*Palaeoxantusia* differing from all known species including *P. kyrentos* (described
by a combination of the following characters: (1) small size, (2) tricuspid teeth, with lateral cusps arranged in a straight line, (3) lack of significant increase in width of posterior teeth, (4) shallow to nonexistent groove between teeth and lingual shelf, (5) greater number of teeth.

*Description of the type.*--The type is a broken and somewhat worn splenio-dentary 2.98 mm. in length as preserved, bearing eight teeth or remnants, of which four are preserved (Figure 6). As in all known xantusiids the Meckelian groove is closed and fused. The broken base of a strong coronoid process forms the posterodorsal edge of the specimen. The lingual surface of the coronoid process bears a moderately developed coronoid incision which reaches the posterior border of the tooth row directly behind the posterior limit of the slightly curved subdental lingual shelf. Between the tooth row and the well developed lingual shelf the bone curves gently medially so that no groove is formed. The anterior inferior alveolar foramen lies beneath the bases of
the second and third teeth from the rear of the tooth row on a flattened portion of the splenio-dentary. The anterior mylohyoid foramen is positioned posterior and just ventral to the anterior inferior alveolar foramen beneath the base of the last tooth. A strong notch in the posterolingual surface of the splenio-dentary for the coronoid reaches forward to within about one and one-half tooth widths of the posterior edge of the tooth row. The bases of the last and anteromost teeth preserved are concave and were presumably being excavated by the now missing replacement teeth indicating typical nonanguinomorphan type of tooth replacement. All teeth and tooth remnants are not in contact, of about the same width, and project about one-fifth of their height above the parapet of the jaw. The crowns are abraded, yet show a squared-off condition with lateral cusps more or less evident. No striations or wrinkles are visible on the sides of teeth of the type, perhaps due to the worn condition of the teeth. Posterolabially a well-developed groove for the adductor musculature reaches forward to about the anteromost level of the notch for
the coronoid on the lingual surface—it does not reach forward, however, to the level of the last tooth in the type. The postcoronoid process is broken off at the level of the coronoid process so there is no way to tell how far the groove for the adductor musculature extended posteriorly on the spleniodentary. A single nutrient foramen is preserved beneath the seventh tooth from the rear.

Referred specimens.—A number of additional splenio-dentaries are available, about half of them from the type locality. All save four are much more fragmentary than the type but by critical comparison of these specimens a range of the variability within this species is discernable. There are at least hints of accessory cusps on all of the specimens whose teeth are not badly eroded. Specimen UCMP 104758 shows clearly what the crowns of uneroded teeth look like. They are broadly triangular with a shallow groove separating the wide central cusp from the narrow lateral cusps. All cusps are arranged in a linear fashion. The sides of the teeth are subparallel,
flaring somewhat near the bases, and possess very fine vertical striations. In the two specimens complete enough to estimate the length occupied by the last ten teeth that distance is 2.10 mm. (UCMP 110312) and 1.65 mm. (UCMP 104534). The distance from the top of the last tooth to bottom of the mandible, for the six specimens from which this measurement could be taken, ranges from 0.57 to 1.58 mm. (mean, 1.30).

The type gives no indication of the total number of teeth in the splenio-dentary. Specimen UCMP 110312, broken anteriorly, has remnants of ten teeth. UCMP 106700, broken posteriorly, clearly has 14 teeth and remnants of teeth. There was probably one more tooth posteriorly, thus the total number of teeth probably was 15. Another approach to this problem is considering the location of the anterior inferior alveolar foramen. In UCMP 106717 it is questionably beneath the last tooth, in UCMP 110314, 110318, and 106752 it lies between the base of the last tooth and next to last tooth. UCMP 110312 has the foramen beneath the next to last tooth, while in UCMP 110311 it lies beneath the bases of the second and third
teeth from the rear; for UCMP 104758 and 109830 it lies beneath the third tooth from the rear of the dental battery. Since in UCMP 106770, with 14 remnants and teeth, the foramen lies beneath the last two remnants, and since the most common position for a foramen lying beneath the bases of two teeth is between the last and next to last teeth, it is reasonable that only 14 teeth were present on the jaw. On the other hand as many as 15 could have existed since in one case a foramen is known from beneath the second and third teeth from the rear.

The dorsal-ventral dimension of the coronoid incision on the lingual surface of the base of the coronoid process is variable. In some (UCMP 110312, 106752) it is nearly as large as the height of the last tooth while in most specimens it is more narrow as in the type. The borders of the coronoid incision vary from well-defined to weakly-defined.

The region referable as a dental gutter (the region beneath the tooth bases and just labial to the subdental shelf) varies from flat-bottomed and smoothly curving in the type to a shallow groove in many
specimens (e.g., UCMP 106770). For most specimens in which the area was preserved the strong notch for the coronoid insertion on the lingual surface of the splenio-dentary extends forward to within the width of two teeth from the rear of the tooth row. The single exception to this is UCMP 104534 (and possibly 104290) in which the notch is slightly more than the width of two teeth behind the tooth row. The extent to which the groove for the adductor musculature reaches forward is somewhat variable. It extends anterior to within the width of two teeth of the last tooth on the labial surface of UCMP 110314; within one tooth width of the last tooth on UCMP 106752; and reaches the level of the last tooth on UCMP 109830, 110311, 104758, 104854, and 110317. The anterior extent of the groove is not visible on UCMP 110312 and therefore does not reach the level of the last tooth. In none of the referred specimens is the postcoronoid process preserved so it is not possible to determine how far the groove for the adductor musculature ran posterior on the process.

There are five broken maxillaries tentatively assigned to this species. All maxillary fragments are
representative of animals about the same size as those represented by the splenio-dentaries. The teeth are pleurodont, widest at about the parapet of the maxillary bone, and with hollowed bases. The only observable difference is that the maxillary teeth have a tendency toward more squared off crowns with relatively more fusion of the narrow lateral cusps to the wide central cusp than in the splenio-dentary teeth. In all other respects maxillary and splenio-dentary teeth are alike. Similarly there is no significant enlargement of posterior maxillary teeth. The last nutrient foramen on the maxilla, as shown by UCMP 104499 and 104827, lies above and between the last and next to last teeth. A strong supradental shelf is present on UCMP 104741 and 104827, the only specimens in which this region is not broken. Along the posteromedial surface of the posterior maxillary process lies a shallow antero-posterior directed depression for insertion of the jugal.

Discussion.—Holman (1972) showed that the Canadian Oligocene species *Palaeoxantusia borealis* may
be closer to *Xantusia* than *P. fera* because of the following characters: (1) *P. borealis* smaller than *P. fera*, (2) large nutritive foramina, four to five in number, irregularly spaced as in *Xantusia* (foramina are small, five in number and regularly spaced in *P. fera*). *P. allisoni* is smaller than *P. borealis*, in fact overlapping *Xantusia* for some measurements. *P. allinosi* (UCMP 106770) has four large more or less regularly spaced nutrient foramina located more anteriorly than in *Xantusia*. *P. allisoni* may therefore on the same criteria as Holman used be considered at least as close to *Xantusia* as is *P. borealis* and probably closer because of its size, tooth count, and geographic occurrence.

Holman (1972) felt that a character that indicated *P. borealis* was closer to *X. vigilis* and *X. arizonae* than *X. henshawi* is the number of teeth on the splenio-dentary. In *P. borealis* the count is 12 to 13 (mean 12.5 for two specimens). For *X. vigilis* Hecht (1956) reported 12 to 14 (mean 12.6) and Holman (1972) reported 13 for 11 specimens. *X. arizonae* had a count of 12 to 14 (mean 13.1)
according to Hecht. *X. henshawi* possesses 14 to 16 (mean 15 for four specimens) (Holman, 1972) and 13 to 16 (mean 14.8) for specimens examined by Hecht (1956). *P. allisoni*, as calculated above, possessed 14 or 15 teeth and is therefore closest to *X. henshawi* by this line of reasoning.

Bezy (1967) reduced *X. arizonae* to subspecific rank within *X. vigilis*. I therefore conclude that the lower Tertiary *Palaeoxantusia* radiation showed as much variety of forms as Recent *Xantusia*.

It is interesting to note that *X. vigilis*, with a reduced tooth count averaging about 13, is considered more primitive according to numbers of derived states from the karyotype study than *X. henshawi*, averaging 15 teeth per splenio-dentary. It is considered more common to evolve from a taxon with more of a given feature (e.g., teeth, toes, legs) to a state with less (e.g., fewer teeth or toothless, fewer toes, reduction of number of limbs). In this case if the chromosome based phylogeny is accepted as correct perhaps the more primitive form merely acquired a particular derived state (fewer teeth)
while the more generally advanced form has simply retained a more primitive condition as regards number of teeth.

Although Holman (1972, p. 1628) indicated that P. borealis evolved from P. fera and in turn possibly gave rise to the recent genus Xantusia this would now seem difficult or impossible unless Xantusia is considered polyphyletic. Even though P. borealis is a near perfect ancestor to Xantusia it lacks sufficient number of teeth to have eventually given rise to X. henshawi. P. allisoni exhibits morphologic features which make it equally as appealing an ancestor of Xantusia as is P. borealis. However, P. allisoni retained a higher tooth count and may therefore be judged more likely closer to being the ancestor. I do not feel that the lateral cusps of P. allisoni interfere with this interpretation since Savage (1955) considered tricuspid teeth primitive for Xantusiids.

The close relation between P. allisoni and the genus Xantusia shows well when considering the smallest specimens of P. allisoni, especially UCMP
104534. This specimen is at least as small as any living adult Xantusia and just as delicate in structure. Known splenio-dentaries of Palaeoxantusia are generally considered robust, not delicate and slender. Ignoring the differences in tooth crowns UCMP 104534 also shows close relation to Xantusia in the retracted anterior extent of the notch for the coronoid on the lingual surface of the splenio-dentary, shallow depression for adductor musculature (very shallow in Xantusia), lack of depression about the splenio-dentary foramina, more posterior position of the last nutrient foramen, and somewhat irregularly spaced nutrient foramina. Although all these characters lie within the range of variation of P. allisoni it is the combination of these states in a smaller variant of P. allisoni that may indicate its affinity to Xantusia.

The presence of a form very close to the direct ancestry of Xantusia (P. allisoni) within the San Diego fauna may be significant paleogeographically. P. allisoni was found within the present geographic distribution of Xantusia and so it may not be that its direct ancestors have ever lived far removed from
the present day center of *Xantusia* distribution (southwestern United States and northwestern Mexico)—a case implied when the more northern fossil species is considered ancestral.

**Palaeoxantusia kyrentos** sp. nov.

**Etymology.**—Greek: kyriakon, Lord's house; entos, within, since the type specimen was found on the property of Shepherd of the Hills Evangelical Lutheran Church.

**Type.**—UCMP no. 106000, nearly complete skull and rami.

**Type locality.**—UCMP V-6871.

**Referred specimens.**—UCMP nos. 104221, 104339, 104688, 104729, 106257, 106751, 109834, 113236, 113237, 113238, 113239.


**Diagnosis.**—*Palaeoxantusia* distinguished by (1) large size, (2) tricuspid teeth which become larger and more blade-like toward the rear of the battery, (3) posterior teeth strongly wrinkled lingually.
Description of the type--

MANDIBLE

**General description.**--The left mandible (Figure 7) has been removed from the skull in order to facilitate description. The compact, rather heavy mandible is composed of four distinct bones, the splenio-dentary, angular, coronoid, and fused surangular-articular-prearticular. The tooth row makes up about 40 percent of the total mandibular length. The Meckelian groove is closed and fused as in other xantusiids. The teeth are pleurodont, projecting about 20 to 25 percent of their height above the parapet of the dentary.

**Splenio-dentary.**--The splenio-dentary is robust compound bone bearing teeth on its dorsolinguinal margin. It is 10.98 mm. in length, measured from the symphysis through the tip of the postcoronoid process. There were thirteen teeth of which three are missing. The teeth are closely spaced, stout and have strong bases which are excavated indicating characteristic nonanguimorph type of tooth replacement. The apices
Figure 7. Mandible and teeth of Palaeoxantusia kyrentos, UCMP 106000: a, labial view; b, lingual view; c, enlargement of the tooth row, labial view.
of the teeth are tricuspid, the cusps being arranged in a linear fashion, with moderately defined anterior and posterior cusps which become less well defined as one progresses toward the anteriormost teeth. The clearly tricuspid nature of the teeth is in contrast to previously described species of Palaeoxantusia. The anteroposterior diameter of the teeth increases markedly toward the rear teeth so that the posteriormost tooth is approximately 3-1/2 times as wide as the anteriormost preserved tooth. Labially the crowns are essentially smooth except that the last several teeth show fine striae. Lingually the tooth crowns bear coarse vertical folds. Distinct vertical ridges separate the broad main cusp from the side cusps. The crowns do not flare.

Beneath the tooth bases is a distinct and well formed shelf which rises to a low ridge that becomes higher at the level of the second tooth from the front to act as symphyseal reinforcement. This shelf is essentially flat bottomed in contrast to the "distinct groove" present in P. fera and P. borealis. There is no indication of a distinct splenial.
The coronoid process is broken and some bone is missing from its lingual surface, however, it was strong and well developed. Despite the breakage the lingual surface of the coronoid process retains the mark of a deep incision which reaches forward to the level of the last tooth. This groove was for the retention of the coronoid which overlaps the dentary in this region. This portion of the coronoid has been broken in the type specimen and the broken piece or coronoid has moved ventrally on the lingual surface of the jaw obscuring the region where the two spleniodentiney foramina are found in other Palaeoxantusia. There appears to be a foramen on the labial side of the dentary very near the mandibular symphysis beneath the second tooth from the front.

There are three mental foramina on the labial surface of the dentary. They are located beneath teeth numbers five, seven, and ten counting from the front. Posterolabially, beneath the coronoid process, is a shallow but wide depression for the insertion of the adductor musculature. This depression continues onto the postcoronoid process and then passes onto the
surangular where the ventral edge of the depression is marked by a sharp ridge. The postcoronoid process is well developed, extending farther posterior than either the posteriormost labial or lingual edge of the coronoid.

**Coronoid.**—A roughly U-shaped bone straddling the mid-dorsal surface of the mandible by means of labial and lingual anterior processes and a lingual posterior process. The anterior labial process possesses a large depression into which the coronoid process of the dentary once fit. Although the process is now broken off and missing, the size of this depression in the coronoid attests to the well developed nature of the coronoid process of the dentary. The bottom edge of the anterolabial process of the coronoid was evidently never covered by the dentary and projected as a narrow splint between the coronoid process and the anterodorsal edge of the surangular just above the anterior surangular foramen.

The anterolingual process of the coronoid fitted into the groove on the lingual surface of the coronoid process of the dentary overlapping it there.
This process of the coronoid extended further in the ventral direction so that it covered the lingual juncture between the surangular and dentary. This portion of the coronoid, broken in the type, now covers the depressed area where the two spleniodentary foramina presumably lie but most likely did not reach this depression in the unbroken state.

The posterolingual process overlies the anterior sutural contact between the prearticular and surangular. This process does not quite form the anterior border of the adductor fossa as the surangular and prearticular contact each other at a point just posterior to the posterolingual process of the coronoid.

The anterior and posterior processes of the coronoid meet each other dorsally to form a strong, slightly rounded dorsal process which possesses a broad, depressed shelf on its posterior edge presumably for insertion of the adductor mandibularis muscles.

Angular.---A small, narrow bone wedged between the posterodorsal surface of the postcoronoid process
of the dentary on the ventral lingual surface of the mandible and the anterior ventral process of the prearticular. The posterior process of the angular, which wrapped around the ventral surface of the mandible, is missing. The posterior mylohyoid foramen is not present on that portion of the angular which was preserved.

