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Lizard Caudal Vertebrae

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The caudal vertebral column in most lizards exhibits linear differentiation with regard to the presence or number, shape, size, and orientation of the transverse processes and their positional relationship to the autotomic planes of fracture. Individual caudal vertebrae may bear one or two pairs of transverse processes or may lack them. The plane of fracture may pass in front of, through, or behind the processes when one pair is present, and passes between the anterior and posterior pairs when two are present. A single pair of processes may be oriented anterolaterally, laterally, or posterolaterally, and paired processes may converge or diverge distally. Sequential change in the caudal vertebrae from sacrum to tail tip is gradual and involves relatively slight modifications in some lizards, but is more often abrupt, takes place within the space of two or three vertebrae, and involves relatively major changes such as the loss or doubling of processes.

The primitive type of lizard caudal vertebra is probably one which bears a single pair of processes located anterior to a plane of fracture. A shift of the plane of fracture to split or pass in front of the processes, the loss of the plane of fracture, the doubling of transverse processes and their subsequent divergence or convergence, and the loss of transverse processes are specializations. All of these specializations have probably arisen more than once in lizards.

The differences observed between genera, generic groups, and families appear not to be correlated with the general form and function of the tail, but follow rather closely along taxonomic lines. The four types of caudal sequences found in lizards of the family Iguanidae are closely correlated with generic groups that have been established on the basis of other anatomical characters.

INTRODUCTION

LIZARD tails exhibit remarkable diversity in their general form and function. The tail may serve as a balancing, prehensile, or swimming organ, in serpentine locomotion, for fat storage, defense, escape, or in territorial or courtship display. Tails vary in proportional length and thickness, in cross-sectional shape, ornamentation and fragility, and in structural details of skeletal support. The functional significance of some structural features is obvious, such as the extremely long neural spines of the caudal vertebrae in *Basiliscus* and *Hydrosaurus*, but they are of so limited and scattered occurrence as to be of little taxonomic or phylogenetic import. On the other hand, the position of the haemal arches and whether or not they are fused to the centra are of questionable functional significance, but are of broad taxonomic interest (McDowell and Bogert, 1954; Camp, 1923).

An important character which is subject to variation in lizards is the linear differentiation of the caudal vertebral column. Primarily involved are differences in the sequential change from sacrum to tail tip in the presence or number and orientation of the transverse processes, and their positional relationship to the plane of fracture when autotomic ability is present. The differences observed between genera, generic groups, and families appear not to be correlated with the general form and function of the

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tail, but follow rather closely along taxonomic lines. My purpose here is to draw attention to the possible use of caudal vertebrae as a taxonomic character by presenting descriptions of the caudal sequences in a number of lizard families, discussing the possible evolution of various types of caudal vertebrae and their sequential arrangements, and, by way of example, applying some of these findings to the family for which the most information is available, the Iguanidae.[1]

Descriptions of caudal vertebrae of lizards are to be found mostly in accounts of individual species (Cope, 1892; Beddard, 1905; Woodland, 1920; Reece, 1923; El Toubi, 1938; Barrows and Smith, 1947; Pratt, 1946; Iyer, 1942; Sibtain, 1938; Ali, 1948, 1949, 1950; El Toubi and Khalil, 1950; Islam, 1956; Furieri, 1956; Quattrini, 1952a, 1952b, 1953, 1954; Ganguly and Mitra, 1958; Holder, 1960; Kluge, 1962; Savage, 1963; Werner, 1965; Etheridge, 1960, 1964a, 1964b, 1965, 1966a, 1966b). There is also a large body of information on the subject of caudal autotomy and tail regeneration in lizards (see citations under Autotomy). It is apparently because of the limited taxonomic scope of these studies that the potential taxonomic value of the caudal sequence has not been recognized.

MATERIALS AND METHODS

The descriptions that follow are based on dry skeletons and radiographs of 211 genera and 682 species representing 19 families of lizards (see Material Examined[2]). Most iguanid species are represented by series of from 10 to over 100 individuals, and series of at least some species were examined in most other families. Low-voltage radiography proved to be a valuable technique, overcoming the difficulty of obtaining complete, intact tail skeletons, especially from lizards capable of caudal autotomy. Low-voltage, or "soft" x-rays are probably best known for their application in industry and medical research, where a high degree of contrast is necessary for the inspection of low absorptive materials. "Soft" x-rays are obtained by delivering a high ma rating at low kilovoltages. A beryllium window tube rather than the

usual pyrex envelope provides the lowest possible inherent filtration. Several instruments were used, the most satisfactory of which was a Balteau Electric Corporation's Baltograph Model 5-50 capable of delivering from 0 to 20 ma throughout a range of 5–50 kv. Kodalith Ortho Type 3 film gave the highest resolution and strongest contrast, but required exposure times of from 5 to 12 min. Kodak Type M industrial x-ray film proved to be satisfactory for most animals, and required much shorter exposure times, from 45 to 90 sec. Most exposures were taken at 5 ma between 15 and 30 kv. Examination of radiographs was best done directly from developed negatives illuminated by a light table under a dissecting microscope.

Dry skeletons were prepared from dry carcasses by dermestid beetles. These were most useful for determining the exact structure of each type of vertebrae, but due to the extreme difficulty of preparing complete, intact tail skeletons the radiographs were more useful in studies of the sequence of vertebral types. Neither dry skeletons nor radiographs are satisfactory for the examination of lizards with heavy osteoderms. Cleared specimens stained with Alizarin might be useful here but were not used in this study.

RESULTS

Six common types of lizard caudal vertebrae are illustrated in Fig. 1. In most lizards all of the caudal vertebrae bear a single pair of transverse processes. The plane of fracture, when present, may pass posterior to (Fig. 1A), through (Fig. 1E), or anterior to (Fig. 1F) the transverse processes. These vertebrae may be conveniently referred to as "single-process" vertebrae. In some lizards the transverse processes of the caudal vertebrae are doubled, and the plane of fracture, when present, passes between the two pairs of processes. The paired processes may diverge distally (Fig. 1C), a type which may be referred to as "diverging-process" vertebrae, or converge distally (Fig. 1D), which may be referred to as "converging-process" vertebrae. The caudal vertebrae of some lizards lack transverse processes entirely (Fig. 1B), and may be referred to as "no-process" vertebrae.

The caudal vertebrae usually undergo serial modification from sacrum to tail tip. The sequential change is gradual and involves relatively slight modifications in some lizards, but is more often abrupt, takes place

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[1] As used in this work, the term "caudal vertebrae" refers to all vertebrae posterior to the sacrum.

[2] Studies of amphisbaenid caudal vertebrae, not covered in this work, are now in progress by Dr. Carl Gans.
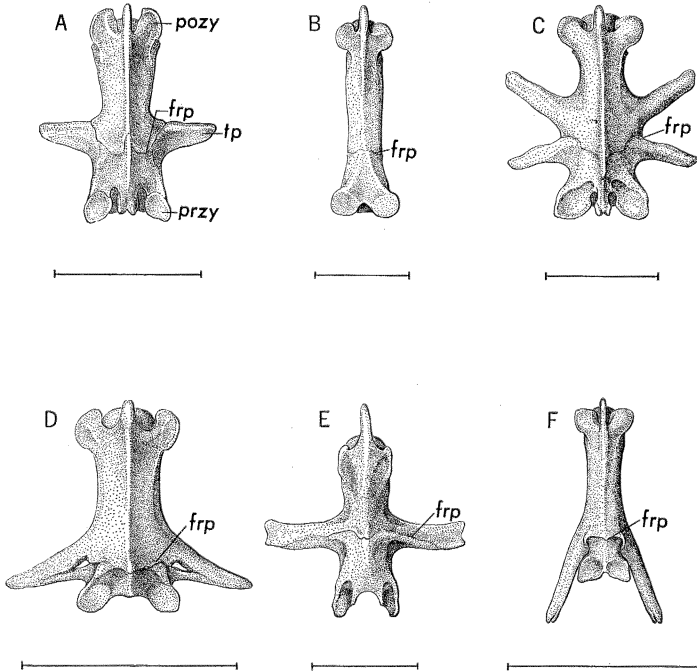
Fig. 1. Six common types of lizard caudal vertebrae in dorsal view as represented by A, *Sceloporus magister*; B, *Basiliscus vittatus*; C, *Dipsosaurus dorsalis*; D, *Ophisaurus ventralis*; E, *Eumeces fasciatus*; and F, *Anolis sagrei*. Horizontal lines equal 0.5 cm. (frp, fracture plane; pozy, postzygapophysis; przy, prezygapophysis; tp, transverse process.)

within the space of two or three vertebrae, and involves relatively major changes. Slight and gradual changes are usually associated with lizards that lack planes of fracture; major and abrupt changes with lizards that have fracture planes. The first few caudal vertebrae are similar in all lizards. They bear a single pair of transverse processes and lack planes of fracture. The remaining vertebrae may be similar to these, or different but all alike, or radical changes may occur within the tail, the column passing through several vertebral types.