**Surangular.**—A prominent smooth bone which fits into the large notch in the dentary between the coronoid and postcoronoid processes. It forms the lateral wall of the very deep adductor fossa. Laterally the dorsal anteriormost edge of the surangular fits into a groove between the anterolabial process and dorsal process of the coronoid. Ventral to the coronoid process of the dentary, at the level of its posteriormost extent in the surangular lies the anterior surangular foramen. The posterior surangular foramen is located just anterior to the well developed precondylar process. A ridge runs anterior from the precondylar process to the coronoid forming the dorsal edge of the surangular. The depression for the adductor musculature on the lateral edge of the
dentary beneath the coronoid process extends posteriorly onto the surangular as a large smooth flattened area with a distinct ridge marking its ventral margin. This ridge grows larger posteriorly until a large wing-like lateral flange is encountered just anterior and ventral to the precondylar process. The surangular is fused ventrally and posteriorly to the articular-prearticular.

Articular-prearticular.--Fused bones which are themselves fused to the surangular dorsally and anteriorly. The posterodorsal portion of this compound bone forms the floor of the glenoid fossa which is elongated anteroposteriorly and climbs up the rear edge of the precondylar process. Ventrally the angular process is large and flattened forming a ventromedially expanded wing connecting the prearticular and retroarticular process. This "wing" is separated from the glenoid fossa by a ridge at the medial border of the fossa and extends to the tip of the rather blunt retroarticular process.
SKULL

General description.--The skull is roughly triangular in dorsal view showing proportions rather typical for the family. In size it is comparable to but not as deep as Klauberina riversiana. It would appear that the depth of the skull was more like that of Xantusia; however, crushing and some distortion may be responsible for the apparent dorsoventral depression. The junctions between many bones of the dorsal surface of the skull have been made difficult to observe because of the poor preservation in this region. A detailed examination of the dorsal surface indicates that although the surface is nearly smooth, apparently a thin encrustation of osteoderms covers the entire dorsal surface of the skull. Osteodermal sculpture consists of sparse pits and a few very low, randomly oriented wrinkles.

Vomers, nasals, septomaxilla and premaxilla were not preserved. The orbits are relatively small; postorbital region broad and flat with the widest
portion of the skull approximately one-half way between the posterior edge of the orbit and the posterior edge of the skull.

The left maxilla along with the attached anterior portion of the left jugal was removed during preparation of the specimen. Description of the maxilla is therefore primarily based on the left maxilla.

**Maxilla.**—A large bone whose external surface occupies much of the side of the snout. It articulates with the frontal, prefrontal, jugal, ectopterygoid and presumably the missing premaxilla and septomaxilla. The external surface rises sharply until near the apex of the nasal process where it bends strongly in a medial direction. There are seven supralabial foramina located above the fifth, sixth, and seventh teeth, with two above the eighth and tenth teeth counting from the front. The flattened dorsal surface of the premaxillary process, which forms the floor of the external naris, is weakly bifid; the lateral portion articulating with the premaxilla and a medial vomerine portion which bears
a weak notch at its anteromedial extremity for contact with the septomaxilla. At the base of the vomerine portion of the premaxillary process near the junction with the base of the nasal process lies an anterior inferior alveolar foramen. The nasal process rises rather steeply from here to its apex forming the lateral wall of the nasal capsule. At the apex there is a small shelf which protrudes to underlap the edge of the unpreserved nasal. The nasal process probably narrowly contacted the frontal posterior to the nasal. The posterodorsal border of the nasal process, although now somewhat broken, was rounded and descended in a dorsally concave manner to the posterior maxillary process which extends laterally over the jugal to the region of the ectopterygoid. The upper edge of the dorsal concavity is overlapped by the prefrontal.

Internally the palatal shelf runs along the entire length of the bone except for the post dental portion of the posterior maxillary process. The palatal shelf is widest just posterior to its midpoint where the prefrontal rises from its dorsal border and
the palatine makes its anteriormost contact with the maxilla. The width of the shelf decreases gently toward its anterior extension but rather rapidly posteriorly to a point behind the last tooth where it terminates. The sulcus dentalis is well developed.

There are ten pleurodont teeth on the maxilla of which nine are preserved. They are in all respects comparable to the dentary teeth except that they are a bit more robust and not quite as tall.

Jugal.--A roughly triangular bone which forms a major portion of the posteroverntal and posterior border of the orbit. The anterior maxillary process fits into a wedge-shaped groove on the medial surface of the maxilla just behind the posteriormost extent of the palatal shelf so that it does not extend forward as far as the posteriormost tooth nor reach the lacrimal. The jugal also contacts the ectopterygoid along its anterolateral margin. At its posterodorsal edge the temporal process broadly contacts the fused postorbital-postfrontal. Across
its entire flat surface the jugal parallels the external surface of the skull so that neither process is inflected. It becomes progressively thinner posterad where it extends far beyond the posterior margin of the maxilla.

**Vomers.**--Not preserved.

**Palatine.**--A sharp ventromedially projecting vomerine process and a broad, blunt laterally projecting maxillary process extend from the anterior portion of this bone. Between the vomerine and maxillary processes in ventral view exists a smooth concave surface that narrows posteriorly. Along the anteromedial two-thirds of the palatine runs a ventral ridge which gradually descends to the apex of the vomerine process. The bevelled lateral edge is wide and rises steeply from the concave surface posteriorly. At a point slightly ahead of the pterygoid process is an anteriorly projecting reentrant into the bevelled lateral edge of the palatine.

The narrow inferior orbital fossa is bordered anteromedially by the palatine, laterally by the ectopterygoid, posteriorly by the pterygoid while,
presumably, only the anteriormost portion is narrowly bordered by the maxilla. The interpalatine area is narrow anteriorly becoming wider posteriorly, however, the interpterygoid vacuity remains nearly the same width posterior to the palatines.

In dorsal aspect the palatine is broad and smooth. A shallow groove runs forward along the anteromedial edge of the bone bifurcating anteriorly so that one branch lies directly beneath the anteriormost extent of the maxillary process while the other branch becomes even more shallow and continues forward along the dorsomedial surface of the vomerine process.

A small palatine foramen pierces the palatine near the lateral border of the maxillary process.

_Pterygoid._--The ectopterygoid process reaches forward nearly to the level of the palatine process; it also extends widely in a lateral direction and remains relatively heavy throughout. The palatine process is separated from the ectopterygoid process by a small anteriorly directed concavity so that it does not project markedly forward beyond the palatine
process-ectopterygoid process juncture. The palatine process is shorter than the ectopterygoid process. The pterygoid abuts the palatine so that there is little overlap of bone. The ectopterygoid process, however, fits into the ectopterygoid bone by means of a large tongue-in-groove suture along the posterior one-third of the ectopterygoid.

As with the palatine, there are no teeth on the pterygoid. The long posterior quadrate process curves gently posterolaterally past the basisphenoid and epipterygoid to contact the quadrate. A slight ridge marks the posterior edge of the quadrate process. The interpterygoid space is relatively narrow-being approximately as wide as the widest portion of the interpalatine space.

Ectopterygoid.--The ectopterygoid is a dorsally concave element forming the lateral margin of the inferior orbital fossa. Its short, wide body gives rise posteriorly to a broadly rounded ventrally projecting medial process which possesses a posteromedially directed spike along its internal edge. This posteromedial spike of the medial process forms the
dorsomedial extent of the groove which the ectopterygoid process of the pterygoid fits into. The broad horizontal medial process exhibits a weak posterior concavity which accommodates the coronoid process of the mandible when it is adducted. The lateral process probably did not contact the palatine along its medial edge but probably did contact the posterior process of the maxilla as well as the jugal. Minor deformation and slippage of bones in this region of the type are the reason for the uncertainty. Dorsally, the ectopterygoid forms the ventral floor of the orbit.

**Frontal.**--The frontals are paired bones with smooth dorsal surfaces indicating an apparent lack of osteoderms. The frontals are comparatively wide anteriorly where the tip of the anterior frontal process has been broken. The process is broken in such a manner that it appears not to have projected strongly anteriorly. The anterior lateral process is not developed as the prefrontal contacts the postero-laterally directed anterior margin of the frontal, here replacing the process and forming the anterior and
anterodorsal border of the orbit. The frontal is concave above the orbit, being widest at the posterior edge of the orbit where it makes an irregular, gently curving contact with the fused postorbital-postfrontal. Contact with the parietal is limited to the sinuous posterior transverse suture. A low supraorbital ridge, the crista cranii, extends posteriorly along the mid-ventral side of each frontal. The bone is not grooved medial to the crista cranii but remains flat where it contacts the corresponding surface of the other frontal.

Prefrontal.--The prefrontal forms the anterior and anterodorsal border of the orbit. The frontal process is sutured with the anterior inferior edge of the frontal within the orbit. Dorsally it contacts the area normally occupied by the expanded anterior lateral process of the frontal.

A stout maxillary process abuts the supradental shelf at the level of the second tooth from the rear. At this point the lacrimal foramen is formed mainly by a notch in the maxillary process of the prefrontal. The lacrimal forms the lateral border
of the lacrimal foramen. Slightly ahead of the lacrimal foramen the prefrontal is broken and missing. The nearly flat, vertical surface of the maxillary process of the prefrontal forms the posterior wall of the nasal cavity.

**Lacrimal.**—The lacrimal is a tiny splint-like bone plastered to the medial surface of the posterior process of the maxilla contacting only the maxilla and prefrontal and forming the lateral border of the lacrimal foramen.

**Parietal.**—The parietals are paired bones with nearly straight anterior, medial and lateral borders. The posterior margin is approximately twice as wide as the anterior margin and ventrally depressed so that it, along with the squamosal and (?) supratemporal, forms posterolateral and posterior temporal cover. The unsculptured dorsal surface has no trace of a parietal foramen. Posteriorly the parietal reaches the level of the occipital condyle. The supratemporal fenestra is completely closed by contact of the parietal with the postfrontal-postorbital and squamosal. Supratemporal processes of the parietal
are virtually nonexistent, protruding no farther in a posterior direction than the posteromedial extremity of each bone.

Postfrontal.—Romer (1956) noted that among xantusiids the postfrontal and postorbital are both present but generally fused. The condition in P. kyrentos is no exception to this rule as these two bones are indistinguishably joined together. The postfrontal portion of the postfrontal-postorbital forms a small part of the posterior border of the orbit. Medially there is a shallow concave contact with the posterolateral extent of the frontal where it meets the parietal.

Postorbital.—I shall refer to that portion of the compound postfrontal-postorbital lying behind the anterior extent of the parietal as the postfrontal. It is well developed, forming most of this compound bone including the greatest part of the lateral border of the temporal region. Contact is made with the squamosal, parietal, postfrontal and jugal. The exact site of contact with the squamosal is equivocal. The left postorbital-squamosal region is highly fractured
and has large areas where bone is missing so that there are no clues as to the nature of the postorbital-squamosal contact here. However, the right side of the skull has questionably, in dorsal view the posterior concave border of the postorbital meets the squamosal at a point about one-third of the way from the rear edge of the orbit and the posterior edge of the skull, approximately one-half way between the medial and lateral margins of the bone. The contact curves gently posteriorly so that the anterior of the squamosal is broadly convex.

Squamosal.--The squamosal is expanded anteriorly, tapering posteriorly where it meets a small chip of bone which may tentatively be identified as the supratemporal. The squamosal articulates with the postorbital, parietal (broadly), (?) supratemporal and quadrate. The contact between squamosal and parietal is responsible for closure of the posterior portion of the supratemporal fenestra.

Supratemporal.--If the small flake of bone articulating with what appears to be a notch in the posterior edge of the right squamosal is correctly
referred to as a supratemporal, it is abnormally wide and unusual in its great external exposure. That this could, however, be the case is supported by the armored appearance of the lateral edge of the temporal region where the widely exposed postorbital and squamosal curve ventrally in a fashion exceeding even that of *Klauberina*. A wide, exposed supratemporal would appear to fit this sort of a pattern. The supratemporal fits between the small supratemporal process of the parietal and the posterior extremity of the squamosal.

**Quadrate.**—The right quadrate is folded up beneath the right squamosal. As preserved, only its posterior concave and ventral surfaces are clearly visible. The quadrate is slightly shorter than the anteroposterior dimension of the squamosal. The single, large concave posterior surface is nearly the same width along the length of the bone. The medial wall thickens ventrally to produce a terminal medial condyle. A lateral condyle is present on the thickened ventral wall of the quadrate and is
separated from the medial condyle by a shallow constriction.

**Epipterygoid.**—Most of the left epipterygoid is exposed. The shaft is rod-like and only very slightly laterally flexed. The ventral end is expanded into an oval shaped articulating surface which fits into a shallow fossa columella on the dorsal side of the pterygoid at about the level of the basipterygoid process of the basisphenoid region of the braincase.

**Braincase.**—So far as can be seen all bones of the braincase are indistinguishably fused. The left paroccipital process is missing, as is the lateral portion of the right. The basisphenoid region is elongate with an anteroventrally projecting, unflared basipterygoid process. The parasphenoid process is broken. The posterior opening of the vidian canal is immediately lateral to the basipterygoid process at the point where the crista prootica reaches the basipterygoid. The basioccipital region has low, rounded ventrally projecting spheno-occipital tubera which lie anteroventral to the well-developed,
elongate occipital recess. Dorsally connected within the recess is the horizontally elongated foramen rotundum. The anterior prootic region has the remains of long cristae prootica which connect directly to the base of the basipterygoid process forming a thin, ventrally projecting sheath which lies lateral and ventral to the recessus vena jugularis. The trigeminal notch region is not exposed. Only the ventral portion of the fenestra ovalis is preserved. The stapes are not preserved.

The crista tuberalis, forming the posterior wall of the occipital recess, rises from the postero­ventral extremity of the sphenoo­occipital tubercle and extends to the basal exoccipital region where it dies out. From about the midpoint of the crista tuberalis a low ridge diverges and curves medially to contact the lateral edge of the occipital condyle. Slightly posterior to the divergence of this ridge from the crista lies an elongated foramen tentatively identified as the vagus foramen.
Discussion.--*P. kyrentos* is larger than *P. fera*, *P. borealis* or *P. allisoni* (see Table 1). The length of the holotype of *P. fera* as measured from the posterolateral tip of the postcoronoid process through the symphysis was 9.6 mm. It was not possible for Holman (1972) to make the same measurement for *P. borealis*. Neither is this dimension available for *P. allisoni*. However, as Table 1 shows, for *P. kyrentos* this distance is 10.98 mm. Similarly, the longest distance between the top of the last tooth and the bottom of the mandible is larger (2.66 mm. mean) for *P. kyrentos* than for *P. fera* (2.1 mm. mean), *P. borealis* (1.75 mm. mean) or *P. allisoni* (1.30 mm. mean). Many of the measurements for *P. kyrentos* are close to the same measurement for *Klauberina riversiana*.

Aside from its larger size *P. kyrentos* is distinguished from *P. fera*, *P. borealis*, and *P. allisoni* by (1) enlargement of posterior teeth, (2) flat bottomed groove between teeth and lingual shelf, and (3) strong vertical wrinkles on the lingual surface of the last two or three teeth. A character that separates *P. kyrentos* from *P. borealis* but not
Table 1
Size Differences between the Species of *Palaeoxantusia*
(* represents measurements from the holotype or measurements taken from published illustrations of the holotype. Numbers of specimens from which the mean was calculated are in parentheses)

<table>
<thead>
<tr>
<th>Species</th>
<th>Dentary length: symphysis to postcoronoid process</th>
<th>Posterior edge of last tooth to symphysis</th>
<th>Distance occupied by 10 posterior teeth</th>
<th>Bottom of mandible to top of last tooth</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. fera</em></td>
<td>9.6 *</td>
<td>5.6 *</td>
<td>4.5 *</td>
<td>2.1 *</td>
</tr>
<tr>
<td><em>P. borealis</em></td>
<td>4.1–4.9</td>
<td>4.6 (3)</td>
<td>4.2 *</td>
<td>1.6–1.9</td>
</tr>
<tr>
<td><em>P. kyrentos</em></td>
<td>10.98 *</td>
<td>6.53 *</td>
<td>5.42 *</td>
<td>2.23–3.10</td>
</tr>
<tr>
<td><em>P. allisoni</em></td>
<td>1.65–2.0</td>
<td>1.88 (2)</td>
<td>0.57–1.58</td>
<td>1.13 (6)</td>
</tr>
</tbody>
</table>
P. allisoni and P. fera is the presence of tricuspid teeth.

The splenio-dentary of P. kyrentos is distinguished from Xantusia by its larger size, robustness, lateral cusps, strong groove for adductor musculature on the posterolateral border of the splenio-dentary, and presence of an angular bone; from Klauberina by its enlargement of posterior teeth, squared off nature of the tricuspid crowns, strength of groove for adductor musculature, and presence of an angular bone (absent in adult Klauberina); from Lepidophyma by the same characters separating it from Klauberina plus the presence of fewer less specialized teeth; from Cricosaura by its larger size, posterior tooth enlargement, nature of the tooth crowns, and fewer teeth.

P. kyrentos appears to differ from P. fera and P. borealis in subjective characters as Klauberina differs from species of Xantusia. On the other hand both Hecht (1956) and Holman (1972) have noted that the robustness of bone and tricuspid nature of the teeth of Klauberina sharply set it off from
**Palaeoxantusia.** With the discovery of *P. kyrentos* this sharp distinction no longer exists.

As a variation in the size and degree of development existing in *P. kyrentos* is UCMP 109834. This specimen is the posterior portion of a broken right maxilla. Five teeth and the alveolus of another tooth are preserved. A portion of the nasal process is preserved as is that portion of a strong palatal shelf preserved above the tooth bases. The posterior edge of the nasal process curves postero-ventrally in a dorsally concave manner suggesting that the last preserved tooth may indeed represent the last tooth in the maxillary tooth row. The bases of the second and fourth to the last teeth are highly resorbed for replacement buds in typical non-anguinomorpham style. Teeth are very robust and large with shafts that are widest about half way from base to crown and taper slightly toward the crowns and bases. The teeth are also closely spaced, touching at their bases. An erosional groove runs across the penultimate lingual surface of the crown in the last three teeth. All teeth are comparatively poorly
preserved, yet in mesial view it is obvious that they are bluntly tricuspid. There are weak lateral crests or "cusplets" separated from the wide, mesially produced central cusp. Weak lingual vertical striae and stronger lateral vertical striae are present on all tooth crowns which are not badly eroded. In dorsal view the crowns present a crude "T-shaped" morphology. The vertical portion of the "T" is lingually directed and relatively wide. There appears to be a terminal valley separating the two sides of the horizontal portion of the "T" crest. The peculiar development of the crown in dorsal view (superficially resembling Contogenys) may be due to wear and (or) erosion of the "T"-shaped crown complex. Externally the tooth bases are separated from an osteoderm encrusted nasal process by a zone of nonornamented bone pierced by a row of mental foramina. The osteo-scutal crust does not extend posteriorly to the orbital border in this specimen but rather gives way to an unsculptured bone surface at and posterior to the level of the second to last tooth.
This specimen (UCMP 109834) differs from the type mainly in its larger size (5.13 mm. in length as preserved) and clearcut osteodermal encrustation of the nasal process. Other minor differences, however, do exist and include: more robust and generally "more developed" teeth of the sort seen in the type specimen, weak lingual and stronger lateral vertical crown striations, and the lack of a marked increase in posterior tooth size. There is a definite graduation in tooth size such that any given tooth is wider than the preceding teeth: given from the posterior to the anterior preserved tooth, widths at the level of the jaw parapet are (all given in millimeters) 0.85, 0.82, 0.74, 0.72, 0.58. Lingual vertical striations as such are not present in the type, however, strong wrinklings of the posterior teeth on the type are present. Lateral vertical crown striations in specimen UCMP 109834 compare to virtually smooth lateral crown surfaces in the type.

An attempt was made to determine if Palaeoxantusia allisoni could be differentiated from P. kyrentos by teeth alone. Since the inflated rear
teeth of *P. kyrentos* are not preserved in most specimens, it was decided to measure the height and width of teeth from the middle of the tooth row for both species. The results, Figure 8, are a significant total separation of the smaller teeth of *P. allisoni* from the somewhat larger teeth of *P. kyrentos*.

**Intrafamilial relationships.**—Savage (1963) divided the Xantusiidae into two subfamilies. Skeletal differences at this level are as follows:

Subfamily Cricosaurinae—nasal bones separated completely by nasal process of premaxilla, which reaches frontal, frontal single, parietal single; squamosal separated from parietal; no epipterygoid process of prootic; anterior palate of incompletely neochoanate type, with fenestra vomeronasalis externa completely surrounded by prevomer; sternum with a definite posterior projection; clavicles hook-shaped without closed foramina; phalangeal formula of hand 2-3-4-4-3.

Subfamily Xantusiinae—nasals contacting one another most of their length, premaxilla not reaching
Figure 8. Differences in tooth size between *Palaeoxantusia allisoni* and *Palaeoxantusia kyrentos*. Measurements are for teeth from the middle of the tooth row: small dots for *P. allisoni*, large dots for *P. kyrentos*. Circled dots represent posterior teeth of two specimens of *P. kyrentos*. 
frontal; two frontals, two parietals; squamosal contacting parietal; with an epipterygoid process from prootic; anterior palate of paleochoanate type; fenestra vomeronasalis externa bordered by premaxilla and maxilla; sternum without a posterior projection; clavicles perforate, with large, completely closed foramina; phalangeal formula of hand 2-3-4-5-3.

The Xantusiinae is broken into two informal groups, the first consisting of Klauberina and Xantusia while Lepidophyrmma characterizes the second. Osteological differences between these groups are as follows:

Klauberina-Xantusia--Orbit not completely roofed over above by frontal; prefrontal extending onto top of head to separate anterior portion of frontal from orbit; postfronto-orbital not expanded medially, gradually decreasing in width posteriorly.

Lepidophyrmma--Orbit completely roofed over by frontal, outer margins of frontal even, not concave; prefrontal restricted to side of head, not separating anterior portion of frontal from upper margin of
orbit; postfronto-orbital expanded medially, not gradually decreasing in width posteriorly.

Savage (1955) constructed a hypothetical composite xantusiid possessing the maximum number of parts within the family but excluding characters held in common to all forms. It is assumed that an individual with all such character states should closely approach the most primitive xantusiid condition. The characters include external features:

1. A pair of frontonasals
2. A median scale
3. A pair of frontals
4. A pair of parietals
5. Two rows of supraoculars
6. A pretemporal
7. Small temporals
8. Small pretymanics
9. Infrafalabials and postmentals distinct
10. First postmental divided
11. Thirty-nine to fifty-two pregulars
12. Small gulars
13. Dorsals homogeneous in size and shape
14. Transverse dorsals 117-153
15. Longitudinal dorsals 63-86
16. Longitudinal ventrals
17. Transverse ventrals 29-35
18. Lamellae under fourth toe 24-29
19. Radials and femorals small
20. Caudals in uniform sized whorls

Osteological features:
21. Cranium with osteoderms
22. Two frontals
23. Two parietals
24. An epipterygoid process on prootic
25. Anterior palate paleochoanate
26. Ectopterygoid and palatine widely separated
27. Basisphenoid and basioccipital distinct
28. Teeth tricuspid
29. Two pairs of xiphisternal ribs
30. Clavicles perforate
31. Phalangial formula of hand 2-3-4-5-3

The recognized recent genera may then be ranked from primitive to advanced by noting the number
of character states for each form that do not agree with the composite ancestor. The following is modified from Savage (1955):

**Klauberina** (eight characters), 1, 6, 7, 12, 18, 19, 26, 29

**Xantusia** (twelve characters), 1, 5, 11, 12, 14, 15, 16, 17, 19, 21, 28, 29

**Lepidophyema** (fifteen or sixteen characters), 1, 2 (sometimes), 5, 7, 9, 11, 13, 14, 15, 16, 17, 18, 20, 21, 26, 29

**Cricosaura** (twenty-three characters), 2, 3, 4, 7, 8, 10, 11, 12, 14, 15, 16, 17, 18, 19, 21, 22, 23, 24, 25, 27, 28, 30, 31

Features observable in the skull of *Palaeoxantusia kyrentos* which differ from the ancestral condition include 21, 26 (questionably), 27.

It then becomes evident that *Cricosaura* is by far the most advanced form since it differs from the hypothetical ancestor by over 80 percent of the listed characters. It would appear from this evidence that *Cricosaura* diverged from the conservative main stream
of xantusiid evolution in the distant past--before other known stocks or their ancestors did.

Klauberina on the contrary is the most primitive living form since it more closely resembles the hypothetical ancestor than all other xantusiids. Xantusia and Klauberina are closely related (or con­generic according to some, see Bezy, 1972, and below). Xantusia might easily be considered to have been derived from a Klauberina-like ancestor. However, a more primitive tooth count in X. henshawi might disallow direct ancestry of Klauberina.

Lepidophyma is moderately highly modified from the ancestral condition. Some members of Lepidophyma, however, retain rounded pupils and are therefore unique among xantusiids in this feature. Lepidophyma must have branched from the primitive xantusiid stock before Klauberina and Xantusia originated in order for Lepidophyma to have developed its high number of derived characters. It is of interest that using only the osteological characters listed above Lepidophyma does not appear to be any more advanced than Xantusia. This points to the
importance of giving weight to certain characters instead of merely relying on numbers of characters when ranking organisms.

Before continuing with the listing of salient characters of P. kyrentos a point of taxonomy within the living Xantusiidae must be mentioned. Recently Bezy (1972) returned Klauberina to Xantusia on the basis of karyotype analysis and thereby reduced the number of recognized living xantusiid genera to three. Although workers of late have become uncomfortably aware of the problem that most species at present are of necessity morphospecies (see Thomas, 1956) the problem remains especially difficult for the paleontologist who must routinely deal with the subtle differences in practice between morphospecies, chronospecies and biospecies. It seems advantageous then for me to here recognize the status of Xantusia (including Klauberina) as a "biotaxon" which may be treated somewhat different than Klauberina plus Xantusia as separate "morphotaxons." The osteology of Klauberina is distinctive. Its geographic extent is unique among xantusiids. I therefore feel that
Klauberina, if only known as a fossil, would be accorded generic significance and so prefer to recognize it as generically distinct in the context of this report.

Savage (1963) constructed a list of characters significant in determining xantusiid intrafamilial relationships. The following are characters present in Savage's list which are also observable in P. kyrentos:

1. Two frontals
2. Two parietals
3. Squamosal contacting parietal
4. Orbit not completely roofed over by frontal
5. Prefrontal extending onto top of head to separate anterior portion of frontal from orbit
6. Lateral margin of frontal concave
7. Postfrontal expanded medially and not decreasing markedly in width posteriorly

Also, the medial edge of the nasal is entire, without a dorsal re-entrant as found in Klauberina, Xantusia or Lepidophyuma. Fitting the preserved right nasal into position anterior to the right frontal
shows clearly that the left nasal did contact the right nasal immediately anterior to the frontal bones thereby indicating that the nasal spine of the premaxilla did not separate the nasals by extending posteriorly to contact the frontals. The prootic is not exposed deep enough to see whether an epipterygoid process was present. However, it appears that the epipterygoid of *P. kyrentos* may contact the prootic, a feature in common with *Klauberina*, *Xantusia*, and *Lepidophyma* but not *Cricosaura* (according to sketches in Savage, 1963). The anterior palate is not preserved.

Characters 1, 2, 3, plus the median contact of the nasals excluding the nasal process of the premaxilla from the frontals place *P. kyrentos* well within the Subfamily Xantusiinae as defined above. The relation of the structure of the anterior palate and prootic as regards subfamilial classification of the fossil will need to remain undefined at present. Characters 4, 5, and 6 place *P. kyrentos* very near the *Klauberina-Xantusia* group, however, character 7 is very *Lepidophyma*-like in *P. kyrentos*. 
Since all Palaeoxantusia show stronger relations to Klauberina-Xantusia than other xantusiids, and since Palaeoxantusia fera has been shown to range back to the Middle Paleocene (Estes, manuscript) then the line leading to Lepidophyyma must have originated by the earliest Tertiary and forms leading to Cricosaura may have been separate well back into the Cretaceous. This line of reasoning independently arrives at the same conclusions that Savage (1955) did using numbers of derived characters.

In summary, the ancestral xantusiid stock became isolated on Cuba, possibly well back in the Cretaceous, and eventually evolved into Cricosaura. The main portion of primitive xantusiid stock remained on the mainland, possibly in the vicinity of what is now southern Mexico and northern Central America. By Latest Cretaceous or Early Paleocene the primitive stock split—with one "branch" eventually giving rise to Lepidophyyma. The other branch of Palaeoxantusia and Palaeoxantusia-like forms migrated North and West. In the northernmost portion of their new range P. fera gave rise to P. borealis. An Oligocene or later
recession of the family's northern geographic extent left only the fossil forms to attest to the early expansion of the family. During the later Eocene in the area which later became southwestern California a Klauberina-like form (P. kyrentos) and a Xantusia-like form (P. allisoni) existed. P. allisoni probably was ancestral to Xantusia which lives in the same area today. Klauberina is perhaps a conservative relic of the family's earlier radiation but is considered by some (Bezy, 1972) as congeneric with Xantusia.

See Figure 8 for a diagrammatic interpretation of intrafamilial relationships.

**Interfamilial relationships**--Postulated relationships of the Xantusiidae to other saurians have been and remain quite tenuous, and are generally unsatisfactory. Cope's (1900) synopsis based on a modified version of his 1864 work marked a new era in squamate classification. His monumental 1900 volume placed the Xantusiidae in the Leptoglossa (teiids, lacertids, xantusiids, gerrhosours, skinks, "Acontiidae," dibamids, and anelytropsids) near the
Figure 9. Diagrammatic representation of xantusiid intrafamilial relationships. Branches are plotted against hypothetical times if divergence from the ancestral stock.
Lacertidae. Fürbringer, the same year (1900) proposed that the "Tejidae" and Xantusiidae be placed together under the Superfamily Tejidae. Camp's (1923) "Classification of the Lizards" marked the beginning of modern lizard systematics. He felt that the Xantusiidae bridged his two great lizard divisions, the Ascalabota and the Autarchoglossa, but placed them among the Scincomorpha of the Autarchoglossa as their most primitive member. Camp stated that the xantusiids were closest to the skinks, teiids and especially the lacertids (all of the Autarchoglossa) but recognized xantusiid similarities to the gekkonids of the Ascalabota. McDowell and Bogert (1954) correctly suspected that future workers would refer the xantusiids to the Gekkota. Romer (1956) conservatively ignored the Ascalabotan-Autarchoglossan dichotomy erected by Camp and preferred to follow Cope by again placing the xantusiids in the Infraorder Leptoglossa. While examining the systematic position of the Pygopodidae, Underwood (1957) considered the Xantusiidae as the only family constituting an unnamed infraorder within the Ascalabota. In the same paper
Underwood replaced Camp's rather unorthodox "Divisions" Ascalabota and Autarchoglossa with the taxonomic status of Suborder. Hoffstetter (1962) nearly agreed with Underwood (1957) but allied the xantusiids with the gekkos as a superfamily within the Infraorder Gekkota. Savage (1963), principally on the basis of his 1955 work, referred them to the Gekkota. St. Girons (1967) allied the family with the Gekkota, while Miller (1966) and Etheridge (1967) thought that closer relationships existed with the Scincomorpha. Although taking care not to place them systematically, Bezy (1972) theorized that xantusiids appeared karyotypically most similar to the Tejidae within the Scincomorpha. It is worthy to note in passing that Bezy (1972) is the only author so far to suggest that xantusiids may well represent relicts of a third major division of lizards.