Gekkonidae and Pygopodidae

(Fig. 2A). The pre-autotomic series are similar in all geckos. The first few post-sacral vertebrae bear long, slender, posterolaterally oriented processes. These are followed by one or two vertebrae bearing somewhat shorter processes, strongly curved in a posterior direction. There are from three to seven vertebrae in the anterior non-autotomic series; the usual number is five. In most geckos all remaining vertebrae are autotomic, the plane of fracture passing immediately behind the processes. The processes of these vertebrae are usually very long and slender, and oriented in a posterolateral direction; in some they are directed anterolaterally. A slender, vertical, secondary neural spine usually straddles the septum and is most prominent on the more anterior autotomic vertebrae. In some gekkonid genera (*Diplodactylus*, *Gymnodactylus*, *Lucasius*, *Cnemaspis*, and *Uroplatus*) transverse processes are absent from all but the first autotomic vertebrae. According to Werner (1965) all autotomic vertebrae of *Alsophylax blanfordii* lack transverse processes. In *Lucasius*, *Cnemaspis*, *Uroplatus*, and *Nephrurus laevis*, and according to Werner (1965), in *Stenodactylus stenodactylus* and *Ceramodactylus doriae*, the autotomy septa are restricted to two or three vertebrae immediately following the anterior non-autotomic series. According to Holder (1960) autotomy septa are absent in *Nephrurus asper*. The total number of caudal vertebrae varies from 18 to 35, though the usual number is about 25.
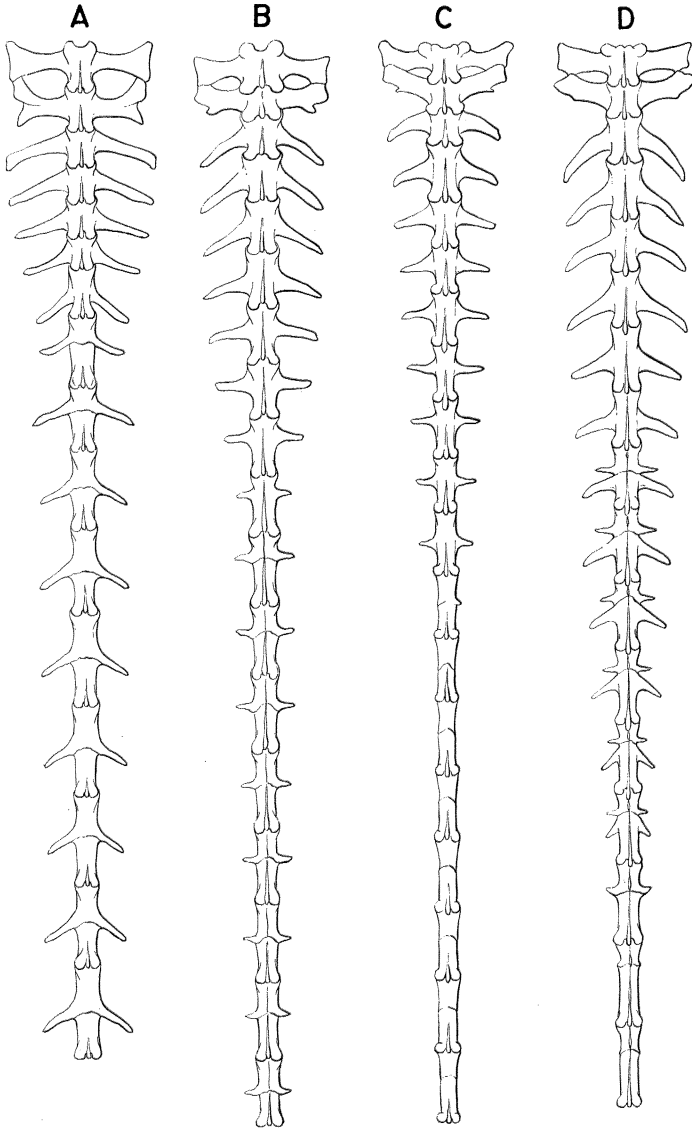
Fig. 2. Sacral and anterior caudal vertebrae in dorsal view of A, *Gekko gekko*; B, *Sceloporus magister*; C, *Basiliscus vittatus*; and D, *Dipsosaurus dorsalis*. Remaining vertebrae in each column are similar to the most posterior vertebra illustrated.

The caudal vertebrae of pygopodids differ from geckos in several minor features. There are five or six anterior non-autotomic caudals, all of which bear straight, flat, postero-laterally oriented processes. Short, flat, laterally oriented processes are present on all autotomic vertebrae, which continue to the end of the tail. The autotomy septa are located just behind the processes, as in geckos. There are 119 caudal vertebrae in a complete tail of *Delma fraseri*, the only pygopodid with a complete tail examined.

Dibamidae and Anelytropsidae

Miller (1966) recently stated that these two families are identical in their cochlear duct structure. The possibility that they are closely allied is also indicated by their vertebral structure. Their caudal vertebrae are very similar in structure and arrangement.

In both families the first two caudal vertebrae each bear a pair of terminally bifurcated processes. In *Dibamus* these are short and stout: in *Anelytropsis* long and slender. These processes arise well forward on the vertebrae, just below and behind the bases of the prezygapophyses. The remaining nonautotomic, as well as all of the autotomic vertebrae each bear a single pair of long, slender, pointed, anterolaterally oriented processes which also arise far forward on the vertebrae. The autotomic septa in both families pass just in front of the bases of the processes, so that each vertebra is divided into a very short anterior segment and a proportionally much longer posterior segment.

Well developed accessory processes extend out from under the articular surfaces of the prezygapophyses of all body vertebrae and the more anterior caudal vertebrae. Structurally and topographically these processes are very similar to the accessory processes of snake vertebrae. I know of no other lizard family in which these accessory processes are present.

About 19 vertebrae are present in the complete tail of *Dibamus argenteus*, the only species examined. The first seven caudal vertebrae are non-autotomic. I have not examined a complete tail of *Anelytropsis*. The longest tail contained 25 vertebrae, and was regenerated beyond that. The first five caudal vertebrae are non-autotomic.

Xantusiidae

(Fig. 3B). The first five or six vertebrae are non-autotomic, each with a single pair of posterolaterally oriented processes which, anterior to posterior, become gradually shorter. The remaining vertebrae are autotomic in all forms examined. The anterior autotomic vertebrae may bear a single pair of processes through which passes the plane of fracture. The anterior and posterior components of the processes then gradually diverge. The anterior components are usually short and slender, the posterior components long and spatulate or rounded. The posterior components become smaller and finally disappear, leaving a single pair of short, pointed processes anterior to the plane of fracture. These remaining processes then also become shorter and finally disappear, leaving the terminal series of vertebrae without processes. This sequence occurs in some

individuals of *Xantusia henshawi*, *X. vigilis*, *Lepidophyma flavimaculata*, *L. gaigeae*, *Klauberina riversiana*, and *Cricosaura typica*. In other individuals of these species and in the single individual of *Xantusia arizonae* examined the anterior non-autotomic series is followed immediately by vertebrae with one pair of processes anterior to the plane of fracture. Reduction and loss of the posterior components of the vertebrae with diverging processes may be accomplished in the space of two or three vertebrae, or may require as many as ten. The single processes may also disappear quickly, or their disappearance may require as many as fifteen vertebrae. The complete tail of all xantusiids contains about 35 vertebrae, of which the first five or six are non-autotomic.

Iguanidae

Four general types of caudal sequences occur in the family. Most iguanid genera have a more or less uniform sequence of vertebrae, each with a single pair of transverse processes (Fig. 2B). The processes of the anterior non-autotomic vertebrae are long and slender, blade-like and posterolaterally oriented. There is an abrupt reduction in size and change in orientation—posterolateral to lateral—of the processes a short distance behind the sacrum. The alteration is accomplished in the space of two or three vertebrae, and usually involves vertebrae between the fifth and fifteenth, counting back from the sacrum. The processes of all remaining vertebrae may also be laterally directed or there may be a gradual alteration of orientation to anterolateral. Processes may be absent from the last few vertebrae of the tail. In this type of sequence the autotomic septa, when they occur, are located just behind the bases of the processes of all vertebrae posterior to the region of abrupt change of orientation and reduction in size of the processes. Autotomy occurs in most iguanid genera with this type of sequence: *Callisaurus*, *Chalarodon*, *Ctenoblepharis*, *Crotaphytus (Gambelia)*, *Cupriguanus*, *Holbrookia*, *Leiocephalus*, *Liolaemus*, *Morunasaurus*, *Ophryoessoides*, *Oplurus*, *Petrosaurus*, *Phrynosaura*, *Phymaturus*, *Platynota*, *Plica*, *Proctotretus*, *Sator*, *Sceloporus*, *Stenocercus*, *Strobilurus*, *Tropidurus*, *Uma*, *Urosaurus*, and *Uta*. A completely non-autotomic sequence of this type occurs in *Crotaphytus*
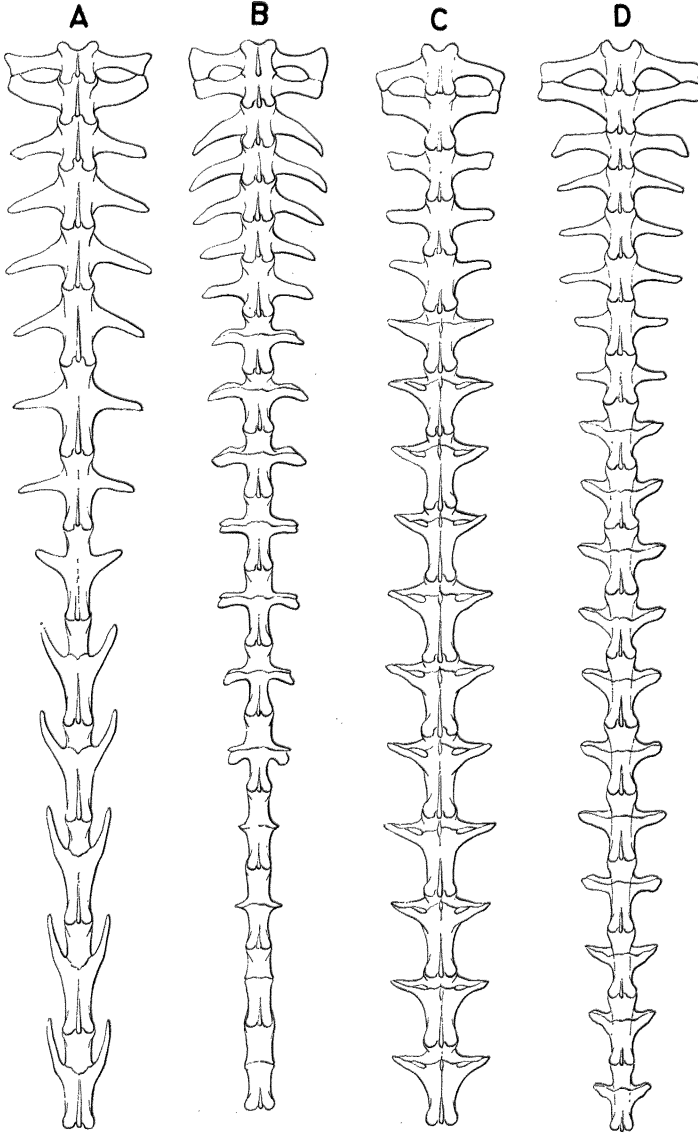
Fig. 3. Sacral and anterior caudal vertebrae in dorsal view of A, *Anolis sagrei*; B, *Xantusia vigilis*; C, *Ophisaurus ventralis*; and D, *Eumeces fasciatus*. Remaining vertebrae in each column are similar to the most posterior vertebra illustrated.