There are a number of characters which have been noted in the past as indicating either ascalabotan or Autarchoglossan affinity which definitely need comment.
McDowell and Bogert (1954, p. 95-97) made a series of statements about the Xantusiidae, some of which could be misleading or are incorrect. They state (p. 95) that the parietals of all xantusiids remain separate. The parietals of *Cricosaura typica*, however, are clearly fused. It is correct to state that in all other xantusiids including *P. kyrentos* the parietals fail to fuse. They state (p. 95) that no pineal foramen is present in xantusiids. The pineal foramen is, however, always present in *Xantusia* and *Klauberina* although it is commonly covered by osteoderms in *Klauberina*. McDowell and Bogert also state that the lacrimal is fused with the prefrontal. Savage (1963) defined this condition for the family as lacrimal "partially or completely fused with prefrontal." The lacrimal of *P. kyrentos*, though reduced, is completely free. McDowell and Bogert further claim that the small ectopterygoid of xantusiids shows gekkotan affinities. Again, examination of all xantusiid genera shows that the ectopterygoid is of normal size when compared to a
number of families that shows no special tendency toward reduction.

Another character supposedly showing gekkotan affinity is the fusion of the angular, surangular, prearticular, and articular. I do not believe that anyone has ever demonstrated that the angular of xantusiids is fused with the other postdentary bones. It is generally considered absent in extant forms. However, the mandible of a newborn *Klauberina riversiana* collected on San Clemente Island showed the angular to be present and partly fused to the dentary (Estes, 1976). The angular is definitely present on the mandible of *P. fera* from the middle Paleocene Tongue River Formation of southeastern Montana (Estes, 1976). *Palaeoxantusia kyrentos* also has a definitely unfused angular. It would appear that the angular bone has been lost or fused in adult forms by the *Xantusia-Klauberina* ancestors after the early Tertiary and therefore must have been lost separately in the three major modern xantusiid "lines" of Figure 8. Removal of the angular from the list of fused postdentary bones leaves only the surangular, prearticular, and
articulare. Fusion of these three bones is not significant in pointing out xantusiid affinities since these bones are commonly fused among many lizards.

McDowell and Bogert further state (p. 96) that "Though not so well developed as in the gekkos and pygopods, the gutter of the dentary internal to the bases of the teeth is present in the Xantusiidae." This is an observation of questionable significance as a moderately well developed dental gutter is present throughout the anguimorphan family Xenosauridae and is widely present among scincomorphans.

Underwood (1957) retracted his 1955 suggestion that the procoelous condition of the vertebrae of gekkos is primitive. He added that he felt that pygopods independently acquired the procoelous condition. Therefore, claims that the primitively procoelous condition of xantusiid vertebrae indicate gekkotan affinities could be of less significance than often thought. Procoely may have originated several times among lizards for purely mechanical reasons. Primitively procoelous vertebrae (small condyle, squarish centra, presence of subcentral foramina, and
possibly enlarged neural canal) in xantusiids might only represent an "arrested stage" of development in one line that developed procoely.

In conclusion, the gekkotan affinity of the family Xantusiidae is questioned. Further study emphasizing character states now known to exist in fossil forms of the Xantusiidae may show the family to lie closer to the Scincomorpha. There is a particularly striking correspondence between the jaws of the early Tertiary scincomorphan *Contogenys* with those of *Palaeoxantusia*. Character states commonly cited to suggest the gekkotan affinity of the Xantusiidae have been shown above to have been erroneously interpreted in several instances.

**FAMILY SCINCIDAE**

**Introduction to the Family**

The most recent subfamilial classification of skinks was proposed by Greer (1970) who recognized four subfamilies. The Scincinae, considered to be the most primitive subfamily, is apparently independently ancestral to the other three subfamilies. Scincines
occur in Asia, Africa (center of abundance is subsaharan Africa and some islands in the western Indian Ocean) and north of Costa Rica in the New World. The Feylininae and Acontinae are specialized burrowers confined to subsaharan Africa. The Lygosominae is present in the Australian region across to southeastern Asia, west to Africa; in the New World they are known from southern and eastern United States south throughout most of South America.

The oldest possible scincids are the questionably referred species *Sauriscus cooki* (Estes, 1964) from the Late Cretaceous Lance Formation of Wyoming and *Contogenys sloani* (Estes, 1969a) from the Cretaceous through middle Paleocene of Montana and Wyoming.

**Paracontogenys** gen. nov.

**Etymology.**—The generic name refers to the resemblance to *Contogenys*.

**Type and only known species.**—*Paracontogenys estesi*, sp. nov.
Diagnosis.--A moderate sized scincoid lizard with blunt, homodont, highly pleurodont teeth that diminish in height above the jaw parapet only slightly toward the rear of the tooth row; tooth crowns spatulate with faint anterior and posterior crests which are the vertical extensions of a labial crown crest; dorsally anteroposteriorly elongate, obtuse V-shaped valley separates two labially convex crests; the lingual crest terminates where the labial crest turns ventral to form the anterior and posterior crests; the Meckelian groove is closed and fused.

Paracontogenys estesi sp. nov.

Etymology.--The specific name honors Dr. Richard D. Estes for his work with fossil lizards.

Type.--A fragmentary right dentary, UCMP no. 113228.

Type locality.--UCMP V-73138.

Referred specimens.--The rear portion of a left frontal, UCMP no. 113224; maxillary fragments, UCMP nos. 106521, 113245, and 113246; a tooth, UCMP no. 104226.

Diagnosis.--As for the genus.

Description.--The type consists of the greatest portion of a right dentary (Figure 10). There are indications of 15 teeth and tooth spaces. Although the dentary is broken anteriorly and posteriorly the last partially preserved alveolus probably marked the location of the last tooth in the jaw. The dorsal edge of the bone is nearly straight and slopes upward to the level of the third preserved tooth from the rear of the specimen. From the level of the third to last tooth posteriorly the dorsal dentary surface rises somewhat steeper. The level of the tooth crowns follows this flexure so that the crowns of the posterior three preserved teeth (and presumably those from this region that are not preserved) extend slightly above the anterior teeth. The posterior teeth are, however, not taller than other teeth. Rather they are slightly reduced in height, especially when viewed externally. Seven
Figure 10. Paracontogenys estesi, UCMP 113228: a, lingual view; b, enlargement of teeth, lingual view. Unidentified anguid, UCMP 113240: c, osteoscute, external view. Pancelosaurus sp., UCMP 113217: d, dorsal view of left frontal.
teeth are preserved with their crowns intact. All teeth are strongly pleurodont and the regularly spaced shafts have parallel edges. Crowns are somewhat flared anteroposteriorly in relation to the tooth shafts and are slightly compressed linguolabially. Weak vertical anterior and posterior crests result from a vertical continuation of the labial crown crest. In dorsal view the crowns present a highly characteristic dual crest and valley or "split-crown" effect. Two obtuse V-shaped crests run anteroposteriorly across the crown so that the apex of the "V" points lingually. Each arm of the "V" is slightly lingually concave. Between the two subparallel crests is a shallow but well developed valley that extends from the anterior to the posterior edge of the crown where the lateral crown crest bends ventrally to form the anterior and posterior crests. The crown valley and lingual crown crest terminate at the level of the ventral inflection of the labial crown crest. Fine vertical striations mark the lingual surface of the crowns while the labial surface is essentially smooth. In lateral view the
crowns are blunt and shouldered with the highest part of the crown centrally placed. The sulcus dentalis is developed into a well formed subdental gutter that has a dorsally projecting lingual margin. Beneath the sulcus dentalis, the Meckelian groove is closed and fused along the entire length of the specimen. Posterior breakage does not allow it to be established if there was a lingual coronoid facet beneath the posterior teeth. Although broken posteriorly, there is no indication that a lateral coronoid lappet existed. The steeper angle of the rear portion of the dentary suggests that a prominent and divergent coronoid process of the dentary was once present, but this cannot be confirmed with the material at hand. The external surface of the dentary was probably smooth (it has since been abraided and deeply scratched) except for three rather large mental foramina which are preserved in a row on the side of the bone. The preserved length of dentary UCMP 113228 is 6.29 mm.

There are five teeth preserved on the maxillary fragment (UCMP 106521). In addition, there
are remnants of four toothless alveoli. The specimen belonged to a somewhat smaller individual than that of the type. However, the teeth are identical in all other respects to those of the type. The bone is smooth externally and lacks indication of osteodermal encrustation. No mental foramina are preserved. The parapet of the jaw is slightly irregular but there is a perceptible slight decrease in height of what are interpreted as posterior teeth. All teeth project about one-fifth of their total height above the parapet of the jaw. The base of one tooth is resorbed for a replacement but indicating direct, vertical replacement. The palatal shelf is well developed and is about the same width along the entire length of the specimen. Internally, at the base of the nasal process, a well developed groove extends along the anterior two-thirds of the specimen parallel to the palatal shelf. The groove becomes shallow and is lost posteriorly.

The posterior portion of a left frontal (UCMP 113224) indicates that the frontals were suturally distinct. Dorsally the frontal is covered
with a moderately thick osteodermal encrustation which is fused to the underlying bone. The osteodermal crust covers the entire dorsal surface, even the orbital rim. The large frontoparietal epidermal scale impressions are separated from the metopic suture by a mesially placed interparietal scale impression. A nearly straight frontoparietal-frontal epidermal scale contact extends anterolateral from the front corner of the interparietal impression. The ornamented surface of the osteoscutal crust is sparsely covered with simple pits and slightly elongate randomly oriented pits separated by large flattened areas. The narrowest preserved width of the frontal, as measured from the orbital margin to midline at right angles to the metopic suture, is 4.61 mm.

Ventrally the most striking feature is the base of a strong, ventrally descending frontal process. The broken base of this process runs from the anterolateral corner of the specimen to a more mesially located point somewhat anterior to the preserved midlength of the specimen. A weak lateral
ridge separates from the base of the descending process one-fourth of the way from its posterior end and curves gently to the orbital margin. Posterior to the lateral ridge is a large depression which lies medial to most of the preserved orbital margin. Medial to the base of the descending process and along its entire length lies an elongate depression which is bounded at the metopic suture by the thickening of a low ridge. Posterior to the rear margin of the descending process the ventral frontal surface slopes dorsad so that the posterior preserved margin is relatively thin.

Discussion.--Although 15 teeth and tooth spaces are preserved in UCMP 113228, it is quite apparent that as many as five or six teeth are missing from the front of the tooth row. The total dentary tooth count was probably about 20 or 21. Thirteen dentary teeth were reported for the holotype of Contogenys sloani (Estes, 1969a). The presence of about 20 or 21 dentary teeth in Paracontogenys estesi
is significantly greater than the number in *Contogenys sloani*.

Although the posterior end of the dentary is not preserved there is some indication as discussed above that a strongly divergent coronoid process existed. The increased tooth number, lingual crown striations, and fused Meckelian groove contrast with the condition seen in *Contogenys sloani* but may simply represent advanced characters perhaps expected in a later member of that lineage. Greer (1970) has placed the Scincinae as the most primitive of scincid sub-families. Greer also stated (p. 179) that *Eumeces* may be the most primitive living genus of skink and may be similar to the ancestor of all skinks. It is therefore interesting to note that Meckel's groove is narrowly open to the symphysis in *E. fasciatus* and *E. skiltoneanus* but closed and fused anterior to the splenial in *E. laticeps*.

Although there may be as many as 46 species of *Eumeces* (Greer, 1970) those listed here are sufficient to demonstrate the variation of Meckel's groove within the genus *Eumeces*. Another example may
be cited: among lygosomine skinks *Leiolopisma laterale* shows intraspecific variability in the closure of Meckel's groove. Of the six skeletons of *L. laterale* examined in the collection of Dr. R. Etheridge, two had a closed and fused Meckelian groove while in four specimens the groove remained narrowly open to the symphysis. Although such variations are present within modern skinks, the presence of significantly more teeth (20 or 21) and minor dental differences taken in conjunction with the closed and fused Meckelian groove of this fossil form suggests generic separation from *Contogenys*.

One of the reasons that Estes (1969a, p. 5) questionably placed *Contogenys* within the Scincidae was the presence of "... the *Eumeces*-like wedge on the posterior border of the maxilla ..." The configuration is the same in *Paracontogenys*. It should be noted that although this wedge is bifurcated in all Recent skinks I have examined, its simple presence is equally as characteristic of xantusiids and may represent one of a number of features allying the Xantusiidae with the Scincomorpha. The presence
of descending processes of the frontal as well as a somewhat greater tooth count and lingually striated crowns in Paracontogenys may link Contogenys closer to primitive extant skinks such as Eumeces.

Ventral parietal flanges are characteristic of all living skinks. The ventral parietal flanges are unknown in Contogenys sloani and Paracontogenys estesi. Thus the absence of flanges in Contogenys and Paracontogenys obscures familial assignment.

Paracontogenys estesi may be distinguished from the only other presently known early Tertiary scincoid, Contogenys sloani, by the presence of a closed and fused Meckelian groove, greater number of dentary teeth, very slightly more flaring crowns, and definite vertical striae on the lingual surface of tooth crowns.

Paracontogenys is questionably referred to the Scincidae because of its resemblance to Contogenys.
FAMILY ANGUIDAE

Introduction to the Family

The present-day range of anguid lizards extends across South America, Central America (including the West Indies) and southern North America; Europe and northern Africa in the Old World as well as southern Asia, Formosa, Sumatra and the outer Hebrides. The family is thus essentially a northern one.

Meszoely (1970) has produced the most recent subfamilial classification of anguid lizards. His scheme recognizes four subfamilies, the Gerrhonotinae, Anguinae, Diploglossinae, and Glyptosaurinae. The categories are essentially the same as those recognized by McDowell and Bogert (1954), however, there are several important changes in the content of McDowell and Bogert's subfamilies: Meszoely placed Xestops in the Glyptosaurinae. He split off the Cretaceous form, Pancelosaurus piger, which was the ancestor of glyptosaurine anguids through a Xestops-like form, and placed it in the Anguinae. Ophisaurus
was removed from the Gerrhonotinae and placed in the Anguinae.

At the other extreme of anguid classification is the arrangement by Kuhn (1940) who recognized two families of lizards usually considered anguid: the Anguidae and the extinct Placosauridae. Several other classifications have been proposed (Cope, 1900; Camp, 1923; Hoffstetter, 1962) but need not be of concern here.

Subfamily Anguinae

Pancelosaurus sp.

Referred specimens.--Left frontals UCMP nos. 113217, 113218, 113220, 113221, 113222, 113223; left parietal UCMP no. 113219.


Description.--The nature of the frontals is best shown by UCMP 113217, the rear portion of a left frontal which is missing the posterolateral corner.

The following description is primarily based on this
specimen, features on other frontal specimens are only noted if they are missing on UCMF 113217 or more clearly shown elsewhere.

The dorsal surface is covered with a thick encrustation of osteoderms, which are fused to the underlying bone. The orbital border is only slightly curved. Along the orbital border, back to about the level of the frontoparietal scale impression, the osteodermal encrustation is recessed so that there is a thin strip where the frontal bone itself is visible. The thin strip of frontal which is visible widens slightly at about the level of the frontoparietal scale and gives the impression that more of the posterolateral corner was also devoid of osteodermal encrustation. A large anteriorly convex frontoparietal scale impression is separated from the metopic suture by a considerably smaller, mesially placed interparietal scale impression. None of the specimens are preserved anteriorly to show the region of nasal bone overlap. The mesial surfaces of all preserved frontals have strong crenulations that indicate that they were suturally distinct.
In lateral view the postfrontal incision extends anteriorly to just slightly behind the prefrontal-frontoparietal scute contact. The somewhat larger prefrontal incision extends back to the area near the narrowest width of the frontal. The narrowest width of a single frontal ranges from 0.80 mm. in UCMP 113223 to 2.17 mm. in UCMP 113217. A characteristic sculpture of irregular pits and ridges marks the entire dorsal osteoscutal surface. Ventrally, somewhat broken but well developed olfactory processes appear to have been widely separated.