(*Crotaphytus*), *Hoplocercus, Leiosaurus, Phrynosoma,* and *Urocentron.*

Short-tailed genera in the above group usually have fewer caudal vertebrae than long-tailed forms, but this is not always true. In some forms elongation of the tail is effected by elongation, rather than increase in the number of the vertebrae. The minimum number is found in *Hoplocercus,* which has 16; the maximum in *Plica,* which has about

60. In those forms with autotomic vertebrae, the anterior non-autotomic vertebrae never number more than one-quarter of the total caudal vertebrae.

The second type of caudal sequence found in the Iguanidae is a short anterior series of non-autotomic vertebrae with a single pair of processes followed by a very long series of vertebrae without processes which may or may not be autotomic (Fig. 2C). At the be-

ginning of the caudal sequence the processes are long and oriented posterolaterally. There is a rapid reduction in size and change in direction (to lateral), after which the processes abruptly disappear. This series may contain from 5 to 15 vertebrae, but contains less than one-quarter of the total vertebrae present in a complete tail. Autotomic vertebrae, when present, include all of those in the series which lack processes, and occasionally the last of the single-process series as well. This sequence occurs in some species of *Anolis*, and in all species of *Corythophanes, Phenacosaurus, Chamaeleolis, Basiliscus, Laemanctus, Enyalius, Enyalioides, Polychrus, Polychroides, Urostrophus,* and *Uranoscodon.* If the terminal single-process vertebra is autotomic in *Anolis*, the septum passes in front of the processes; in *Basiliscus, Enyalioides,* and *Uranoscodon* it passes behind the processes. Autotomy and autotomy septa are absent in *Phenacosaurus, Chamaeleolis, Corythophanes, Laemanctus, Enyalius, Polychrus, Polychroides, Urostrophus,* and in some species of *Anolis* with this type of sequence. Ontogenetic restriction, but not complete loss, of autotomy occurs in *Basiliscus, Uranoscodon,* and *Enyalioides* (see discussion under Autotomy).

The total number of caudal vertebrae lies between 40 and 50 in most lizards with this type of sequence. There is a maximum of 87 in *Polychrus* and a minimum of 35 in some species of *Anolis*. There are usually fewer (5–10) single-process vertebrae in the forms with autotomy than in those without autotomy (8–15).

Two iguanid genera, although listed as having the first type of sequence, appear to be somewhat intermediate between the first and second types. There are about 60 caudal vertebrae in *Plica*. The first 15 bear single processes but autotomy begins some distance (eight vertebrae) before the processes are lost. The caudal vertebrae of *Leiosaurus* are non-autotomic. About 35 vertebrae are present in a complete tail. The anterior 17 or 18 (about half) bear processes; the remaining vertebrae do not.

The third type of sequence is found only in some species of *Anolis* and in the related genera *Tropidodactylus, Chamaelinorops, Anisolepis,* and *Aptycholaemus* (Fig. 3A). All of the caudal vertebrae are single-process but differ from those of the first iguanid type in several respects. The sequence begins with the usual short series of non-autotomic vertebrae having long, posterolaterally oriented processes. Following these there is an abrupt change in orientation of the processes—to lateral then acutely anterolateral—after which the vertebrae continue to the end of the tail with very little change other than a slight reduction in the length of the processes. The anterolaterally oriented processes are unusual in being terminally bifurcate in the vertical plane. Autotomy, when present, begins at the position of change in process orientation. The planes of fracture pass anterior to the bases of the processes. (Note: in the first iguanid type the fracture planes are posterior to the processes.) Autotomy is present in all species of *Anolis* with this sequence, and in *Tropidodactylus.* Autotomy and autotomy septa are lacking in *Chamaelinorops, Anisolepis,* and *Aptycholaemus.*

The final type of iguanid caudal sequence contains four different vertebral types (Fig. 2D). From the sacrum back these are: 1) vertebrae bearing a single pair of long posterolaterally oriented processes, followed by 2) vertebrae with two pairs of processes, a short anterior pair oriented anterolaterally and a longer posterior pair oriented posterolaterally, followed by 3) vertebrae with one pair of processes, usually the anterior pair of the preceding series, followed by 4) vertebrae with no processes. The single processes of the first series become shorter and more nearly lateral in direction. The double processes become shorter and their bases move slightly apart. Following the loss of one pair of processes from the double process vertebrae, the remaining pair become shorter and eventually disappear, leaving the fourth and terminal series of vertebrae which lack processes. The double nature of the processes of the second series is often anticipated in the more posterior vertebrae of the first series by incomplete or asymmetrical separation of their single processes.

An autotomic sequence of this type is found in *Iguana iguana, Ctenosaura, Cyclura, Enyaliosaurus, Sauromalus,* and *Dipsosaurus.* In these forms the planes of fracture pass between the processes of the second series, and in front of or behind the single processes of the third series depending on whether the anterior or posterior pair of the second series has been lost. Planes of fracture are also present in the terminal no-process series.

The fourth type of iguanid sequence is also found in *Iguana delicatissima, Conolophus, Amblyrhynchus,* and *Brachylophus,* but their tails are non-autotomic. The transitions between vertebral series are more gradual and unilateral anomalies more frequent in these forms which have lost autotomy. Vertebrae with two pairs of processes (the second series) show a wide range of variation in these forms. The two pairs are short, nearly lateral, widely separated and often united distally in *Conolophus* and *Brachylophus.* They are divergent but united proximally in *Amblyrhynchus.*

The tail is shortest in *Sauromalus,* with about 35 vertebrae. There are about 50 caudal vertebrae in *Dipsosaurus, Enyaliosaurus, Conolophus, Amblyrhynchus,* and *Cyclura,* about 60 in *Brachylopus,* about 70 in *Ctenosaura,* and about 85 in *Iguana.*

Agamidae

The caudal sequence in all agamid lizards consists of an anterior series of vertebrae with a single pair of processes followed by a series of vertebrae which lack processes. The relative number of vertebrae in each series is variable. When the anterior single-process series is short, the transition from this to the no-process series is abrupt. When the anterior series is long, the transition takes place by gradual anterior to posterior reduction and eventual loss of processes. The anterior series is relatively short in most agamids, including all arboreal forms. The following average ratios of single-process to no-process vertebrae obtain in the species examined: *Lophura,* 15 : 70; *Calotes,* 12 : 49; *Physignathus,* 12 : 52; *Draco,* 10 : 50; *Agama,* 10 : 25; *Diporiphora,* 17 : 40; *Acanthosaura,* 11 : 29; *Otocryptis,* 8 : 25; *Aphaniotus,* 10 : 14; *Japalura,* 13 : 22; *Chlamydosaurus,* 17 : 25; and *Goniocephalus,* 11 : 29. The anterior series is relatively long in the following: *Amphibolorus,* 21 : 15; *Moloch,* 14 : 5; *Uromastix,* 25 : 9; and *Phrynocephalus,* 35 : 3.

Functional autotomy by way of fracture planes does not occur in agamids. Secondary neural spines are present in some *Agama,* rising vertically above the transverse processes. In some species of *Agama* the tail is fragile, but breakage is nearly always intervertebral, in which case regeneration is not extensive and does not involve the production of a calcified rod of cartilage as in normal regeneration following breakage of a fracture plane.

Chamaeleontidae

The caudal sequence in this family is similar to that found in the short-tailed agamids, except for a different change in orientation of the processes. The processes of the anterior caudal vertebrae are long and slender, posterolaterally oriented and pointed downward. The processes gradually decrease in length and change in orientation—to lateral and then to anterolateral—and from downward to horizontal. There are no autotomy septa and no secondary neural spines.

The following ratios of anterior single-process vertebrae to posterior no-process vertebrae obtain in the single examples examined: *Chamaeleo dilepis,* 45 : 4; *C. bitaeniatus,* 33 : 10; *C. jacksoni,* 40 : 7; *C. chamaeleon,* 50 : 8; *C. zeylanicus,* 60 : 2; and *Brookesia kersteni,* 21 : 2.

Teiidae

The caudal sequence in most teiid lizards is the complex type described above as the fourth iguanid sequence: a single-process series, followed by a diverging-process series, followed by a second single-process series, terminating in a no-process series. Two other types of sequence are of less common occurrence; one in which the second single-process series is lacking, and one in which both this and the diverging-process series are lacking. Autotomy occurs in all teiids examined. Autotomy septa are present in all vertebrae except the short anterior single-process series.

The anterior non-autotomic vertebrae bear long, slender posterolaterally oriented processes. In most teiids these are followed by a short series of diverging-process vertebrae with short, laterally oriented anterior processes and long posterolaterally oriented posterior processes. The plane of fracture passes between the two pairs of processes. The next series of vertebrae usually bear a single pair of processes, the anterior or posterior pair of the preceding series, depending upon which pair has been lost. In most of the smaller forms, *i.e.,* the microteiids, it is the posterior pair that is lost. The remaining processes then gradually change in orientation from lateral to posterolateral and become gradually shorter until they finally disappear, leaving a short terminal series of

no-process vertebrae. This sequence occurs in *Anadia, Placosoma, Proctoporus, Bachia, Gymnopthalmus, Tretioscincus, Argalia, Neusticurus, Heterodactylus, Euspondylus, Echinosaura,* and *Leposoma,* and in the larger genera *Callopistes* and *Tupinambis.* A similar sequence, differing only in that it is the anterior, rather than the posterior pair of processes that have been lost from the diverging-process vertebrae, occurs in *Cnemidophorus, Dracaena, Ameiva,* and *Kentropyx.*

The diverging-process series is absent in *Teius* and *Dicrodon.* In *Teius* the anterior non-autotomic series is thus followed immediately by autotomic vertebrae bearing a single pair of processes posterior to the plane of fracture. These processes are posterolaterally oriented, gradually become shorter and eventually disappear. The remaining vertebrae lack processes. In *Dicrodon,* all of the autotomic vertebrae lack processes.

Lacertidae

Two general types of caudal sequences occur with about equal frequency in this family. One sequence contains (anterior to posterior) single-process, diverging-process, single-process, and no-process series. In the second type of sequence the diverging-process series is absent, the anterior non-autotomic single-process series being followed immediately by autotomic single-process vertebrae, followed in turn by a terminal series of no-process vertebrae. Autotomy is present in all forms examined, and involves all vertebrae except the usual anterior series.

The four-part sequence occurs in *Lacerta, Psammodromus, Algyroides, Acanthodactylus,* and *Ophisops.* The anterior parts of the processes of diverging-process vertebrae are short and laterally directed. The posterior parts are long and blade-like, oriented posterolaterally. The posterior parts of the processes abruptly disappear, leaving a short series of single-process vertebrae with their processes anterior to the plane of fracture. The terminal vertebrae are without processes.