The left rear portion of a single parietal (UCMP 113219) is the only specimen of this element preserved. It is broken anteriorly at the level of the parietal foramen and is also clearly broken along the midline. There is no doubt that before breakage the parietals were azygous. The anterior two-fifths of the specimen is covered with an osteoscutal crust possessing the same sculpture as the scutes on the frontals. The imprints of portions of the interparietal, paired parietal and occipital epidermal
scales are visible on the sculptured surface. Not much is left of the interparietal scale area. The parietal foramen is located near the apex of the triangular interparietal impression. Parietal-occipital scale impressions contact extends medially at right angles from the lateral edge of the parietal to contact the interparietal near its posterior corner. Parietal scale impressions are therefore completely separated by the interparietal impression along the entire length of all three scale impressions. The posterior border of the parietal table is strongly concave and there is evidence of a prominent medial notch. Laterally, the parietal border is smoothly concave indicating that the supratemporal fenestra was open. The base of the supratemporal process is wide; that portion of the supratemporal process preserved is flattened dorsally but very slightly concave ventrally. Although the distal portion of the supratemporal process is broken, the general configuration of the process suggests that it was slightly expanded laterally.
Ventrally, a strong anterior ridge curves toward the midline as it continues posteriorly. If both such ridges (left and right sides) were considered simultaneously they would be seen to converge postero-medially to form a triangle. The parietal fossa was a deep, anteriorly elongate pit extending forward from the apex of the triangle just mentioned. A low posterior ridge follows the lateral border of the suprtemporal process but grades into a wide flattened space before it contacts the anterior ridge.

The osteoscutes referred to this form are rectangular, longer than wide and covered with irregular, elongate pits and grooves similar to those on frontals and parietals. An unsculptured transverse gliding surface makes up roughly the anterior one-fourth to one-third of each scute. Thin to moderately prominent lateral bevels are located on the sides of each scute. One bevel is dorsally placed and the other ventrally placed on the overlapping lateral body osteoscutes; both bevels are dorsally located in middorsal, somewhat fan-shaped, posteriorly expanded scutes. About two-thirds of the osteoscutes possess
a slightly asymmetrical keel on the outer sculptured surface. The keel is symmetrically placed only on middorsal scutes. About one-third of the scutes referred to this form lack keels and appear somewhat flatter than the moderately dorsally convex keeled forms. There are two to three small foramina on the underside of all scutes. Frequently when only two foramina are present they are both beneath the level of contact between the external gliding surface and the sculptured surface.

Discussion.---This form is referred to the genus *Pancelosaurus* because of a combination of character states: pitted and grooved nature of cephalic and body osteoscutes, general arrangement of frontal and parietal dermal scute markings, a relatively large interparietal epidermal scale impression separating the large frontoparietal scale impressions, great similarity of the configuration of the ventral parietal surface to *Pancelosaurus piger*, and distinct frontal bones.
Comparison with Lance Formation *P. piger* shows the San Diego form to be considerably smaller. Frontals and parietals of the San Diego form are consistently slightly less than one-half the length and considerably smaller in mass than known *P. piger*. Although the general nature of dorsal sculpture of the osteoscutes is characteristic of *Pancelosaurus* in the Cretaceous Paleocene, Eocene, and Oligocene forms, it is generally finer and slightly more complex in the Eocene form. Ventral comparison of parietals of *P. piger* and the San Diego form shows striking similarity. Minor differences, however, do exist: the ridges posterolaterally bounding the parietal fossa are shorter and apparently nondiverging in the San Diego form and the posterolateral ridge on the ventral parietal surface is much weaker in the San Diego form than in *P. piger*. Dorsally the contact between parietal and occipital epidermal scale imprints is at a much more obtuse angle in the San Diego form so that the occipital epidermal scale marking is not triangularly shaped but rather forms a posterior transverse band on the sculptured portion
of the parietal table. Parietals of the Oligocene form, \textit{P. pawneensis}, are unknown.

Specimen UCMP 113217 is quite comparable in size to material comprising the type of \textit{P. pawneensis} (KU specimen no. 1281). Other frontals of the local form are somewhat smaller in minimum interorbital distance than the type; however, at least one of the two partial skulls referred to \textit{P. pawneensis} by Meszoely (1970, p. 118) is smaller than the type.

Despite the similarities noted, certain diagnostic elements are not known to be associated with the San Diego form that would positively identify it as \textit{P. pawneensis}. For instance, the primary difference between \textit{P. piger} and \textit{P. pawneensis} is the presence of pointed teeth in the later. Toothed elements have not been identified for the San Diego \textit{Pancelosaurus}. Additional material might show the presence of a new species of \textit{Pancelosaurus} but because of the scanty material available it is preferable not to name it.

Keeling has not been demonstrated for osteoscutes of \textit{Pancelosaurus piger} or \textit{P. pawneensis}.
While numerous scutes of *P. piger* are known, only a single (unkeeled) osteoscute has been referred to *P. pawneensis*. Evidently *P. piger* gave rise to the glyptosaurines through *Xestops* (Meszoely, 1970). Presumed *Xestops* osteoscutes are all keeled; many other glyptosaurines possess keels and some genera (for example *Gerrhonotus*) may show both keeled as well as nonkeeled osteoscutes. An Eocene *Pancelosaurus* (or related genus) might, therefore, possess keeled osteoscutes.

I suggest that the arrangement of the two major types of osteoscutes on the body of the San Diego *Pancelosaurus* were arranged such that dorsal body osteoscutes were keeled and ventral ones were nonkeeled. This follows the arrangement described by Meszoely (1975) for *Ophisaurus hallensis*, a middle Eocene European anguine, as well as some Recent forms such as *Gerrhonotus*.

It is probable that more than one species of lizard may be represented by the osteoscutes here referred to *Pancelosaurus*. Although all scutes resemble the description given above, some are thinner
and flatter (especially some unkeeled scutes), some show a more poorly developed pattern on the sculptured surface with fewer and less deeply imprinted grooves (a portion of these may be the result of erosion of the scute surface), and some show more branching of the grooves along with fewer rounded pits. I believe that certain of these scutes may be beyond the range of normal variability expected for a single species, but better material would be necessary to demonstrate the presence of another taxon.

Subfamily Glyptosaurinae

**Referred specimens.**—Left dentary, UCMP no. 104253; teeth, UCMP nos. 104628, 104865; numerous unnumbered osteoscutae.

Description.--The dentary (UCMP 104253) is robust and 15.91 mm. in length as preserved; it bears 14 teeth and tooth spaces of which ten teeth are preserved (Figure 6). There may have been one more tooth posteriorly, however, the curvature of the subdental shelf indicates that probably the entire toothed portion of the dentary is preserved. Meckel's groove is ventral anteriorly and widely open to the symphysis. There is no subdental gutter, the crista dentalis grades directly into the medial surface of the dentary at the bases of the teeth. The intra­mandibular septum is well developed but broken posteriorly so that it is not clear if there was a free ventral border. The ninth tooth from the front is the tallest. There is a decline in tooth height anteriorly and posteriorly. In lateral view it can be seen that the anterior teeth project higher above the parapet of the jaw than the posterior teeth. Besides being shorter, the posterior teeth are more robust and more swollen at the crowns than anterior teeth. All teeth are pleurodont, labially and lingually striated at the crowns, and the basal
nutrient foramen is interdental in position. The anterior half of the base of the fourth preserved tooth from the front was resorbed by a now missing tooth bud. The crowns of anterior teeth are blunt, shouldered, slightly incurving, very slightly recurved, and more pointed as one proceeds anteriorly in the tooth row. Posterior tooth crowns are swollen, they possess worn remnants of anteroposterior directed ridges placed slightly to the lingual side of the crown, and they seem much more worn than anterior teeth. Tooth bases are in contact but do not appear crowded together at the level of the jaw parapet. Externally the dentary is smoothly rounded and unsculptured except anteriorly where it is pierced by three mental foramina. The individually referred teeth match in all respects those of the dentary described above.

The osteoscutes are all covered with tubercular mounds or pustules. Body scutes are subrectangular, longer than wide, and have anterior gliding surfaces making up one-fourth to one-third of the length of each scute. There is almost always
some indication of lateral suturing along the edges of the scutes, in fact evidence of lateral suturing is generally more developed than lateral beveling. Some scutes are keeled, the keels are asymmetrical in all but middorsal scutes and extend from an antero-mesial position posteriorly to the left or right corner, depending on the side of the animal from which they came (see Meszoei, 1970). Exceptionally long and posteriorly tapering scutes are interpreted as having come from appendages, particularly the tail. Cephalic and some neck scutes are polygonally shaped and centrally convex to nearly flat. Cephalic and body osteoscutes commonly show the tubercles arranged into concentric bands.

Discussion.--This material can be referred to the anguid subfamily Glyptosaurinae on the basis of the tuberculated osteoscutes. Below the sub-familial level, however, the use of tuberculated osteoscutes is of little help. Also unfortunate is the fact that at present glyptosaurine anguids cannot be distinguished by dental characters at the generic
level. A more refined assignment would require knowledge of the frontals or parietals as presently defined by Meszoely (1970). The genus Peltosaurus is not known from sediments older than the Oligocene (Meszoely, 1970), so I shall assume that the San Diego glyptosaurine material does not belong to either P. abbotti or P. granulosus.

Although there is a normal range in size of osteoscutes of one species (or individual) the preserved scutes show a markedly bimodal distribution of size. Both large and smaller scutes may be present at a given locality, or only one size may be present. The larger osteoscutes I believe are probably beyond the size limit for known Xestops scutes. For this reason alone I suggest that, if there are in fact two glyptosaurine forms present, as I suspect, the smaller one may be Xestops. The remaining known North American large Eocene glyptosaurine lizards include Melanosaurus (one species), Arpadosaurus (one species), and Glyptosaurus (eight species).

At least some keeled scutes are known from each species of Glyptosaurus; only a few body
osteoscutes are known from Melanosaurus but one is keeled; some scutes of Arpadosaurus are also keeled. All known Glyptosaurus neck and body scutes and at least some from Melanosaurus plus those illustrated for Arpadosaurus by Meszoely (1970) show tubercles arranged in parallel rows around the periphery of the scute. Therefore, some of the scutes from each of the three genera resemble those from the San Diego specimens. The large form then could be a representative of any of the three genera or possibly a new one.

Unidentified anguid

_Referred specimen._--UCMP no. 113240, a single osteoscute.

_Locality._--UCMP loc. V-72179.

_Description._--The osteoscute is subtriangular in shape with very blunt corners (see Figure 10). It is about the same size (3.9 mm. in greatest diameter) as the glyptosaurine osteoscutes from the fauna but shows no indication of exterior-placed pustules. The
scute is slightly externally convex, with a darker center that gives rise to radiating, nearly straight but branching shallow channels most of which reach the lateral scute edges. About twenty well marked foramina are scattered across the external surface. Many, however, are concentrated in the central raised portion of the scute. The lateral edges are smooth, but not bevelled and there are a few foramina which pierce the thick lateral surfaces. About ten large pit-like foramina are randomly placed on the concave ventral surface.

Discussion.—This single slightly abraded osteoscute does not seem to be referable to any of the known species in the fauna. Although its long axis is nearly twice that of Recent *Anguis fragilis*, the radiating pattern compares favorably with *A. fragilis* except for the lack of tiny external pustules. UCMP 113240 compares favorably with the general shape of the postparietal in *Anguis*, *Ophisaurus*, and *Ophioides*. UCMP 113240 is, however, more equant than postparietals of the three modern
genera. The radiating pattern of the fossil osteoscutum is also common among skinks. However, the osteoscutes of skinks are compound whereas the fossil scute clearly is not. Finally, the surface sculpture and placement of foramina compares very well with a mid-dorsal osteoscutum of *Anguis fragilis* illustrated by Camp (1923, Figure 93).

The scute is tentatively placed within the Anguidae because of its large size, thickness, and surface sculpture resemblance to scutes of Recent *Anguis fragilis*.

Discussion of this form is included only to show the existence of another lizard in the fauna. Comparison with *Anguis* in no way suggests close relations.

**FAMILY VARANIDAE**

*Introduction to the Family*

The extant genus *Varanus* lives in parts of Africa, Arabia, southern Asia, the East Indies, Australia, the Marshall, Caroline and Fiji Islands.
In addition, although no varanid is presently native to North America, they did live there from Late Cretaceous through Oligocene time.

The family Varanidae is separated from other Squamata by a combination of: postorbital and supratemporal skull arches present, few osteoderms, non-autotomic tail vertebrae, presence of parietal foramen, presence of a mandibular jaw hinge, nine cervical vertebrae, and no groove in the teeth.

Two subfamilies have been distinguished:

1. Varaninae—teeth not present on palatal bones; no zygosphene or zygantra on the thoracic vertebrae.

2. Saniwinae—teeth present on the palatine and pterygoid; vestigial zygosphene always and zygantrum sometimes present on thoracic vertebrae.

The genera *Saniwa*, *Palaeosaniwa*, and *Megalania* belong to the subfamily Saniwinae.

*Saniwa* Leidy, 1870

*Saniwa* may be distinguished by its recurved, trenchant, spaced teeth without serrations, and
elongate thoracic vertebrae without marked ventral longitudinal channels on the centra. *Saniwa* is presently known only from the Eocene to Oligocene of North America.

*Saniwa brooksi* Brattstrom, 1955

Referred specimens.--Vertebrae: UCMP nos. 104223, 104341, 104355, 104635; dentary fragments: 110329, 110330; questionably referred teeth: 104257, 113247, and 113248; caudal vertebrae LACM 55928 and 55930.

Localities.--UCMP locs. V-71184, V-71211, V-72157, V-72158; CIT 249.

Revised diagnosis.--The ventral surface of thoracic vertebrae are slightly convex transversely and nearly straight in lateral view. The neural spine extends far posteriorly and is inclined posteriorly. Two times the height of the condyle is greater than width across the condyle. No ridge surrounds the condyle; the condyle does not descend beneath the ventral surface of the centrum.
Description.--The two thoracic and two caudal vertebrae are characteristically varanoid. The slightly concave ventral margins of centra of the elongate caudal vertebrae in lateral view descend to their ventralmost extent directly beneath the postzygapophyses. A paired tubercle for attachment of the missing caudal chevron is present on the ventral centrum margin just anterior to the condyle. In transverse section the ventral margin of the centrum is slightly concave. The concavity is the result of a median ventral canal which is best developed on the posterior half of the centrum and extends between the tubercles. A single set of subcentral foramina lie just lateral to this median central canal below the level of the posterior extent of the transverse process. The cotyle is transversely elliptical, less than twice as wide as high, and faces directly forward. The condyle is likewise transversely elliptical, posterodorsally facing, not separated from the centrum by a ridge, and does not extend beneath the ventral surface of the centrum.
Dorsally a very low median ridge runs posteriorly on the neural arch from a point just behind the level of the prezygapophyses. This low ridge rises gently until it reaches the approximate midpoint of the vertebra in lateral view, where it rises more steeply to form the well developed neural spine. Although the extremity of the neural spine is somewhat broken in both caudal vertebrae the indication is that the neural spine was flat-topped and extended in a posterior direction at least as far as the postzygapophyses but probably not as far as the posterior level of the condyle. Anterior and posterior edges of the neural spine are subparallel, posteriorly inclined and straight.

A low subrounded ridge extends posteriorly with diminishing strength from the anteriorly placed transverse process, disappearing on the lateral portion of the centra just anterior to the condyle. Only the bases of the transverse processes are preserved although there is an indication that they projected in a slightly anterior direction as well as laterally. A slight anterior slant to the transverse
processes of the posterior two-thirds of the caudal vertebrae of Recent varanids is not uncommon. Another very low ridge connects the prezygapophyses with the postzygapophyses. Neither caudal vertebra shows an autotomic fracture plane.

The two thoracic vertebrae lack the subcentral canal. The ventral surface of the centra of these specimens is smoothly convex, and the centra taper smoothly posterior to the condyle, which is not separated from the centra by a ridge.