The three-part sequence, from which the diverging-process series is absent, has been found in *Tropidosaura, Ichnotropis, Eremias, Nucras, Holaspis, Scapteira,* and *Latastia.* Autotomic single-process vertebrae with short laterally directed processes anterior to the plane of fracture immediately follow the usual anterior non-autotomic single-process series. The processes of these vertebrae

gradually become shorter and finally disappear, leaving the terminal series without processes.

I have examined only single representatives of the lacertid genera mentioned above, and therefore, have no information concerning intraspecific or intergeneric variation. The family as a whole shows considerable variation in the total number of caudal vertebrae and the number of vertebrae allotted to each series.

Cordylidae (including Gerrhosauridae)

The caudal sequence shows considerable variation in this family. One general type of sequence is found in the zonures *Gerrhosaurus, Zonosaurus, Platysaurus, Zonurus,* and *Tetradactylus,* another type in *Cordylus,* and still another in *Chamaesaura.*

The caudal sequence of zonures consists of an anterior series of single-process vertebrae, followed by a series of diverging-process vertebrae, followed by a terminal series of no-process vertebrae. Vertebrae of the second and third series are autotomic, the plane of fracture passing between the two processes of the second series. The orientation and relative size of the two pairs of processes of the diverging-process vertebrae are variable and may alter within the series. In *Gerrhosaurus* and *Zonosaurus* the anterior processes of the first vertebra of the diverging-process series are short, pointed, and oriented anterolaterally; the posterior processes long and posterolaterally directed. The anterior processes rapidly increase in length (anterior to posterior) and change in orientation to lateral. This change is accompanied by a sudden decrease in length of the posterior processes and is accomplished within the space of three or four vertebrae. On all remaining vertebrae of this series (about 30–40) the anterior processes are longer than the posterior ones. The terminal no-process series in these genera contain an additional 30–40 vertebrae.

In *Platysaurus* and *Zonurus* the diverging-process vertebrae are relatively uniform. The anterior processes are short and anterolaterally oriented; the posterior processes long and posterolaterally oriented. The diverging-process series contains about 8–10 vertebrae in these genera, and the terminal no-process series contains an additional 15 vertebrae. The diverging-process series of *Tetradactylus* shows still a different pattern. The vertebrae are all alike, with long anterolaterally ori-

ented anterior processes and short laterally oriented posterior processes.

The caudal sequence in *Cordylus* is very similar to that found in skinks, consisting of a short anterior series of non-autotomic vertebrae followed by a long series of autotomic vertebrae which bear a single pair of processes split, but not separated by, the plane of fracture. The first few anterior non-autotomic vertebrae bear short, flat laterally oriented processes. There is a gradual change in direction of the processes to anterolateral within this series. The plane of fracture unequally divides the single processes of the autotomic vertebrae into a short narrow anterior part and a longer, wider posterior part. This series is usually followed by a short series of no-process vertebrae. A complete tail contains from 15 to 20 vertebrae.

The caudal sequence of *Chamaesaura* differs from all of the above types, and indeed appears to be unique. The tail is very long and contains over 80 vertebrae. There is first a series of about 15 non-autotomic vertebrae with laterally oriented, distally expanded processes. The shape and orientation of these processes remains essentially unchanged into the autotomic series, where they are split tip to tip by the transverse septa. These anterior autotomic vertebrae are of the skink type (Fig. 1E). As the column continues posteriorly a notch soon appears in the expanded distal part of each process. The notch continues to deepen, separating the single split processes into diverging anterior and posterior parts, until near the end of the tail the vertebrae are of the diverging-process type. Accompanying the structural changes is a very gradual reduction in the length of the processes until, near the seventy-fifth vertebrae the processes finally disappear.

Scincidae

Because of the obscuring effect of heavy osteoderms in this family, interpretation of radiographs has been difficult. Unfortunately, I have been able to check my interpretations with dry vertebrae in only a few forms. The descriptions which follow need to be verified by examination of dry vertebrae.

At first glance, the caudal sequence in most skinks appears to consist of a uniform series of vertebrae of which the first four to six are non-autotomic. On closer inspection one finds that the fracture plane passes through the transverse processes, unequally dividing them into a narrow anterior part and a wider posterior part (Fig. 3D). In some skinks the septum appears (in radiographs) to pass entirely in front of the processes, but inspection of dry vertebrae show them to be of the usual skink type described above. In a few skinks, however, the septum actually does pass entirely in front of the processes: *Brachypodus* and some species of *Acontias*, *Mabuya*, and *Emoia*. In *Chalcides*, *Ophiomorus*, and *Egernia depressa* the anterior and posterior parts of the processes are separated at their bases by a slight gap. The separation appears not to be as great as in the vertebrae of anguids (Fig. 1D), feyliniids, and anniellids. In *Egernia cunninghami* the posterior part of the processes is deeply bifurcate distally so that the unbroken vertebra resembles a diverging-process vertebra; the plane of fracture, however, passes anterior to the bifurcation.

When seen together (in an unfractured vertebra) the anterior and posterior parts of the processes appear to form a single, unbroken process. This process is directed laterally in *Eumeces*, *Chalcides*, *Leiolopisma*, *Mabuya*, *Tiliqua*, and *Tropidophorus*; anterolaterally in *Acontias*, *Brachypodus*, *Neoseps*, *Scelotes*, *Scincus*, *Sphenomorphus*, and *Tribolonotus*. Because of the high incidence of broken tails, I can offer little information on variation in the total number of caudal vertebrae. Most skinks appear to have between 30 and 40; a maximum of 56 was found in *Brachypodus* and a minimum of 22 in *Acontias*. Autotomy is present in all of the scincids examined except *Egernia depressa*.

Anguidae, Anniellidae, and Feyliniidae

Except for certain anguids the caudal sequence in these families consists of a short anterior series of single-process vertebrae followed by a long series of vertebrae with double, converging processes (Fig. 3C). The processes of the anterior series are usually short, slender, pointed, and more or less laterally oriented. The remaining vertebrae are relatively uniform in structure, showing only a gradual overall decrease in size toward the end of the tail. The anterior parts of the processes are short, slender, pointed, and laterally oriented. The posterior parts of the

processes are long, wide at their base but pointed distally, and oriented anterolaterally. The anterior and posterior parts of the processes are separated at their bases. Distally, the anterior pair intercept the anterior border of the posterior pair, where they fit into a shallow groove. When present, the plane of fracture passes vertically between the two parts of the processes.

The vertebrae with converging double processes described above are identical to those found in certain scincids (*Chalcides, Ophiomorus*) except that in the latter the separation of the bases of the processes is not as great. Two anguids, *Diploglossus monotropus* and *Sauresia sepsoides*, differ from most other members of the family in having skink type autotomic caudal vertebrae. The less typical scincid type found in *Brachypodus*, in which the plane of fracture passes entirely in front of the processes, is found in some species of *Celestus*.

Autotomy occurs in all of the forms examined with the exception of *Ophisaurus apodus* and *O. compressus*. No planes of fracture are present in these species and their tails do not appear to be fragile.

Helodermatidae, Xenosauridae, Lanthanotidae, and Varanidae

In these families all of the caudal vertebrae bear a single pair of processes and never have planes of fracture. The processes of the anterior vertebrae are long and flattened, and oriented posterolaterally. From anterior to posterior the processes become gradually shorter and change in orientation, first to lateral then anterolateral. The change in orientation of the processes to anterolateral is slight in *Heloderma, Lanthanotus*, and *Shinisaurus*. It is strong in *Varanus* and *Xenosaurus*. Autotomy planes of fracture do not occur in any lizards of these families.

There are from 60 to 110 caudal vertebrae in *Varanus*, from 30 to 40 in *Heloderma*. In the single individuals examined there are 69 caudal vertebrae in *Lanthanotus borneensis*, 43 in *Shinisaurus crocodilurus*, and 40 in *Xenosaurus grandis*. Data for *Shinisaurus* are from radiographs published by McDowell and Bogert (1954).

AUTOTOMY

Caudal autotomy in most lizards is facilitated by a plane of fracture that passes through the centrum and at least part of the neural arch. The plane of fracture is formed by a septum of cartilage or connective tissue that develops postembryonically, or at least late in embryonic development after ossification has taken place. Studies of autotomy in lizards have been concerned mostly with the structural mechanism, and with the regeneration of the tail that follows (Gegenbaur, 1862; Muller, 1863; Fraisse, 1885; Cope, 1892, 1900; Werner, 1896; Gadow, 1901, 1933; Hooker, 1912; Terni, 1920, 1922; Woodland, 1920; Slotopolsky, 1922; White, 1925, 1935; Korschelt, 1927; Barber, 1944; Pratt, 1946; Cagle, 1946; Fitch, 1954; Quattrini, 1952a, 1952b, 1954; Kamrin and Singer, 1955; Hughes and New, 1959; Roulet, 1959; Goss, 1961; Simpson, 1964; Moffat and Bellairs, 1964). Fracture planes like those in lizards also occur in *Sphenodon* and have been reported in the Jurassic rhynchocephalians *Homoeosaurus* and *Sapheosaurus* (Price, 1940), and regeneration of the tail following autotomy in *Sphenodon* has been studied by Boulenger (1888), Byerly (1925), Barbour and Stetson (1929), and Ali (1941). From the point of view of the present study, the works of these authors are of little value in deciding which of the various caudal vertebra types are primitive and which are advanced, and whether or not caudal autotomy itself is primitive in lizards. Certain aspects of autotomy which, I believe, are helpful in this regard are discussed below.

Caudal vertebrae with planes of fracture always begin some distance posterior to the sacrum. The hemipenes, slips of the pelvic musculature, and other important organs are accommodated in the base of the tail, supported by at least a short series of non-autotomic vertebrae. These always bear a single pair of transverse processes, usually oriented laterally or posterolaterally. Vertebrae in the immediate postsacral region are functionally more closely associated with the sacral and last few presacral vertebrae than with the remaining vertebrae of the tail. Holder (1960) has called them "pygals" in geckos where, as in most other lizards with autotomic tails, the anterior non-autotomic vertebrae are sharply distinct from the autotomic vertebrae, referred to by Holder as "postpygals." However, the distinction between pygals and postpygals cannot be made in dry skeletons or radiographs of many lizards, especially those which lack fracture planes. The beginning of the autotomic series is marked by the appearance of frac-

ture planes, and usually by an abrupt modification in the condition of the transverse processes. At this point the processes may alter in orientation, shape and size, a second pair of processes may appear, or processes may disappear altogether. In contrast, the transverse processes of most lizard groups that do not have autotomic vertebrae show little or no serial modification. Exceptions are found among iguanids and agamids with non-autotomic tails, and will be discussed later.