The neural spine of neither specimen is well preserved. However, the left postzygapophysis of UCMP 104635 is preserved to show it extending posterior to the posterior level of the condyle. The neural spine of UCMP 104223 extends farther posterior than the postzygapophyses. However, the condyle is not preserved so it is impossible to see the relation between the posterior extent of neural spine, postzygapophyses and condyle on a single specimen. Zygosphenes are not preserved. The zygantra are wide and well developed. The paradiapophyses are solid, vertically elliptical, inclined slightly
anteroventrally, fused with and directly below the prezygapophyses. A ridge extends anterior from the ventral margin of the diapophyses to the lateral margin of the cotyle which is transversely elliptical and faces directly ahead. Two times the height of the cotyle is wider than its width. No ridge surrounds the cotyle which does not extend below the level of the centrum. The neural canal is restricted posteriorly.

Several small jaw fragments and unattached teeth (UCMP 104257, 113247, and 113248) are questionably referred to this species. The teeth are fang-like and recurved. Complex infolding is present on both lingual and labial sides of the tooth bases extending slightly less than one-half way up the teeth. The bases are expanded and give rise to sharp pointed crowns that are oval to nearly circular in cross section near the tooth tips. A well developed anterior, vertical ridge and shallow groove-like constriction make the teeth look more laterally compressed than they actually are. The groove-like constriction on the anterior edge just lingual to the
ridge is superficially *Heloderma*-like. However, here the teeth are not relatively heavy, large, and very wide based as they are in Heloderma. The "groove" in these fossil teeth is so shallow and wide open that I cannot believe it ever functioned as a poison duct. Admittedly, diagnostic bones such as maxillae, premaxillae, and more complete dentaries are lacking, but there is nothing positive on the other hand to establish the presence of a helodermatid in the San Diego Eocene herpetofauna.

**Discussion.**—The vertebrae appear to fall into the size range of an animal represented by the size of the type specimen (LACM [CIT] no. 5117) of *S. brooksi* Brattstrom (1955) from LACM (CIT) loc. 249. The questionably referred jaw fragments and teeth, however, present an enigma for they are all very small with tooth heights in the range of 2 mm. It is possible that since varanid remains in the collection are exceptionally rare to begin with, that this size differences might represent a collection bias. There is little at this time upon which to establish the
existence of a second varanid in the fauna. Therefore the question of how many varanids are in the fauna cannot be definitely established with the material at hand.

The caudal vertebrae agree well with the variation expected within the species. Referred thoracic vertebrae agree in all respects except size with the type specimen, also a thoracic vertebrae; the referred specimens are somewhat smaller. The caudal vertebrae may quite confidently be assigned to *S. brooksi*. Characters of the caudal vertebrae differ from the type only as would be expected due to differentiation along the vertebral column. It is important to note that the type and the vertebrae at hand show a slightly convex ventral surface to the centrum while there is a subcentral groove running along the length of the caudal vertebrae. Comparison to Recent Varanus shows that this is a common, in fact expected, range of variation within an individual. Nevertheless, the existence of a slightly convex ventral surface of the centrum should be
removed from the specific diagnosis as characterized by Brattstrom (1955).

The discovery of new specimens referred to S. brooksi does not basically change its relations as stated by Brattstrom (1955, p. 146). Brattstrom concluded that S. brooksi is closely related to S. ensidens and S. paucidens.

Hecht (1959) made the statement that "Many species of Saniwa have been described, but it is difficult to evaluate the status of these species and even more difficult to allocate the specimens." A re-evaluation of Saniwa and perhaps the Saniwinae is sorely needed.

ORDER AMPHISBAENIA

FAMILY RHINEURIDAE Berman, 1973

Unidentified Genus and species

Referred specimens.—Vertebrae, UCMP nos. 104522, 109861, 109944, 113249; questionably referred dentary fragments, UCMP nos. 104757, 104760, 104790, 110413, 110414, 110415, 110416, 110417, 110418,
110419, 110420, 110421, 113234, 113250; maxillary fragment UCMP no. 110422; questionably referred premaxillary fragments UCMP nos. 113235 and 113251.


Description.--The vertebrae are small with tiny neural crests but lacking true neural spines. The neural arch is low and marked by an anterior thickening of the neural crest that extends forward to a position even with the anterior level of the prezygapophyses. Posteriorly the neural arch gives rise to a mesial flattened process which extends beyond the posteromost extent of the postzygapophyses. In dorsal view the prezygapophyses project laterally from the vertebra at a more acute angle than do the postzygapophyses. The articulating surface of the prezygapophyses are subrhomoboidal in shape. Suboval synapophyses, present on the ventral surface of the prezygapophyses, are not produced dorsoventrally and do not extend below the ventral edge of the procoelous centrum. Centra have parallel lateral edges,
are flat bottomed, and possess a pair of anteriorly placed subcentral foramina in UCMP 109861, 104522, and the UCMP 113249. The corresponding portion of 109944 is chipped and only one foramen is preserved. Condyle and cotyle are wider than tall; the width is a little over two times the height. The condyle of UCMP 109944 is very slightly wider than the centrum, is not set off from the centrum by a constriction, and projects directly ahead. The articulating surface of the postzygapophyses are subrhombic but considerably smaller than the prezygapophyses. In lateral view the neural arch is slightly concave at mid-vertebral level.

All dentaries are questionably referred for reasons discussed below. The most complete dentary is UCMP 113234. It contains seven teeth and remnants of one more posterior tooth. Judging from the dorsal curvature of the subdental shelf there were probably no other teeth in the unbroken specimen; thus the dentary tooth count in the unbroken state was most likely eight. Teeth are attached to the dentary in a subpleurodont to subacrodont manner; tooth bases
are indistinct and a medullary cavity can be clearly seen only at the base of the next to last preserved tooth. The teeth are simple, unicusp, and laterally compressed with oval bases in cross-section. Long axes of the tooth cross-sections are all oriented parallel with the exterior surface of the dentary. Posterior teeth are most anteroposteriorly expanded than the anterior teeth. Tooth size is somewhat variable. However, the next to last tooth is clearly largest. UCMP 110414 shows that the last tooth was the smallest. Teeth of UCMP 104790, 110414, 110419, and 113234 are moderately wide spaced, however, the teeth of UCMP 110413 and 110415 are spaced more closely-touching one another at and below the level of the parapet of the dentary. In medial view the teeth are subtriangular (especially in specimens other than UCMP 113234) to simply rounded at the crowns. In all specimens the tooth edges taper convexly from the strong bases toward centrally placed tips. Anterior teeth were taller than other teeth, but did not project farther above the jaw parapet because of their anterior tilt. All teeth project about one-half of
their height above the jaw parapet; teeth of UCMP 110413 curve gently medially as they rise from their bases in contrast to the rather vertical condition of teeth on other specimens.

The lingual surface of the dentary has a widely open, ventromesially placed Meckelian fossa. Several anterior dentary fragments (especially UCMP 110415 and 113234) show that the Meckelian groove remained open to the symphysis. Beneath the bases of the last two teeth on the dorsal edge of the Meckelian fossa lies a well developed articulating facet for the anterolingual process of the coronoid. There is a large excavation on UCMP 110414 posterior to the tooth row, presumably for the insertion of the surangular and prearticular. The posterolingual excavation of UCMP 110414 reaches forward to the level of the facet for the anterolingual process of the coronoid. The edges of the excavation in UCMP 110414 and 113234 are, however, irregular and heavily worn indicating that it may have been artificially enlarged by breakage and abrasion. The sulcus dentalis is moderately to poorly developed.
Laterally the dentary was short and relatively deep. The lateral surface is more or less flattened posteriorly, lacks sculpture and is pierced by six mental foramina in UCMP 113234. Four of the foramina are in a row and subequally spaced; two are in a second row below the upper four foramina. The anteromost foramin in the bottom row is large, elongate and placed nearly at the symphysis.

Lateral view of the upper margin of the dentary is slightly dorsally concave, but all specimens are broken posteriorly so that it is impossible to determine the strength of the coronoid process. The posterolateral portion of UCMP 110413, 110414, and 113234 shows no dorsal groove, indicating that a coronoid lappet onto the dentary was absent. In dorsal view the labial surface of the dentary is nearly straight, as are all but the first two teeth of the tooth row.

Five poorly preserved teeth are present on UCMP 113235, a questionably referred fragment of Premaxilla. The median tooth of UCMP 113235, as well as that of the unnumbered premaxilla fragment, is
enlarged. There are weak lateral crests, the teeth are rounded in cross section, and the tooth shafts are subparallel. Each of these three features contrasts with the condition of posterior dentary teeth.

**Discussion.**--The vertebrae are clearly amphisbaenian-like in their shape, depression of neural arch, flattening, straight-sided centra, and prominently projecting zygapophyses. There is a great similarity of vertebrae of *Rhineura floridana* to those of the fossil. The Rhineuridae was elevated to familial rank by Berman (1973) who also noted that there has been little change in the vertebrae of amphisbaenians since the Eocene. Amphisbaenian vertebrae are, therefore, of little value in generic diagnosis.

The absence of a coronoid lappet onto the dentary poses a problem since all rhineurines have been considered to possess the lappet (Estes, 1965). The wide open Meckelian groove most closely approaches the condition of Recent *Bipes biporus*, although a
Meckelian groove open to the symphysis could be interpreted as merely the retention of a primitive state. Meckel's groove in *Amphisbaena fuliginosa* is also open to the symphysis; *Rhineura floridana* always shows a closed and fused Meckelian groove. In his description of *Spathorhynchus fossorium*, the most primitive rhineurid presently known, Berman (1973) did not report if the Meckelian groove was open anterior to the splenial. The San Diego fossil amphisbaenian bears eight dentary teeth as in *S. fossorium* but contrasts with *S. fossorium* in lacking any indication of the coronoid lappet.

The San Diego fossil amphisbaenian is referred to the family Rhineuridae on the basis of vertebral character and the pleurodont method of tooth implanation. The questionably referred dentaries indicate that the fossil form lacked a coronoid lappet but possessed a wide open Meckelian groove contrasting with presently known rhineurine amphisbaenians. These two character states could be interpreted as retained primitive ones and, in combination with the large number of dentary teeth, might indicate that the
San Diego fossil form was morphologically more primitive than middle Eocene Spathorhynchus fossorium. It is also possible that the dentaries represent a different species than the vertebrae do. However, since there is at this time a single type of dentary and a single vertebral type plus the fact that all amphisbaenian material has been recovered from only three localities, two of which are very closely associated, I prefer at present to view all the amphisbaenian material as constituting a single taxon.

Because of the possibility of more than one species being represented, the recent trend to base amphisbaenian species on more than vertebrae alone, and the relatively little value of vertebrae in generic diagnosis, the San Diego amphisbaenian is allocated to the Rhineuridae as genus and species indeteminate.

Berman (1973) included Rhineura floridana and all the presently known fossil North American amphisbaenians, except for the hyporhinids, in the Rhineuridae. The middle to late Paleocene Oligodon-tosaurus wyomingensis presents the exception to Berman's statement. Estes (1965) referred
Oligodontosaurus to the Amphisbaenidae but now considers it to be the only member of a distinct family (Estes, personal communication, 1975). Reference of the San Diego later Eocene amphisbaenian to the Rhineuridae would therefore not be unexpected.

North American Tertiary amphisbaenians are known from a rather restricted area including parts of South Dakota, Nebraska, Colorado and Wyoming plus the John Day Formation of Oregon (Berman, 1973) and the Cypress Hills Formation of Saskatchewan (Holman, 1972). The presence of a later Eocene amphisbaenian from San Diego considerably extends the known range of the group.
INTERPRETATIONS AND DISCUSSION

Lower Vertebrate Faunal List

The following lower vertebrates have been identified from localities within the Friars Formation, Mission Valley Formation, and Santiago Formation (UCMP locality V-72088). Identifications for forms other than the lizards are tentative. Following the name of each taxon (except the lizards) is an indication of the number of elements represented.

Class Osteichthyes

Infraclass Holostei

Lepisosteus cf. L. spatula (one tooth)

Infraclass Teoeostei

Unidentified remains (numerous teeth, about six vertebrae, and five otoliths)

Class Chondrichthyes

Order Galeiformes

Odontaspidae

Odontaspis sp. (two teeth)

Sphyrnidae? (two teeth)
Order Squaliformes
  Squalidae
    Squalus sp. (one tooth)
Order Rajaformes
  Rhinobatidae
    Rhinobatus sp. (12 teeth)
  Rajidae
    Raja sp. (nine teeth)
  Dasyatidae
    Dasyatis sp. (two teeth)
  Myliobatidae
    Myliobatis sp. (18 teeth)

Class Amphibia

Suborder Neobatrachia
  Pelobatidae
    Cf. Eopelobates (four urostyles, three jaw fragments)
  Rhinophrynidae? (one vertebra)
  Undetermined neobatrachian (five jaw fragments, nine vertebrae)

Class Reptilia

Order Chelonia
  Trionychidae
Trionyx sp. (numerous plates)

Testudinidae or Baenidae

at least one form (two individuals)

Order Squamata

Gekkonidae?

Unidentified gen. and sp.

Xantusiidae

Palaeoxantusia allisoni

Palaeoxantusia kyrentos

Iguanidae

Parasauromalus olseni

Form A

Form B

Agamidae

Tinosaurus cf. T. stenodon

Scincidae

Paracontogenys estesi

Anguidae

Unidentified gen. and sp.

Pancelosaurus

Unidentified glyptosaurine

Varanidae
Saniwa brooksi

Biodae

Boavus affinis (about a dozen vertebrae
at least one unidentified gen. and sp.
Anillidae?
cf. Dunnophis (about six vertebrae)

Order Amphisbaenidae

Rhineuridae

Gen. and sp. indeterminate

Order Crocodylia

Crocodylidae

Pristichampsus sp. (about 15 teeth)

Unidentified alligator (a few teeth)

The questionable rhinophrynid is represented
by a single vertebra. The presence of weak opistho-
coely in the vertebra of an apparently mature
individual is suggestive of the Rhinophrynidae. The
centrum is not at all flattened which is suggestive
of the holochordal (primitive) condition rather than
the flattened epichordal (derived) condition.
Comparison of Faunas

The later Eocene lizard fauna of the greater San Diego area may be compared with two other North American early Tertiary faunas. The Bridgerian Tabernacle Butte fauna of Wyoming (Hecht, 1959) and the early Oligocene Cypress Hills fauna of Saskatchewan (Holman, 1972) contain diverse saurian elements as well as representing geographically the nearest well known lower vertebrate faunas temporally subequivalent to the San Diego fauna.

Perhaps the most striking difference between the three faunas is that both the San Diego and the Tabernacle Butte faunas lack any extant lizard genera (Rhineura from Tabernacle Butte excepted) while the Cypress Hills fauna contains a primitive species of Crotaphytus (see Table 2). Six representatives of extant genera are known from the Oligocene Cypress Hills herpetofauna, none are known from the San Diego herpetofauna and only Rhineura is known from the Tabernacle Butte herpetofauna. All three faunas are modern with respect to families represented. The Cypress Hills fauna is considerably "more modern" at
Comparison of the Lizards from the Tabernacle Butte Fauna (Bridgerian), the San Diego Fauna (Uintan), and the Cypress Hills Fauna (early Oligocene). Taxa marked by * were not correctly identified or have been shown to be absent.

<table>
<thead>
<tr>
<th>TABERNACLE BUTTE</th>
<th>SAN DIEGO</th>
<th>CYPRESS HILLS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Not represented</td>
<td>GEKKONIDAE?</td>
<td>Not represented</td>
</tr>
<tr>
<td>Gen. &amp; sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>XANTUSIIDAE</td>
<td>XANTUSIIDAE</td>
<td>XANTUSIIDAE</td>
</tr>
<tr>
<td><em>Palaeoxantusia fera</em></td>
<td><em>P. allisoni</em></td>
<td><em>P. borealis</em></td>
</tr>
<tr>
<td><em>P. kyrentos</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Not represented</td>
<td>IGUANIDAE</td>
<td>IGUANIDAE</td>
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<tr>
<td></td>
<td><em>Parasauromalus</em></td>
<td><em>Cypressaurus</em></td>
</tr>
<tr>
<td></td>
<td><em>olseni</em></td>
<td><em>hypsodontus</em></td>
</tr>
<tr>
<td></td>
<td>Form A</td>
<td>Form A</td>
</tr>
<tr>
<td></td>
<td>Form B</td>
<td></td>
</tr>
<tr>
<td>AGAMIDAE</td>
<td>AGAMIDAE</td>
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</tr>
<tr>
<td><em>Tinosaurus stenodon</em></td>
<td><em>Tinosaurus</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>cf. T. stenodon</em></td>
<td></td>
</tr>
<tr>
<td>Not represented</td>
<td>SCINCIDAE</td>
<td>Not represented</td>
</tr>
<tr>
<td></td>
<td><em>Paracontogenys estesi</em></td>
<td></td>
</tr>
<tr>
<td>TABERNACLE BUTTE</td>
<td>SAN DIEGO</td>
<td>CYPRESS HILLS</td>
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</tr>
<tr>
<td><strong>TEIIDAE</strong></td>
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<td>Not represented</td>
</tr>
<tr>
<td>Gen. &amp; sp. indet.*</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>ANGUIDAE</strong></td>
<td>ANGUIDAE</td>
<td>ANGUIDAE</td>
</tr>
<tr>
<td>Xestops</td>
<td>Glyptosaurines</td>
<td>cf. Peltosaurus</td>
</tr>
<tr>
<td>Dimetoposaurus</td>
<td>1 or more species</td>
<td></td>
</tr>
<tr>
<td><em>wyomingensis</em></td>
<td>Pancelosaurus sp.</td>
<td></td>
</tr>
<tr>
<td>Peltosaurus sp.*</td>
<td>Undetermined gen. &amp; sp.</td>
<td></td>
</tr>
<tr>
<td>Melanosaurus sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>VARANIDAE</strong></td>
<td>VARANIDAE</td>
<td>Not represented</td>
</tr>
<tr>
<td>Saniwa grandis</td>
<td>Saniwa brooksi</td>
<td></td>
</tr>
<tr>
<td>Saniwa sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>PARASANIWIDAE</strong></td>
<td>Not represented</td>
<td>Not represented</td>
</tr>
<tr>
<td>Parasaniwa sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>RHINEURIDAE</strong></td>
<td>RHINEURIDAE</td>
<td>RHINEURIDAE</td>
</tr>
<tr>
<td>Lestophis sp.</td>
<td>Gen. &amp; sp. indet.</td>
<td>Lestophis nr.</td>
</tr>
<tr>
<td>Rhineura</td>
<td></td>
<td>L. anceps</td>
</tr>
<tr>
<td></td>
<td></td>
<td>one other form</td>
</tr>
</tbody>
</table>
the generic level, however, especially when the entire herpetofauna is considered.

The San Diego herpetofauna is clearly the most diverse with about 22 species being represented; 18 species are known from the Tabernacle Butte and 16 species from the Calf Creek herpetofaunas. In addition, sharks and rays are not known from the Tabernacle Butte or Calf Creek total faunas.

The list of species presented in the Tabernacle Butte herpetofauna by Hecht (1959) needs modification: *Tinosaurus stenodon* is incorrectly listed as *Tinosaurus stenodon* and *Dimetoposaurus wyomingensis* has been shown to be a synonym of *Xestops vagans* by Meszoely (1970) who also stated that *Peltosaurus* is only known with certainty from the Oligocene of North America.

A questionable gekkonid is present in the San Diego fauna. Each fauna contains species of the xantusiid *Palaeoxantusia*. Iguanid lizards make up an important part of the San Diego and Calf Creek faunas. In contrast, only a small fragmentary iguanid dentary (now lost) and an iguanid frontal not determinable
to species are known from the Tabernacle Butte fauna (Estes, personal communication, 1975). Iguanids are present in Wasatchian sediments of Wyoming (Gauthier, personal communication, 1975) and so were probably more widespread in North America during the Bridgerian. The questionable skink Paracontogenys is known only from the San Diego fauna. Paracontogenys appears morphologically intermediate between Late Cretaceous to middle Paleocene Contogenys sloani (Estes, 1969a, 1976) from the Rocky Mountain Region and primitive extant Eumeces-like skinks. The agamid Tinosaurus, present at Tabernacle Butte and in San Diego but not at Calf Creek, represents the most recent record of a North American agamid lizard. Sympatry of agamids and iguanids in the San Diego fauna is unusual considering their total geographic separation in modern faunas. Despite Hecht's (1959) statement to the contrary, teiid remains seem to be absent from all three faunas (fide Estes, for the Tabernacle Butte fauna). The Calf Creek fauna is the most depauperate in terms of anguid lizards, with Peltosaurus being the only form present; two Bridgerian anguids have
been described and three are questionably known from the San Diego later Eocene. Varanids are absent from the Calf Creek local fauna, Parasaniwa is present only in the Tabernacle Butte fauna. Rhineurine amphibiaenids are present in all three faunas.

**Geologic Age of the San Diego Lizard Fauna**

Two lizard species present in the San Diego fauna are also present in the Paleogene faunas from the Rocky Mountain region. Parasauromalus olseni is known to range from the Wasatchian to Bridgerian in Wyoming. Tinosaurus cf. T. stenodon was reported from "Horizon C or higher, Bridger formation, Middle Eocene" by Gilmore (1928, p. 31). However, Rocky Mountain region specimens probably referable to Tinosaurus are known to range back in age to Wasatchian (Gauthier, personal communication, 1975). A brief comparison with material from the Bridger Formation of Wyoming being studied by Dr. R. Estes shows that San Diego iguanid, Form A, and an undescribed Bridger iguanid may be conspecific. The presence of Parasauromalus olseni, Tinosaurus cf.
T. stenodon, and iguanid, Form A, in the San Diego fauna suggests a Bridgerian age.

*Palaeoxantusia* is known to range from the middle Paleocene (Estes, 1976) to the early Oligocene (Holman, 1972), but the two species present in San Diego are endemic. *Pancelosaurus* is known from two species, *P. piger* ranging from Late Cretaceous to late Paleocene (Estes, 1964, 1976) and *P. pawneensis* from the middle Oligocene of Colorado (Meszoely, 1970). Differences in sculpture on the external side of frontals referred to *Pancelosaurus* sp. in the San Diego fauna suggest that the San Diego *Pancelosaurus* material may represent a new species. However, since toothed elements are presently unknown for the San Diego form, its specific allocation remains uncertain at this time.

Like the species of *Palaeoxantusia*, the San Diego varanid is apparently known only from the San Diego and Sespe faunas (Brattstrom, 1955, 1958). The unidentified anguid and *Paracontogenys* estesi are progressive forms suggesting relations with more modern faunas. *Paracontogenys* estesi may help to link
Contogenys sloani with primitive unquestioned skinks. Contogenys sloani is known to range from the Late Cretaceous to middle Paleocene (Estes, 1969) but the genus may range into the early Eocene of Wyoming (Contogenys-like material is presently being studied by Mr. J. Gauthier at San Diego State University). Therefore, the unidentified anguid, Paracontogenys estesi, and questionably Palaeoxantusia allisoni, P. kyrentos, and Saniwa brooksi weakly suggest an advance over typical Bridgerian faunas. Advancement over the Bridgerian Tabernacle Butte fauna is also suggested by the absence of Palaeoxantusia fera and Parasaniwa.

The San Diego Eocene mammalian fauna has been considered to suggest an early Uintan (of Wood and others, 1941) North American land mammal age by Lillegraven (1973), Novacek (1973) and Uintan by Black and Dawson (1966). Lillegraven (1973, p. 30) noted that mammalian fossils from the Friars and Mission Valley formations ... are more primitive than Uintan fossils from the Laguna Riviera localities, from Ventura County and from most of the Rocky Mountain sites.
However, the fossils seem not to be so primitive as to be considered "Bridgerian," the next older land mammal age.

The primitive nature of the San Diego Eocene insectivores (Novacek, 1973) does not alter the conclusions of Lillegraven; neither does the nature of the San Diego Eocene lizard fauna.

Coastal southern California, especially between Los Angeles and San Diego, presents a unique situation in which marine and nonmarine stratigraphic sequences may be correlated. Kennedy and Moore (1971) revised the stratigraphy of the San Diego Cretaceous and Eocene. They divided the local Eocene into two major parts, the La Jolla Group and the Poway Group. Vertebrate fossils have been recovered from the Scripps Formation (rarely) and Friars Formation of the La Jolla Group as well as the Mission Valley Formation of the Poway Group. The stratigraphic relations proposed by Kennedy and Moore (1971) are presented here as Figure 11. The dominantly nonmarine Friars Formation is partly contemporaneous with the principally marine Ardath Shale and Scripps Formation. On the basis of calcareous nannoplankton, Bukry and
Kennedy (1969, p. 43) suggested that the Ardath Shale correlates with the "upper part of the lower middle Eocene Discoaster sublodoensis Concurrent-range Zone."

Steineck and Gibson (1971) reported an early middle Eocene age for the Ardath Shale (old Rose Canyon Shale Member of the La Jolla Formation) and a late middle Eocene age for the Poway Conglomerate (part of the old Poway Formation) based on planktonic foraminifera. Steineck, Gibson, and Morin (1972) concluded that the Ardath Shale is early middle Eocene and that the "Poway Conglomerate" (sampled from a marine lens in the Stadium Conglomerate at the Fenton Material Quarry, Mission Valley) is late middle Eocene in age. They further stated that the unnamed unit of Milow and Ennis (1961), now the Friars Formation, is apparently equivalent to the Morozovella lehneri zone (medial middle Eocene), although direct evidence is lacking.

Foraminiferal faunules have also been described from the Ardath Shale and Poway Conglomerate by Cushman and Hanna (1927), Cushman and Dusenberry
(1934), Gibson (1971), Mallory (1959), and Shepard et al. (1957).

A problem of some significance emerged when Steineck and Gibson (1971) presented evidence that classical "Ulatisian" and "Narizian" stages, represented in San Diego by faunas from the Ardath Shale and Poway Conglomerate, respectively, are time transgressive. Steineck and Gibson suggested that the Ulatisian stage ranges in age from late early Eocene to early middle Eocene (instead of the standard concept of middle Eocene) and the Narizian stage ranges in age from early middle Eocene to late middle Eocene (instead of the standard concept of late Eocene). They further noted (p. 479) that

... none of the Narizian sequences for which planktonic foraminiferal or nannoplankton data is available are late Eocene in age. Instead upper Eocene strata in California are represented in the superjacent Refugian stage (considered Oligocene by Mallory, 1959, and Lipps, 1967).

The argument presented by Steineck and Gibson (1971) is that Mallory's (1959) stages and zones are based on benthonic foraminiferal assemblages which could be time transgressive, and indeed are shown to
be so by planktonic biostratigraphy. It was further suggested that Mallory's system be abandoned in favor of more reliable means of dating such as planktonic foraminifera or calcareous nannoplankton.

A series of replies and discussions soon appeared (McWilliams, 1972; Steineck and Gibson, 1972; Phillips, 1972; Gibson and Steineck, 1972) which mainly rejected Steineck's and Gibson's findings.

Steineck (personal communication, 1975) has observed that micropaleontologists have in general continued to use Mallory's scheme in the classic sense simply accepting any Ulatisian benthonic assemblage as middle Eocene and so forth. Work emanating from the University of California at Santa Barbara and the University of California at Berkeley has simply ignored the findings of Steineck and Gibson (1971).

Evidence supporting the contention of Steineck and Gibson (1971) that the Pacific Coast foraminiferal stages of Mallory (1959) are significantly time transgressive has accumulated, for instance Steineck and Jervey (1971), Bandy (1972), and Gibson (1972,
Gibson (personal communication, 1975) stated that the United States Geological Survey is currently using Steineck's and Gibson's (1971) definition of the lower Tertiary stages and zones. Gibson's communication continued,

The furor has died over the assignment of "stages" and our (Steineck and Gibson) way is now more or less the accepted view. There are still a smattering of die hards but they too are wavering in our favor as more evidence becomes available.

Lillegraven (1973, p. 30) has noted that because of Steineck's and Gibson's findings, a change in the present concept of time intervals represented by land mammal ages is possible. Lillegraven continued:

The mammalian fossils from the upper parts of the Friars and Mission Valley formations strongly suggest an early "Uintan" (of Wood et al., 1941) North American land mammal age. . . . Although the "Wood Committee" intentionally avoided equating the "North American land mammal ages" with time intervals, usage has grown to consider the "Bridgerian" as "middle Eocene" and the "Uintan" as "late Eocene." If, as Steineck and Gibson suggest, the Ulatisian and Narizian are far older than previously thought, then the concept of the "Uintan" must be broadened to include some of the middle Eocene as well as nearly the entirety of the late Eocene. If this were true, the duration of the Uintan would be significantly increased.
Although the problem with the marine section is not yet settled, it appears that it may now be possible to formalize an increase in the time interval represented by the Uintan land mammal age to include much of the middle Eocene as well as nearly all of the late Eocene. Using the correlation results of Steineck and Gibson (1971) a suggested maximum age for the Uintan would be from early middle Eocene to late Middle Eocene. For this reason I prefer to follow Novacek (1973) in using the term "later Eocene" instead of the traditional "late Eocene" (e.g., Black and Dawson, 1966) as applied to the San Diego Uintan vertebrate fauna.

The primitive nature of the San Diego Eocene lizards does not conflict with a "pre-late Eocene" age for the local vertebrate fauna.

Faunal Distribution

Fossil lizards have been recovered from the dominantly nonmarine Friars Formation (the uppermost unit of the La Jolla Group) and the Mission Valley Formation which lies above and interdigitates with
the Stadium Conglomerate of the Poway Group. Overlying the Mission Valley Formation and Stadium Conglomerate but within the Poway Group is the Pomerado Conglomerate and its included Miramar Sandstone Member which were considered upper Eocene units by Peterson and Kennedy (1974). No vertebrate remains have as yet been discovered within the Pomerado Conglomerate.

One locality, V-72088, from the northern end of Camp Pendleton Marine Corps Base near Camp Onofre has also yielded fossil lizards. Locality V-72088 is here considered to belong to the Santiago Formation. Discussion of reasons for this assessment are made in a following section.

Twenty-two localities have yielded fossil lizards from the combined Friars, Mission Valley and Santiago formations. Table 3 summarizes the presence-absence distribution data by locality. Fossil lizard remains were, in general, too fragmentary to prepare a listing of minimum numbers of individuals present at any given localities.
### Table 3

**Distribution of Taxa by Locality (Presence or absence data given only)**

<table>
<thead>
<tr>
<th>Taxa</th>
<th>SANTIAGO FM.</th>
<th>FRIARS FM.</th>
<th>MISSION VALLEY FM.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gekkonidae?</td>
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<tr>
<td>Parasauromalus olseni</td>
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<tr>
<td>Iguanid Form A</td>
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<tr>
<td>Iguanid Form B</td>
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<tr>
<td>Tinosaurus cf. T. stenodon</td>
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<tr>
<td>Palaeoxantusia allisoni</td>
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<tr>
<td>Palaeoxantusia kyrentos</td>
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<tr>
<td>Paracontogenys estesi</td>
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<tr>
<td>Pancelosaurus sp.</td>
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<td></td>
<td></td>
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<tr>
<td>Unidentified anguid</td>
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<td></td>
<td></td>
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<tr>
<td>Gyptosaurines</td>
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<tr>
<td>Saniwa brooksi</td>
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<tr>
<td>Rhineuridae</td>
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</table>
A summation of Table 3 shows that *Parasaurromalus olseni*, iguanid, Form B, *Tinosaurus* cf. *stenodon*, and *Palaeoxantusia allisoni* are present within each of the three formations. No form is restricted to the Friars Formation of locality V-72088 and no form from the Friars Formation is absent in the Mission Valley Formation, although five species are present in the Mission Valley Formation but absent from the Friars Formation. Eight species are present in the Mission Valley Formation that are lacking in the Santiago Formation (V-72088). A total of five species are known from the Santiago Formation, seven are present in the Friars Formation and 13 are present in the Mission Valley Formation. Only the Mission Valley Formation possesses species restricted to it, these include the questionable gekkonid, iguanid, Form A, *Paracontogenys estesi*, the unidentified anguid, and the rhineurine amphisbaenid. A number of these are small, fragile, or rare forms that may represent either a collection bias (more time spent collecting from the Mission Valley Formation) or a different environment of deposition reflected by the
common occurrence of finer-grained fossil-bearing sediments in the Mission Valley Formation. I do not believe that a single reason explains the situation, nor do I believe that a comparison of one probable channel deposit (V-72088) with roughly a dozen localities from the Mission Valley Formation is valid since several environments may be represented in the Mission Valley sample. Processing of samples from the localities, however, showed one striking difference between V-72088 and most other localities; V-72088 sediments contained large percentages of medium-to-coarse-grained sand particles. The difference in sediment type may be directly responsible for the faunal content of locality V-72088 as compared with the more diverse fauna from fine-grained Mission Valley Formation localities.