Planes of fracture, when present, are usually found in all vertebrae posterior to the first few non-autotomic vertebrae. Functional autotomy may, however, become ontogenetically restricted to a few vertebrae, or disappear entirely as a result of progressive replacement of the cartilaginous septum with bone. In such cases fusion begins at the top of the neural arch, and extends down through the centrum. A vertebra is no longer functionally autotomic when fusion has reached the level of the transverse processes; i.e., if sufficient pressure is exerted to break the tail, it will come about by intervertebral separation rather than by the fracture of a vertebra. When fusion is complete, strong pressure may cause the vertebra to fracture, but breakage will occur elsewhere than along the line of fusion. Fusion begins in the posterior region of the tail, progressing forward as the individual becomes older. The caudal sequence of a subadult contains vertebrae in all stages of fusion, the more anterior autotomic vertebrae showing the least amount. After the individual has reached adult size, a short series of functionally autotomic vertebrae may remain (e.g., Sauromalus) so that autotomic ability is restricted to a short segment near the base of the tail, or all of the autotomic vertebrae may become fused (e.g., Iguana iguana), leaving the tail entirely non-autotomic.

Extensive regeneration of the tail, including the production of a rod of calcified cartilage replacing the vertebral column, occurs normally after autotomy involving separation at the fracture plane. Regeneration following an intervertebral break is rare, and when it does occur the regenerated part is seldom more than a few mm long and lacks a calcified cartilaginous rod. Extensive regeneration, including the production of a cartilage rod, may, however, occur in lizards which do not possess fracture planes, pro-

viding the break actually involves trauma to a vertebra and not simple intervertebral separation. I have seen this type of regeneration in Brachylophus fasciatus and Agama agama, neither of which possesses planes of fracture. Even in the Crocodilia (Caiman crocodilus) regeneration may occur following actual breakage of a caudal vertebra (Dathe, 1960). Regeneration following the experimental cutting of the tail at sites other than the plane of fracture, either intervertebral or intravertebral, has been described by Woodland (1920), Slotopolsky (1922), and Moffat and Bellairs (1964).

According to Morgan (1901) caudal autotomy is a highly specialized protective mechanism on the part of the lizard, and is a result of adaptation to prevailing environmental conditions. This view is also held by Pratt (1946), who stated, "It is of interest that it does not occur in any species in which the tail possesses a definite and specialized function, such as swimming or grasping, since under these conditions it would prove to be a distinct disadvantage by causing mechanical instability." Woodland (1920) stated that caudal autotomy does not occur in lizards in which the tail has distinct use for purposes other than protection, and Boring et al. (1948) stated that "Those lizards which practise caudal autotomy are those whose tails are of no distinct use. . . ." These observations are clearly not in accord with the facts. For example, the powerful, compressed tail of Dracaena used in swimming, the prehensile tail of Abronia, the long serpentine tail which provides much of the locomotor power in some species of Ophisaurus, and the tails with large fat reservoirs must be considerable assets, yet all are capable of autotomy. It is apparent that the selective value of autotomic ability is very high, for within populations it is used frequently. In a population of Sceloporus olivaceous, 35.3% of adult females and 50% of adult males had lost their tails in nature (Blair, 1960). Boring et al. (1948) found 50% of 106 Takydromus septentrionalis and 33% of Gekko swinhonis collected for their studies had regenerated tails. My own studies of other species yield the following percentages of tail loss in adults: Uta stansburiana hesperis, 72% of 35 specimens; Sceloporus occidentalis, 45% of 53 specimens; Dipsosaurus dorsalis, 31% of 124 specimens; Sator grandaevus, 30% of 64 specimens.

Within most families of lizards planes of fracture are either universally present or absent, the most notable exception being the family Iguanidae. They are present in all species examined in the families Gekkonidae, Pygopodidae, Dibamidae, Anelytropsidae, Xantusiidae, Feyliniidae, Cordylidae (including Gerrhosauridae), Lacertidae, Teiidae, and Anniellidae. They are present in almost all species examined in the Anguidae and Scincidae. They are absent in all species examined in the families Agamidae, Chamaeleontidae, Xenosauridae, Helodermatidae, Varanidae, and Lanthanotidae.

The faculty of facile tail loss is present in some lizards that do not have fracture planes, for example in some species of *Agama*. Breakage is almost always intervertebral and is rarely followed by regeneration. This type of fragility apparently corresponds to that found in certain snakes and small mammals. Snakes of the colubrid subfamily Sibynophinae show a large percentage of individuals with mutilated tails (Taylor, 1954; Taylor and Elbel, 1958). Fragility of the tail is apparently characteristic of both New World (*Scaphiodontophis*) and Old World (*Sibynophis*) members of the subfamily. Taylor and Elbel (1958) suggested that autotomy is possibly a subfamily character of the Sibynophinae, and a primitive situation that harks back to some saurian ancestor of these snakes. I have examined the caudal vertebrae of these genera and find no evidence for the presence of autotomy septa. Breakage of the tail, although it occurs readily, is always intervertebral and never involves regeneration. In an unrelated snake genus, *Pliocercus*, the tail is also excessively fragile, and, as in the sibynophines, breakage is always intervertebral. In view of the absence of planes of fracture and the intervertebral mechanism by which autotomy is effected, it is much more likely that fragility of the tail in the snakes has been derived independently of the autotomic ability of lizards.

The question arises, then, as to whether autotomic ability by means of fracture planes is to be considered a specialized condition within lizards, that is, whether it has arisen a number of times within different phyletic lines, as Morgan (1901), Pratt (1946), and Wiener and Smith (1965) imply, or whether it is a primitive condition in lizards, having been lost independently in different phyletic lines. Autotomic ability through use of frac-

ture planes in lizards and rhyncocephalians involves not only the formation of autotomy septa, but also structural modifications of the muscles, connective tissue, and blood vessels (see especially Quattrini, 1952a, 1952b, 1953; Furieri, 1956; Boring *et al.*, 1948). That this complex mechanism has evolved independently in rhynchocephalians and in a number of groups of lizards seems unlikely. More probably, it had its evolutionary origin in pre-saurian times, possibly in some common eosuchian ancestor of both lizards and rhynchocephalians, and its absence in some modern lizards is the result of evolutionary loss. In view of its obvious selective advantage in a great variety of lizards, it would seem that if it were possible to regain fracture planes and all of the other anatomical modifications necessary for this type of autotomy that it would have re-evolved in many lizards whose ancestors had lost these specializations. This ought to be especially true, *e.g.*, in lizards of the family Agamidae, in which, instead, tail autotomy is now by means of an intervertebral mechanism.

I suggest, therefore, that fracture planes were primitively present in lizard caudal vertebrae, and that they have been lost in xenosaurs and the ancestors of platynotans, in the acrodont ancestors of agamids and chamaeleontids, in a very few skinks and anguids, and repeatedly in the family Iguanidae. As pointed out earlier, in some lizards which lack planes of fracture the entire caudal sequence is rather uniform, with no abrupt alterations in the form, number, or presence of transverse processes (xenosaurs, platynotans, some chamaeleontids, and some agamids), while in others there is a marked change in the transverse processes at the position where, in their close relatives, fracture planes do occur (anguids, skinks, most agamids, and most iguanids). The latter condition implies, I believe, a relatively recent loss of fracture planes.

EVOLUTION OF THE CAUDAL SEQUENCE

In the majority of lizards the tail functions primarily as an accessory locomotor and balancing organ. The problems involved in locomotion and balance vary with respect to behavior, habits, and size of the animals and the tail performs these functions in a variety of ways. The diversity of general form and structure of the tail reflects these functional differences in balance and locomotion as well

as other specialized functions superimposed on them. A number of special tail functions have been independently evolved in different lizard families and within the same families. That is, adaptive radiations within different groups have resulted in similarities of general form and function of the tail in quite unrelated lizards. The tail is used as a prehensile organ in at least five families: Agamidae (*Cophotis, Hylagama*), Iguanidae (*Phenacosaurus, Anolis homolechis*), Chamaeleontidae, Anguidae (*Abronia*), and Scincidae (*Corucia*). A vertically compressed, paddle-like tail used in swimming occurs in the Varanidae (*Varanus salvator* and others), Iguanidae (*Amblyrhynchus*), Teiidae (*Dracaena*), and Agamidae (*Hydrosaurus, Physignathus*). A heavy tail with sharp, stout spines is found in the Scincidae (*Tribolonotus, Egernia stokesii*), Agamidae (*Uromastix*), Iguanidae (*Enyaliosaurus, Hoplocercus,* and others), and Cordylidae (*Cordylus* and others). A high, sail-like fin appears in the Iguanidae (*Basiliscus,* some *Anolis*), and Agamidae (*Hydrosaurus*). In a number of lizards with the limbs reduced or absent the tail is long and slender, considerably longer than the body, and provides most of the propulsive force for serpentine locomotion: Anguidae (*Anguis, Ophisaurus, Ophioides*), Anniellidae (*Anniella*), Pygopodidae, and Cordylidae (*Chamaesaura*). The tail is used for fat storage to some extent in all lizards. Extremes of this function are found in most Gekkonidae, Helodermatidae, some Scincidae, *etc.* It is immediately clear that when unrelated lizards with tails of similar form and function are compared with respect to the vertebral structures described previously, there is no correlation between tail function and caudal sequence.

Conversely, when related lizards with tails of different form and function are compared, a close correlation appears between caudal sequence in these lizards. For example, a complex sequence containing single-process vertebrae followed by diverging-process vertebrae, then single-process, and finally no-process vertebrae is found in a number of iguanid genera: a depressed, short-tailed saxicolous genus (*Sauromalus*), a small, terrestrial, occasionally bipedal desert genus (*Dipsosaurus*), several long, slender-tailed arboreal genera (*Iguana, Brachylophus, etc.*), and a large, semi-marine paddle-tailed genus (*Amblyrhynchus*). In spite of the great vari-

ety of body-form, size, habits, and presumably tail function, the caudal sequence is essentially the same in all. Within the Anguidae are limbless forms with very long tails (*Ophisaurus*), arboreal lizards which use their tail as a prehensile organ (*Abronia*), a short-tailed terrestrial form (*Diploglossus*), *etc.* Yet, the caudal sequences in all anguids are similar. Thus, the caudal sequence appears to be a relatively conservative feature of the lizard skeleton, and a potentially valuable systematic character.