Stratigraphic Position of V-72088

The Uintan vertebrate bearing locality from the northern end of Camp Pendleton Marine Corps Base near Camp Onofre (V-72088) has been referred to the
"Santiago?" Formation (Lillegraven, 1975). The locality is composed of primarily coarse-grained sands with green to brown clay chips. The entire hillside on which the locality is situated shows cross-bedding in the sands, some gravel lag and a complex intermixing of the clay chips. The vertebrate bearing sands overlie and interdigitate with blue-green to green-brown clayey mudstones with a nearly monospecific (gastropod) marine invertebrate fauna. Deposition at V-72088 probably took place along the edge of a delta which was building out into a quiet, shallow marine environment. The monospecific invertebrate assemblage may be explained by assuming a fresh-water dominated (brackish) "interchannel" situation.

The geology of the Oceanside-Carlsbad-Vista region has recently been mapped by Wilson (1972). He shows that stratigraphic units characteristic of the Santa Ana Mountains sequence mesh with and generally overlie those characteristic of the San Diego sequence (Figure 12). The interfingering of Santa Ana Mountain region lithostratigraphic units with typical San Diego
Figure 11. Stratigraphic relations of formations in the San Diego coastal area. From Kennedy and Moore (1971).

Figure 12. Stratigraphic relations of formations in the Oceanside-Del Mar area. After Wilson (1972).
Figure 13. Relation of middle Eocene depositional environments in the Oceanside-Del Mar area. After Wilson (1972).
units occurs about one-half way between the San Diego and Santa Ana Mountain areas. San Onofre, located near V-72088, is nearly three-fourth of the way from San Diego to the Santa Ana Mountains, so one might logically expect closer relations of V-72088 with the Santa Ana Mountain sequence. Miocene (and possibly Oligocene) units are known to occur within the confines of Camp Pendleton Marine Corps Base (Boss et al., 1958), however, both Oligocene and Miocene rock units are unknown from the San Diego Basin proper. Finally, Wilson (1972, p. 119) suggested that one of the main factors controlling the boundaries between the predominantly marine (Santiago B, Torrey, Delmar) and non-marine (Santiago C) facies was a prominent east-west sub-Lusardi (possibly sub-La Jolla) topographic high. This boundary between the depositional regimes occupied the position where the Santiago Peak volcanic mass, the Point Loma and Lusardi Formations, and the Green Valley Tonalite jut out north of Canyon de las Encinas. It appears to have served as a barrier to deposition from the middle through the upper Eocene. North of the barrier, deposition of the Santiago (A, B, and C) took place in middle through upper Eocene. South and southwest of the barrier, the Torrey and Santiago B sandstones, and the Delmar and Santiago B mudstones were laid down.

Within the San Luis Rey and Encinitas quadrangles Wilson (1972) divided the Santiago Formation
into three characteristic members. Members A and B represent brackish water lagoonal and nearshore-shelf environments of deposition, respectively. The uppermost member (C) recognized by Wilson corresponds well with vertebrate locality V-72088 near Camp Onofre. Because of the sedimentological correspondence, presumed age relations, and stratigraphic relations (see Figure 14) locality V-72088 is here referred to the Santiago Formation, Member C of Wilson (1972).

Faunal evidence from Wilson's Member A led him to conclude that there was an age correlation with the upper parts of the Delmar Formation and Torrey Sandstone as well as the Ardath Shale of the San Diego sequence and the marine sandstone portion of the type Santiago Formation in the Santa Ana Mountains. The major portion of Member B was correlated with the Scripps Formation, however, an upper tongue of Member B was considered correlative with the Mission Valley Formation. Member B was considered by Wilson (1972) to be the lithologic and age equivalent of the Friars Formation and correlative with the upper nonmarine
Figure 14. Correlation of Eocene sedimentary formations between the San Diego coastal area and the Santa Ana Mountains. After Wilson (1972).
facies of Yerkes and others (1965) and English (1926) in the Santa Ana Mountains.

Since the upper part of the Mission Valley Formation (to which Santiago Formation Member B was correlated) is time equivalent to the upper Eocene Pomerado Conglomerate of Peterson and Kennedy (1974), a significant portion of Wilson's Member B (and therefore Member C) may be significantly younger than perceived by Wilson. Following this line of reasoning, correlation of Santiago Members B and C, at least in part, with the upper Eocene Pomerado Conglomerate and Miramar Sandstone Member may be a distinct possibility. Such a conclusion would not go against Lillegraven and Wilson (1975) in that the mammalian fauna at V-72088 may be somewhat younger than at the localities from San Diego. I do not believe that the Uintan lizard fauna of San Diego and V-72088 shed any light on this problem for reasons mentioned earlier.
Regional Depositional Patterns

In the later Eocene the San Diego region marked the westward termination of a major river valley called the Ballena Channel by Minch (1970, 1972). The local Ballena and Las Palmas gravels represent one of two major suites of middle to late Eocene channel deposits found on the "old erosion surface" of the Penninsular Ranges of Baja California and southern California. The Table Mountain and El Rodeo gravels represent the Second Suite of channel deposits. Minch (1972) estimated that the source elevation of the channel system could have been 4,000 m. (roughly 12,000 ft.) in the later Eocene.

Peaks in the probable source area today range from 2,000 to 3,000 m. while valleys range from 1,000 to 2,000 m. Using these figures as a possible minimum for the Eocene, Minch (1972) determined that a gradient of 5 to 10 m./km. would be possible but that the gradients near the western end of the present erosion surfaces may have been as low as 2 to 5 m./km. The major part of the load of such a river, which
included the "Poway type" clasts, would be transported only during flood periods.

The San Diego area gravels of the later Eocene conglomerate lithosome (Stadium Conglomerate and most of the Pomerado Conglomerate) are considered to be dominantly nonmarine delta or fan-delta with sandstone lenses representing marginal marine to fluvial sand bars (Peterson, 1971; Peterson and Kennedy, 1974). The western portion of the Mission Valley Formation is marine, while the eastern portion is nonmarine. Kennedy and Moore (1971) considered the Mission Valley Formation to represent a nearshore shelf environment of deposition. It is more likely that the Mission Valley Formation represents a complex of nearshore marine, marine embayments, coastal floodplain and occasional minor channel depositional environments. The Friars Formation sands which lie under and interdigitate with the Stadium Conglomerate were considered "lagoonal" by Kennedy and Moore (1971), but based on its vertebrate fauna and local channels might more properly be considered fluvial dominated and "lagoonal" only in regard to its physiographic aspect.
A hypothetical panorama of later Eocene San Diego area depositional environments would therefore include low gradient, but periodically violent, westward-flowing river systems crossing low lying terrain to the east (Peterson and Kennedy, 1974). The river systems fed locally-derived fine material (Peterson, 1971) and exotic "Poway type" clasts into a dominantly nonmarine conglomeratic delta complex and coastal plain bordering nearshore shelf, estuarine, and lagoonal conditions to the west. Intertonguing of the sandstone and conglomerate lithosomes in the upper part of the section was probably due to a combination of changes in rate of sediment influx and changes in rates of submergence according to Peterson (1971).

In the Oceanside region such a panorama has also been developed by Wilson (1972). His picture (Figure 13) for middle and later Eocene time includes San Diego marine facies which may be traced south as a sequence including the Torrey barrier bar flanked on the east by the Delmar Formation "lagoon," and on the west by the marine silts and clays of the Ardath.
Shale. In the south the Delmar Formation was deposited as fossiliferous muds in brackish water which lapped onto the basement complex. The Torrey barrier complex was diluted by nearshore sands of Member B of the Santiago Formation in the north and offshore. Brackish to fresh water, restricted lagoonal muds of Member A of the Santiago Formation were deposited near dominantly nonmarine Santiago C sands in the north. Santiago B marine sands were deposited west of other units around the east-west topographic high and continued offshore to the southwest.

The San Diego and Oceanside area vertebrate fauna has been recovered from a nearshore environment not represented by other known North American later Eocene vertebrate faunas (Lillegraven, 1973) and may thus explain some of the apparent endemism of the fauna. Although the San Diego lizard fauna is distinct, it does not indicate extraordinary isolation from other known Paleogene lizard faunas. Of the 13 lizards and related forms known from the San Diego Eogene, seven (or questionably eight)
species are probably generically equivalent to forms known from the Eocene and Oligocene lower vertebrate faunas of the Rocky Mountain region. At the species level, three from San Diego are referable (two questionably) to other known Eocene lizard faunas.

**Paleoclimate**

The Eocene palinspastic reconstruction of Smith and others (1973) did not utilize data taken from west of the San Andreas Fault system but showed the Gulf of California in its present configuration. Right lateral displacement across the San Andreas fault system was not considered in the reconstruction of Smith and others (1973). Minch (1972) suggested that the peninsula of Baja California has moved 365 km. northwestward from the mainland of Mexico since the early Tertiary. Removing 365 km. of displacement parallel to the major San Andreas lineament could account for about 2-1/2° of latitude. Subtracting this difference from the postulated Eocene latitude of San Diego by Smith and others (1973) leaves a corrected Eocene latitude for San Diego at about 32°
to 33° North, almost exactly the same latitude that San Diego now occupies.

Major climatic deteriorations in the middle latitudes following the Cretaceous and early in the Oligocene were described by Wolf and Hopkins (1967). Wolf (1971) recognized major climatic fluctuations in the latter half of the Eocene which was, however, the most equable epoch within the Tertiary. Major "turnovers" in the mammalian fauna have been reported from the Late Cretaceous, Eocene through early Oligocene, and early Miocene (Lillegraven, 1972). Doerner (1969) and Hornaday (1965) postulated a Paleogene climatic deterioration at the Ulatisian-Narizian provincial stage boundary within the Santa Barbara Embayment which they correlated with the middle-upper Eocene transition. Based on data from planktonic foraminifera, Steineck (1971) described a marine climatic change from warm-temperate to temperate and correlated this event as well as the one reported by Doerner (1969) and Hornaday (1965) with the lower-middle Eocene boundary as defined by Steineck and Gibson (1971). A similar study by Steineck and
Jervey (1971) also lends support to the concept of a bipolar middle Eocene cooling interval.

It is quite clear from the summary above that when discussing climate during the Paleogene, or Eocene for that matter, one must carefully delimit the time interval being considered.

The middle Eocene coastal plain which drained into the San Diego Embayment was characterized by a climate comparable to modern monsoonal forests tending toward tropical savanna woodland-type plant assemblages, with no grass (Lowe, 1974). Vegetation was sparse in interchannel areas and was concentrated in river valleys and along coastal lagoons. A savanna woodland and mixed savanna-monsoon forest vegetated the coastal mountains and surrounding plain, respectively. The average annual temperature was near 20° C (less than 6° C between warmest and coldest months); the annual precipitation averaged 140 cm. (60 inches) falling mostly in the summer with a comparatively dry winter (Lowe, 1974). The coastal San Diego region then represented a "subtropical"
fairly wet and warm climate during Ardath Shale time based on its flora.

An analysis of pollen from the Mission Valley Formation (Carr, 1975) indicates a possible drying trend toward seasonally dry climates and an implication that streams were also becoming seasonally dry.

Analysis of Eocene caliches within the Mission Valley Formation led Pierce (1974) to suggest that a tropical wet and dry climate (resulting in a savanna) best described conditions prevailing during deposition of the Mission Valley Formation. Pierce concluded that if a tropical wet and dry climate existed during the later Eocene in the San Diego area, it would explain the occurrence of mammalian (and other vertebrate) fossils within the caliches. He continued (p. 77):

The animals apparently lived in a river valley or flood plain. During the wet season, material was washed down from locally derived volcanics and granitoid rocks. During the droughts, caliche formed from capillary action in the soils. During the next rainy season, more material was added, covering the previous caliches. This cycle would repeat itself again and again, thus preserving the layered and nodular caliches.
Novacek (1973) also postulated a savanna-type environment to help explain the diversity of the San Diego later Eocene mammalian fauna.

The presence of a trionychid turtle, the other turtle, crocodilians, and possibly the amphibians within the San Diego area later Eocene sediments indicate that free water was available throughout the year. Even if the streams were becoming more and more seasonally dry during later Eocene time in San Diego, faunally important "pools" remained present throughout in the dry season and were most likely situated within the comparatively thickly vegetated river valleys. The large boid and crocodilians probably indicate a lack of seasonally cold conditions. Incidentally, the large size of the local boid is documented by vertebrae as well as by LACM 1723, which includes the postdentary portion of a mandible 39 mm. long as preserved.

In my opinion, attempts to indicate the ecological preferences or climatic implications of the later Eocene lizard fauna would be little more than guesswork.
In summary, the paleoclimate of Paleogene San Diego may have changed from a humid tropical climate with monsoonal forest-like vegetation to a semi-arid climate (in the broad sense) accompanied by savanna or steppe-type vegetational cover during the later Eocene. Peterson and others (1975) suggest that this climatic change to generally drier conditions may represent the same event that Frakes and Kemp (1972) reported as taking place within the Oligocene.
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ABSTRACT

Eocene nonmarine and marginal marine formations located in western San Diego County, California, have yielded a diverse lower vertebrate fauna. Fossil lizards made up a significant portion of the fauna at many localities.

Dentary fragments of a gekkonid are questionably referred to the family Gekkonidae. Three iguanids have been identified. *Parasauromalus olseni* is represented by jaw fragments and teeth. It was previously known only from the Wasatchian and Bridgerian of Wyoming. A second iguanid has a well developed coronoid lappet, a large splenial, 30 to 32 tricuspid dentary teeth, and a Meckelian groove that is closed for a space but opens anteriorly. A third iguanid has 25 to 28 tricuspid dentary teeth and Meckel's groove is closed and fused. The agamid *Tinosaurus cf. T. stenodon* is represented only by teeth. Two new species of the extinct xantusiid *Palaeoxantusia* are represented, one by a nearly
complete skull and associated mandibles, the other by dentary fragments. The new genus *Paracontogenys* is questionably referred to the Scincidae because of its resemblance to the Cretaceous and Paleocene genus *Contogenys*. *Pancelosaurus* sp. and an unidentified form are referred to the anguid subfamily Anguinae. At least one member of the subfamily Glyptosaurinae is present. An extinct varanid, *Saniwa brooksi*, is known from a few vertebrae and dentary fragments. A generically undetermined member of the amphisbaenian subfamily Rhineuridae is also present.

The San Diego mammalian fauna has been considered to suggest an early Uintan North American land mammal age. The San Diego Eocene lizard fauna is somewhat advanced over typical Bridgerian faunas and therefore also suggests an early Uintan age.

In the San Diego area gravels of the later Eocene conglomerate lithosome are considered dominantly nonmarine deltaic with fluvial developed sand bars. The coastal region of San Deigo marked the western termination of the later Eocene Ballena Channel. Much of the river load, including the "Poway
type" clasts, would have been transported only during flood periods. Crocodilians, trionychid turtles and possibly the frog remains indicate that free water was available throughout the year.

The Mission Valley Formation probably represented a complex of nearshore marine, marine embayments, coastal floodplain and occasional minor channel depositional environments. Although the Friars Formation has been considered "lagoonal" its vertebrate fauna and local channeling indicate fluvial domination of the depositional environment.