A uniform sequence of vertebrae with single processes is of wide occurrence in reptiles. It is present in many lizards, and in all snakes, turtles, crocodilians, and rhynchocephalians, and in many extinct groups. Except in the Sauria, the only other type of sequence found in reptiles is one containing a short anterior series of single-process vertebrae followed by a long series of no-process vertebrae. The plane of fracture passes behind the transverse processes in the autotomic vertebrae of rhynchocephalians and many lizards. I believe this to be evidence for the primitive nature of a simple, uniform single-process series in which the planes of fracture, when present, are behind the transverse processes.

Vertebrae without transverse processes might have evolved in several ways: by direct loss from primitive single-process vertebrae, by loss of first one and then the other parts of processes from two-process vertebrae, or loss of both simultaneously, or by loss of single processes following a forward shift of the plane of fracture. There is evidence that no-process vertebrae have been derived a number of times by all of these means.

A single-process : no-process sequence is found in a number of iguanid genera. The first autotomic vertebra in this sequence is usually the first no-process vertebra, but there is occasionally a short process on one side of the first autotomic. When this condition occurs in all genera except *Anolis*, the short process is anterior to the fracture plane; when it occurs in *Anolis* this short process is posterior to the fracture plane. Within the Iguanidae, autotomic single-process vertebrae with the processes posterior to the plane of fracture occur only in anoles; in all other iguanids with autotomic single-process vertebrae the plane passes behind the processes. Thus, it appears that no-

process vertebrae of *Anolis* were derived after the forward shift of the fracture plane while in all other iguanids they were derived directly from the primitive single-process type.

Autotomy does not occur in some iguanid genera with a single-process : no-process sequence; in these, therefore, the above argument cannot be applied. Nevertheless, in such genera as *Phenacosaurus* and *Chamaeleolis* which are closely related to *Anolis*, this sequence was probably derived after a shift in the fracture plane (which then was lost).

Elsewhere among lizards, single-process vertebrae in which the septum passes entirely in front of the processes occur in *Dibamus* and *Anelytropsis*. This may also represent a modification of the primitive single-process vertebrae by a forward shift of the septum. Superficially, the autotomic caudal vertebrae in these lizards are very similar to the converging-process vertebrae of anguids, anniellids, feyliniids, and some scincids. They differ only in that slender anterior parts of the processes are absent. Thus, an alternative derivation would be the loss of the anterior parts of the processes of converging-process vertebrae.

A single-process : no-process sequence occurs in some agamids, some teiids, and some lacertids. Autotomic vertebrae do not occur in any of the agamids. However, it seems reasonable that the no-process series in this family is the result of direct modification of the single-process vertebrae by loss of processes. Derivation of a no-process series in the Teiidae and Lacertidae was probably not quite so simple, involving the loss of first one and then the other process of diverging-process vertebrae. Evidence for this assumption will be presented later.

I have mentioned that single-process vertebrae in which the transverse septum passes in front of the processes are confined, in the Iguanidae, to certain species of the genus *Anolis*. This type may represent a modification of the primitive single-process type by a forward shift of the septum, or may be a modification of the diverging-process type in which the anterior parts of the processes have disappeared. The latter would require that, in addition to the loss of the forward processes, the posterior ones would have to undergo a 90° forward rotation. A direct modification of the primitive type by a simple shift in the septum seems to be the simplest explanation for the derivation of this type.

Vertebrae with a single pair of processes through which the plane of fracture passes, found in scincids, xantusiids, and some cordylids, appear to be directly derived from single-process vertebrae by a forward shift of the septum. They may be considered structurally intermediate between diverging or converging-process vertebrae and the primitive single-process type.

A caudal sequence containing diverging-process vertebrae occurs in several groups which are generally supposed to be unrelated. They are found in some iguanids, xantusiids, teiids, cordylids, and lacertids. There appear to be two possibilities as to the origin of these vertebrae. The first is that a second pair of processes developed posterior to the plane of fracture; the second, that the transverse septum shifted to a position so that the single processes were split transversely, and that the anterior and posterior components of the processes later diverged. The frequent occurrence of certain intermediate types of vertebrae at the beginning of diverging-process series indicates, I believe, that the second interpretation is correct. The first autotomic caudal vertebra of a sequence containing diverging-process series is usually the first vertebra of that series. It occasionally happens, however, that the septum of the first autotomic vertebra is incomplete, only partly separating what is clearly a single pair of processes. The septum may separate diverging processes on one side of the vertebra but pass through the middle of a single process on the other. Intermediate conditions are occasionally found in which only the proximal parts of the processes are divergent. Anomalous vertebrae of this sort have been found in all lizard families in which a diverging-process sequence occurs. This condition is taken as evidence that the processes on either side of the transverse septum are actually anterior and posterior parts of a single pair of processes, rather than two different pairs, one of which has appeared *de novo*.

The modification of diverging-process vertebrae appears to have followed several different courses in the various groups which have them. These are: reduction and loss of the anterior processes, reduction and loss of the posterior processes, and reduction and loss of both pairs of processes. Reduction of

either or both pairs of processes appears to follow a definite pattern, *i.e.*, from the end of the sequence to the beginning. I shall discuss each family separately.

In iguanid lizards with a diverging-process series the anterior processes are always much smaller than the posterior ones. The posterior processes are usually the first to disappear; *i.e.*, the diverging-process series is followed by vertebrae with a single pair of processes, and that pair is the anterior one. The reduction and loss of posterior processes happens very abruptly, and in such a way that the anterior processes of the following single-process vertebrae clearly represent only the anterior parts of the original processes, rather than entire processes which have not been affected by a shift in the septum.

Non-autotomic diverging-process vertebrae are confined to the iguanid genera *Conolophus*, *Amblyrhynchus*, and *Brachylophus*. Savage (1958) has indicated that these genera are quite closely related to other iguanid genera with autotomic diverging-process vertebrae. Ontogenetic restriction occurs to some extent in most of the lizards of this group, and in the larger forms (*Iguana*, *Cyclura*), may continue until no functional autotomic vertebrae remain. The loss of autotomy in the Galápagos and Fiji members of the group almost certainly occurred after the shift of the septum and subsequent divergence of the anterior and posterior parts of the processes. This loss may indicate that the selective value of autotomic ability is now outweighed by the importance of some other function of the tail.

Several modifications of the diverging-process sequence have occurred in the family Teiidae. In the microteiid genera, and in some others, the posterior processes have disappeared from some of the more posterior vertebrae, an alteration like that described for some iguanids. In other teiids the anterior processes disappear first. The caudal sequence in a few teiids contains no diverging-process vertebrae, and consists only of single-process autotomic vertebrae in which the septum passes in front of the processes. It is impossible to determine with certainty whether these vertebrae were derived from diverging-process vertebrae by loss of the anterior processes, or, as in the anoles, by a shift of the septum all the way forward of the processes. In at least one teiid genus (*Dicrodon*) the autotomic series is entirely

without processes. There is no way of knowing whether these vertebrae were derived by a direct modification of the single-process vertebrae (simple loss of processes) or whether they represent modified diverging-process vertebrae from which both anterior and posterior parts have been lost. In view of the considerable reduction, but not complete loss, of either anterior or posterior processes in many teiids, it seems more likely that the primitive teiid autotomic series consisted of diverging-process vertebrae, and that single and no-process autotomic vertebrae in this family have been derived from these by the loss of one or both pairs of processes.

A situation similar to that in the teiids is also found in the family Lacertidae. Diverging-process autotomic vertebrae are present in some lacertids, and when they are, they are frequently followed by single-process vertebrae with the septum posterior to the processes. In other lacertids all of the autotomic vertebrae are single-process. Thus, there appears to be a tendency for the posterior parts of the divided processes to be lost. When all are lost, the remaining anterior parts give the series a superficial resemblance to the primitive single-process series.

In the family Cordylidae, single-process vertebrae do not follow the diverging-process vertebrae, so that no problems arise from loss of single pairs, as in the iguanids, lacertids, and teiids. The almost limbless genus *Chamaesaura* represents a curious exception. The autotomic series begins with typical cordylid single-process vertebrae which are gradually modified until the series ends with typical cordylid autotomic diverging-process vertebrae. If my previous interpretations of complex sequences are correct, then the condition of the anterior autotomic caudal vertebrae is always more primitive than the condition of the posterior ones. The situation in *Chamaesaura* is in keeping with this hypothesis, since diverging-process vertebrae were presumably derived from something similar to the vertebrae of most modern skinks.

Except for the frequent occurrence of several skink-like vertebrae at the beginning of the autotomic series, the xantusiid sequence is very much like that found in certain iguanids, lacertids, and teiids. Autotomic diverging-process vertebrae are followed by single-process vertebrae from which the posterior processes have been lost, and

these in turn by no-process vertebrae. As in other groups with this type of sequence, the xantusiids may originally have had a uniform autotomic series of diverging-process vertebrae, subsequently modified by the reduction and loss of first posterior, then anterior processes.

Interpretation of the converging-process series presents few difficulties. Converging-process vertebrae occur only in Anguidae, Anniellidae, and Feyliniidae. There is virtually no structural or serial modification in these three families. The only question which arises concerning this sequence is: from what type of caudal sequence was the converging-process series derived?

With regard to this question, the vertebrae of most skinks are excellent structural intermediates between the primitive saurian single-process vertebrae and the specialized converging-process vertebrae. Anomalous first autotomic vertebrae similar to those found in diverging-process series are occasionally found in converging-process series (Fig. 3C). The anterior and posterior parts of the anomalous vertebrae are not separated at their bases, so that they appear very much like parallel-process vertebrae. Furthermore, converging-process vertebrae occur in a few skinks, but with less separation between the anterior and posterior parts of the process. The derivation of converging-process vertebrae from skink-like vertebrae thus seems reasonable.

In summary, except for the first few caudal vertebrae which always have single processes and are non-autotomic, the primitive caudal sequence is considered to be autotomic with single pairs of processes anterior to the fracture plane. This sequence is found today in the Iguanidae, Gekkonidae, and Pygopodidae. As indicated in Fig. 4, this sequence has been modified in several different ways:

1) Loss of the fracture planes, either directly or following any one of the following modifications (Iguanidae, Agamidae, Chamaeleontidae, Varanidae, Helodermatidae, Xenosauridae, Lanthanotidae).

2) Direct loss of the transverse processes (Iguanidae, Agamidae).

3) A shift of the fracture plane to split the transverse processes into anterior and posterior parts without further modification (Scincidae, Cordylidae, Xantusiidae).

4) Divergence of the anterior and posterior

parts of the split processes (Cordylidae, Teiidae, Lacertidae, Xantusiidae, Iguanidae).

5) Basal separation and distal convergence of the anterior and posterior parts of split processes (Anguidae, Anniellidae, Scincidae, Feyliniidae).

6) Loss of anterior and/or posterior parts of split processes (all families in 4 and 5 plus ? Dibamidae and ? Anelytropsidae).

7) Shift of the fracture plane anterior to the transverse processes (Iguanidae, anoles only).

8) Loss of processes following complete anterior shift of the fracture plane (Iguanidae, anoles only).

CAUDAL VERTEBRAE AND IGUANID RELATIONSHIPS

Among the larger families of lizards the structure of caudal vertebrae is best known in the family Iguanidae; 55 genera and 413 species were examined. The generic and generic group relationships have most recently been studied by Savage (1958) and Etheridge (1959, unpubl. Ph.D. thesis, 1964b, 1965). Although some of our generic groupings are still tentative, a comparison of caudal types with these groupings will illustrate the potential taxonomic usefulness of caudal vertebrae.

The genera of iguanid lizards examined are listed in Table 1 according to their caudal vertebrae types, and are grouped according to some of the generic groups suggested by Savage and myself. In somewhat over half of the genera the caudal vertebrae are of the primitive type: a single pair of processes located, when fracture planes are present, anterior to the plane of fracture. These include all of the sceloporines, their close ally *Phrynosoma*, and their more distant allies *Crotaphytus* and *Gambelia*, all of the tropidurines, both Malagasy genera, and several genera of uncertain affinities. Although these genera share the same caudal vertebra type this does not necessarily indicate that they form any sort of natural group, for it is the primitive type that they share. However, it is important to note the conservatism within the sceloporines and tropidurines and their respective allies, for these 23 genera probably do constitute a major, natural branch of iguanids (Etheridge, 1964b, 1965).

Within the anoles and their allies there are two distinctive caudal vertebrae types:
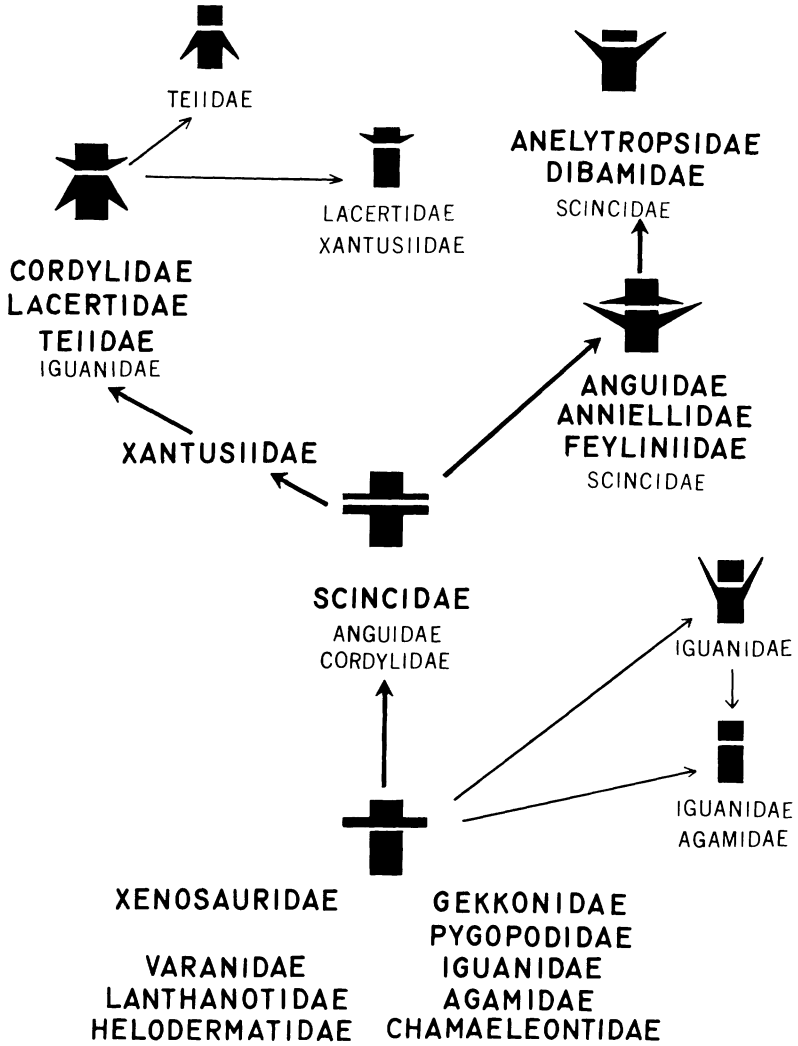
Fig. 4. Evolution of caudal vertebra types in lizards, represented diagrammatically. Family names in large print are below the vertebral type found in most or all members of that family. Family names in small print are below the vertebral type found in a relatively small number of genera in that family. Major trends are indicated by bold arrows, minor trends by narrow arrows.

1) a single pair of anterolaterally oriented, terminally bifurcate processes located, when fracture planes are present, posterior to the plane, and 2) transverse processes lacking, but when fracture planes are present, the first autotomic vertebra may have a short pair of processes posterior to the fracture plane. About half of the species of *Anolis* and several other genera have the first type, the other half of the species of *Anolis* and several other genera the second. The taxonomic and geographic distribution of these two vertebral types reflects what appears to

be an early and basic dichotomy in this major branch of iguanid lizards. (Etheridge, unpubl.).

Vertebrae which lack transverse processes are also found in basiliscines and several other genera of uncertain affinities, but differ from those found in certain anoles in occasionally having short processes on the first autotomic vertebra, located anterior to the plane of fracture, indicating that the processes have been lost independently in at least two phyletic lines.

Caudal vertebrae with two pair of diverg-

TABLE 1. GENERIC GROUPS AND GENERA OF UNCERTAIN AFFINITIES IN THE FAMILY IGUANIDAE LISTED ACCORDING TO TYPE OF CAUDAL VERTEBRA. Asterisk indicates absence of fracture planes; asterisk in parenthesis indicates that fracture planes are present in some species and absent in others.

Single Pair of Processes Anterior to Fracture Plane		Single Pair of Processes Posterior to Fracture Plane	No Processes	Double Pair of Processes with Fracture Plane in Between
sceloporines and their allies	tropidurines and their allies	anoles and their allies	anoles and their allies	iguanines
Callisaurus	Ctenoblepharis	Anolis (Beta)	Anolis (Alpha) (*)	Amblyrhynchus*
Holbrookia	Leiocephalus	Tropidodactylus	Chamaeleolis*	Brachylophus*
Petrosaurus	Liolaemus	Chamaelinorops*	Phenacosaurus*	Ctenosaura
Sator	Ophryoessoides (*)			Conolophus*
Sceloporus	Phrynosaura	Anisolepis*	Polychrus*	Cyclura
Uma	Platynotus	Aptycholaemus*	Polychroides*	Dipsosaurus
Urosaurus	Plica	Urostrophus*		Enyaliosaurus
Uta	Proctotretus			Iguana (*)
	Stenocercus		basiliscines	Sauromalus
Phrynosoma*	Tropidurus			
	Urocentron*		Basiliscus	
Crotaphytus*			Laemanctus*	
Gambelia			Corythophanes*	
	uncertain affinities		uncertain affinities	
Madagascar iguanids	Cupriguanus		Enyalius*	
	Hoplocercus*		Enyalioides (*)	
Chalarodon				
Oplurus	Strobilurus		Uranoscodon*	
	Leiosaurus (*)		Morunasaurus	

ing processes are unique, within iguanids, to the iguanine genera. At the very least they provide an additional diagnostic character for iguanines, and furthermore suggest the interesting possibility that iguanids may be somewhat more closely allied to the teiid–lacertid–cordylid line than our present autarchoglossan–ascalabotan dichotomy (Camp, 1923) implies, a belief which I share with Dr. Max Hecht (pers. comm.) and Dr. Richard Estes (pers. comm.).

DISCUSSION

Although data on the caudal vertebrae of many families of lizards are still far from complete, certain patterns of possible phylogenetic significance appear to be worthy of comment. The arrangement of higher categories of lizards proposed by Underwood (1957) is followed in the discussion below.

Among the families of autarchoglossans autotomy is absent in all of the platynotans and in xenosaurs. The caudal sequence in these families is an undifferentiated series of single-process vertebrae. With few exceptions autotomy is present in the remaining diploglossans and in scincomorphs, and in almost all of them the transverse processes

are split by the plane of fracture. The transverse processes are split but otherwise unaltered in most skinks and in a few anguids and cordylids. The anterior and posterior components of the split processes diverge in all but a few of the lacertoids (cordylids, lacertids, and teiids), and converge in anniellids, feyliniids, most anguids, and a few skinks. The anterior components of the processes have been lost in some teiids and skinks, and the posterior components have been lost in some lacertids.

Primitive autotomic vertebrae with a single pair of processes anterior to the plane of fracture do not occur in any autarchoglossan; such vertebrae in lacertids are almost certainly derived by the loss of posterior components. Split processes, therefore, appear to be generally characteristic of autarchoglossans which possess autotomy. The skink type vertebra is the most primitive of the split process vertebrae and, since autotomy is presumably more primitive than its absence in lizards, the skink type vertebra may be considered the most primitive autarchoglossan type. The lacertoid and anguid type vertebrae are easily derivable from this by divergence or convergence of the processes. Loss of the plane of fracture in a skink type ver-

tebra would result in a single-process verte-
bra as occur in those autarchoglossans which
lack autotomy.

Among ascalabotan lizards, the geckos,
pygopodids, chamaeleontids, and most aga-
mids and iguanids have a sequence of undif-
ferentiated caudal vertebrae with a single
pair of processes. Planes of fracture, when
present, are posterior to the processes in
geckos, pygopodids, and most iguanids; frac-
ture planes are absent in agamids and cha-
maeleontids. Except in iguanids, this se-
quence has been modified only by the loss
of some of the transverse processes (in many
agamids and a very few geckos). Loss of
processes has also occurred in some iguanids,
as well as shifting of the plane of fracture to
split the processes, or to a position anterior
to them. The lacertoid type of diverging-
process vertebrae occurs in those iguanids
(the iguanines) with split processes, but the
skink and anguid types do not. Possibly, the
ancestors of iguanine iguanids possessed the
structurally intermediate skink type verte-
brae, even though no such iguanid survives
today.

Primitive autotomic caudal vertebrae with
the plane of fracture posterior to the proc-
esses, therefore, are generally characteristic
of primitive ascalabotans. Alteration of this
type has occurred mostly by the loss of frac-
ture planes or processes, or both, the only
exceptions being within the iguanids.

Xantusiids were placed among the au-
tarchoglossan families by Camp (1923), but
were provisionally included in the ascala-
botans by Underwood (1957). Their caudal
vertebrae appear to be structurally inter-
mediate between the skink and lacertoid
types. If their affinities lie with the ascala-
botans, then certainly it is with gekkotans
rather than with iguanids, the only family
in which lacertoid type vertebrae occur. If
their affinities lie with the autarchoglossans,
then it is specifically with teiids or skinks.
The evidence from caudal vertebrae, there-
fore, favors an autarchoglossan relationship
for xantusiids.

Dibamids and anelytropsids were also
placed among the autarchoglossans by Camp
(1923), but provisionally included in the
ascalabotans by Underwood (1957). Their
caudal vertebrae most closely resemble those
of skinks in which the anterior components
have been lost. Among ascalabotans similar
vertebrae occur only in some anoles, and in

these the processes are terminally bifurcate.
The placement of dibamids and anelytropsids
in the Autarchoglossa is therefore supported
by the structure of their caudal vertebrae.

MATERIAL EXAMINED

Listed below are the genera of lizards examined
by radiography, as dry skeletons or as cleared
and stained preparations. The number of spe-
cies examined in each genus is indicated in
parentheses.

Gekkonidae: *Coleonyx* (3), *Eublepharis* (1),
Hemitheconyx (1), *Holodactylus* (1), *Coleodacty-
lus* (2), *Gonatodes* (5), *Lepidoblepharis* (1),
Pseudogonatodes (2), *Sphaerodactylus* (6), *Aristel-
liger* (1), *Bavayia* (1), *Ceramodactylus* (1), *Cne-
maspis* (1), *Cyrtodactylus* (2), *Diplodactylus* (1),
Gehyra (1), *Gekko* (2), *Gekkolepis* (1), *Gymno-
dactylus* (2), *Hemidactylus* (1), *Heteronota* (1),
Lepidodactylus (2), *Lucasius* (1), *Nephrurus* (1),
Oedura (1), *Pachydactylus* (1), *Palmatogecko* (1),
Phelsuma (5), *Phyllodactylus* (2), *Phyllurus* (1),
Ptenopus (1), *Ptyodactylus* (2), *Quedenfeldtia*
(1), *Rhotropella* (1), *Saurodactylus* (2), *Steno-
dactylus* (1), *Tarentola* (1), *Thecadactylus* (1),
Tropidocolotes (2), *Uroplatus* (2), *Wallsaurus*
(1).

Pygopodidae: *Delma* (1), *Lialis* (1).

Dibamidae: *Dibamus* (1).

Anelytropsidae: *Anelytropsis* (1).

Xantusiidae: *Cricosaura* (1), *Klauberina* (1),
Lepidophyma (2), *Xantusia* (3).

Iguanidae: *Amblyrhynchus* (1), *Anisolepis* (4),
Anolis (164), *Aptycholaemus* (1), *Basiliscus* (4),
Brachylophus (1), *Callisaurus* (1), *Chalarodon*
(1), *Chamaeleolis* (1), *Chamaelinorops* (2), *Co-
nolophus* (2), *Corythophanes* (3), *Crotaphytus*
(2), *Ctenoblepharis* (1), *Ctenosaura* (4), *Cupr-
iguanus* (2), *Cyclura* (5), *Dipsosaurus* (1), *Enya-
lioides* (7), *Enyaliosaurus* (2), *Enyalius* (4),
Gambelia (1), *Holbrookia* (3), *Iguana* (2),
Laemanctus (1), *Leiocephalus* (20), *Leiosaurus*
(4), *Liolaemus* (34), *Morunasaurus* (2), *Ophryoes-
soides* (10), *Oplurus* (2), *Petrosaurus* (3), *Phena-
cosaurus* (3), *Phrynosoma* (14), *Phrynosaura* (1),
Phymaturus (1), *Platynotus* (1), *Plica* (2), *Poly-
chroides* (1), *Polychrus* (5), *Proctotretus* (3),
Sator (2), *Sauromalus* (6), *Sceloporus* (29), *Steno-
cercus* (14), *Strobilurus* (1), *Tropidodactylus* (1),
Tropidurus (17), *Uma* (4), *Uranoscodon* (1),
Urocentron (4), *Urosaurus* (4), *Urostrophus* (1),
Uta (2).

Agamidae: *Agama* (3), *Amphibolurus* (3),
Aphaniotis (1), *Acanthosaura* (1), *Calotes* (1),
Ceratophora (1), *Chlamydosaurus* (1), *Dendra-
gama* (1), *Diporophora* (1), *Draco* (2), *Gonio-
cephalus* (1), *Japalura* (1), *Liolepis* (1), *Lophura*
(1), *Lyriocephalus* (1), *Moloch* (1), *Otocryptis*
(1), *Phrynocephalus* (2), *Physignathus* (1), *Psam-
mophilus* (1), *Tympanocryptis* (1), *Uromastix* (2).

Chamaeleontidae: *Brookesia* (1), *Chamaeleo*
(6), *Microsaura* (1).

Scincidae: *Acontias* (2), *Brachypodus* (1),
Chalcides (2), *Dasia* (3), *Egernia* (6), *Emoia* (4),
Eumeces (12), *Hemiergis* (2), *Leiolopisma* (2),
Lygosoma (1), *Mabuya* (3), *Melanoseps* (1), *Neo-
seps* (1), *Ophiomorus* (1), *Otosaurus* (1), *Rho-
dona* (1), *Riopa* (1), *Scelotes* (1), *Scincus* (1),

Sphenomorphus (1), *Tiliqua* (2), *Tribolonotus* (1), *Tropidophorus* (2).

Feyliniidae: *Feylinia* (1).

Cordylidae: *Chamaesaura* (1), *Cordylus* (4), *Gerrhosaurus* (2), *Platysaurus* (1), *Tetradactylus* (1), *Zonosaurus* (1), *Zonurus* (1).

Lacertidae: *Acanthodactylus* (1), *Algyroides* (1), *Eremias* (1), *Holaspis* (1), *Ichnotropis* (1), *Lacerta* (1), *Latastia* (1), *Nucras* (1), *Ophisops* (1), *Psammodromus* (1), *Scapteira* (1), *Takydromus* (1), *Tropidosaura* (1).

Teiidae: *Ameiva* (3), *Anadia* (3), *Argalia* (1), *Bachia* (1), *Callopistes* (1), *Cnemidophorus* (12), *Dicrodon* (1), *Dracaena* (1), *Echinosaura* (1), *Euspondylus* (4), *Gymnopthalmus* (1), *Heterodactylus* (1), *Kentropyx* (2), *Leposoma* (1), *Neusticurus* (4), *Placosoma* (3), *Proctoporus* (7), *Teius* (1), *Tretioscincus* (1), *Tupinambis* (2).

Anguidae: *Abronia* (1), *Anguis* (1), *Barisia* (1), *Celestus* (6), *Diploglossus* (2), *Elgaria* (2), *Gerrhonotus* (1), *Ophiodes* (1), *Ophisaurus* (5), *Sauresia* (1), *Wetmorena* (1).

Anniellidae: *Anniella* (1).

Xenosauridae: *Xenosaurus* (1), *Shinisaurus* (1).

Helodermatidae: *Heloderma* (2).

Varanidae: *Varanus* (6).

Lanthanotidae: *Lanthanotus* (1).

ACKNOWLEDGMENTS

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Growth and Size of the Western Fence Lizard (*Sceloporus occidentalis*)

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Growth in *Sceloporus occidentalis* occurs mainly between the first and second hibernation periods, slowing down markedly, and in some individuals ceasing, after the third hibernation period. Winter growth rate is very low. Age classes can be recognized on the basis of snout–vent length (SVL) with considerable accuracy until mid-summer following the second hibernation. There is a highly significant correlation between SVL and clutch size in females and between SVL and weight in both sexes. In juveniles and first-year individuals there is considerable variation in length, which by late summer or early fall becomes much reduced in first-year animals. Size variation remains low in older classes. There is a high degree of correlation between SVL and mean size of prey items utilized until first-year animals reach a length of about 50 mm. It seems probable that this correlation reduces competition for food among juveniles and first-year animals.

INTRODUCTION

FITCH (1940) described briefly the major features of growth in the western fence lizard (*Sceloporus occidentalis*) at Berkeley, California, and near Medford, Oregon. He found that there are three major periods of growth in this species: a period of rapid growth between hatching and entrance into the first hibernation period; the second, when most of the growth takes place, between the first and second hibernation periods; and the third, in which individuals reach adult size and apparently stop growing, following the second hibernation period. It is the purpose of this paper to discuss in greater detail some features of the growth of this species and to treat some aspects of growth not considered by Fitch.

METHODS

The data were derived from a study of a marked population on an area of about five acres at the Hastings Reservation, northern Monterey County, California. The study was carried out between April 1959 and October 1965, save for an absence between December 1960 and July 1961. After initial capture by noosing, each lizard was toe-clipped for permanent identification and color-marked for ready field identification. Sex was established on the basis of presence or absence of large postanal scales (males and females, respectively). Autopsy of 150 individuals of all ages confirmed the complete reliability of this criterion in this species. Snout–vent length was measured to the nearest 0.5 mm at initial capture and at each subsequent recapture. Since western fence lizards become exceptionally wary after repeated noosing, individuals were recaptured only when it was necessary to renew color marks which had been lost through wear, fading, or molt. Although data on length had to be gathered in this random fashion, the total of 1880 individuals captured, many with fairly extensive recapture records, yielded some information on growth and size. Weights were taken from individuals