

Evolutionary aspects of tail shedding in lizards and their relatives

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Introduction

The majority of lizards are able to shed (autotomize) part or most of their tail and subsequently regenerate it. This autotomy, which can often be repeated a number of times, usually occurs when a lizard is attacked by a predator, although it may sometimes take place in intraspecific conflicts. The frequent efficacy of autotomy in allowing escape is well known to anyone who has tried to catch lizards and is supported by the recovery of detached tails, but not their owners, from the stomachs and crops of predators (Cott 1957) and by direct observation of encounters between lizards and their enemies (Congdon, Vitt and King 1974). Yet, notwithstanding its frequent survival value, autotomy is not present in all lizards and, in those where it is, the facility with which breakage takes place is very variable. There are differences between taxa, between different ontogenetic stages of the same species and even within the same individual over short periods of time.

Presence or absence of autotomy and variations in the ease with which it takes place are often explained in adaptive terms, inclination to autotomy being assumed to be determined by natural selection (see for example Vitt, Congdon and Dickson 1977). However, although such explanations are often quite convincing, there is a risk of ignoring the possibility that historical factors may sometimes be more important than present ones; thus absence of autotomy might sometimes be due to loss in the distant past rather than to its having no positive survival value at present. Furthermore, explanations tend to be cast predominantly in terms of variation in the cost of tail loss, for instance that very useful tails are rarely shed while apparently less useful ones frequently are. Many cases do not fit such analyses largely because, as will be argued here, it is to be expected that any variation in the benefits of autotomy would be just as significant as cost variation.

In this paper, the distribution and history of caudal autotomy are considered and an attempt is made to analyse the factors determining the facility with which it takes place or whether it takes place at all. A number of aspects of autotomy are then interpreted in terms of this analysis including: total loss of autotomy and its redevelopment, restriction of autotomy to the tail base, ontogenetic and short-term changes in autotomy threshold, variation in tail fragility between different species and the interpretation of incidences of autotomy in populations, and the possible function of conspicuous tail colouring in autotomy.

Mechanisms of caudal autotomy and regeneration

The term, caudal autotomy, is used here to describe fracture of the tail that occurs in a regular and predictable way at distinct regions of weakness. Its

mechanisms are described in detail by Bellairs and Bryant (in press) and will consequently only be dealt with briefly here. In the majority of lizards, autotomy can occur throughout the tail distal to the basal, pygal series of vertebrae. It takes place at pre-formed areas of weakness, the autotomy or fracture planes, that cross each vertebra transversely. In the soft tissues surrounding the vertebra, the autotomy plane follows the myoseptum that separates adjacent segments of axial musculature and the segments of fat that often lie between these and the vertebra itself. In some cases, there may also be clear regions of weakness in the skin corresponding to the autotomy planes (reported by Woodland 1920, in the gecko *Hemidactylus flaviviridis* and by Quattrini 1954, in the lacertid *Podarcis sicula*; they are also present in some *Agama* species). The total strength of a particular autotomy plane dictates the maximum tensile or torsional force that can be applied to that part of the tail before breakage occurs. This relatively large force seems to be necessary to produce autotomy in unconscious or dead lizards (which corresponds to Slotopolsky's 1922, concept of passive rupture), but much smaller stimuli are usually sufficient in conscious animals. Here natural autotomy is an active process involving a sequence of differential contractions of the various muscle segments bordering the fracture plane. These cause the anterior attachments of the muscle segments to tear away from the myoseptum and the vertebra to break. Autotomy can often be initiated by lightly grasping or touching the tail without actually pulling or twisting it; indeed in some cases the tail may possibly be shed before any contact is made by a pursuer. The stimulus necessary to produce autotomy often varies considerably within the same individual, suggesting that there is a high degree of neurological control of the autotomy threshold in conscious animals. Blood loss following autotomy may be reduced by sphincters in the caudal artery (reported by Woodland 1920 in *Hemidactylus flaviviridis*) and valves in the caudal vein (reported by Winchester and Bellairs 1977 in *Lacerta vivipara* and by Quattrini 1954, in *Podarcis sicula*).

Autotomy is usually followed by regeneration but the neomorph tail differs in structure from the original one: the vertebrae are replaced by a cartilaginous tube that may become calcified, the arrangement of muscles is different and the amount of fat present is often increased. The cartilaginous tube arises from the vertebra that underwent autotomy but not necessarily from the transverse surface initially exposed by this process. In at least some lizards the remaining anterior part of the vertebra undergoes some distal ablation before regeneration occurs (first reported by Werner 1967, in *Hemidactylus turcicus*).

In *Sphenodon* the mechanism of autotomy and regeneration is generally similar to that found in most lizards. Amphisbaenians that shed the tail also have intravertebral autotomy at a preformed fracture plane but regeneration does not follow (Gans 1978). Most agamid lizards do not autotomize at all, but in those that do, it occurs *between* vertebrae, not through them, and may or may not be followed by regeneration. When this occurs, it is like that found in other lizards. The tails of the great majority of snakes are non-autotomous but intervertebral breakage without regeneration occurs in a few species (p. 134). Tail structure in species with intervertebral autotomy is usually quite like that of non-autotomic forms: typically there is little, if any, fat around the vertebrae and the muscle segments are more elongate and more interdigitating than in animals that autotomize intravertebrally. It is also possible that the actual mechanism of breakage and its neurological control are less sophisticated.

How the facility with which autotomy takes place may be altered

It is probable that intravertebral autotomy is the primitive condition in squamate reptiles and that loss or a substantial reduction of the ability to shed all or part of the tail is a derived feature (p. 134). Loss or reduction can take place in a number of ways, the most obvious being by whole or partial fusion of the anterior and posterior sections of each vertebra across the fracture plane, so that its inherent weakness is lessened. This may occur in all the post-pygal vertebrae or only the more distal ones. Etheridge (1967) points out that, when such fusion occurs during ontogeny, it proceeds from the tip of the tail forwards and, in each vertebra, from the top of the neural arch downwards. Vertebral fusion is easy to detect in skeletal material and often in radiographs as well, so it is widely used as an indicator of restricted autotomy. However, ease of autotomy may be reduced by stronger attachment of the muscle segments to the myosepta and loss of planes of weakness in the skin, if originally present. These modifications usually accompany vertebral fusion but sometimes occur in forms where intravertebral autotomy planes are still present (p. 130). As we have seen, neurological factors also seem able to change autotomy thresholds. While all these mechanisms seem able to reduce the facility with which autotomy takes place, they may not be unidirectional in their action, although this would not necessarily apply to fusion of the autotomy planes in the vertebrae once it is established throughout ontogeny.

Of the various possible mechanisms for changing the facility with which autotomy occurs, all seem able to act on evolutionary and ontogenetic time scales, producing differences between taxa and between different ontogenetic stages of the same taxon. But only neurological factors are likely to be effective on shorter time scales.

Distribution of autotomy mechanisms among lizards and their relatives

Much of the data in this summary comes from Etheridge (1967). New information presented here is based on osteological and spirit specimens in the collection of the British Museum (Natural History) and on radiographs prepared from them.

Lizards

Fracture planes occur in virtually all post-pygal vertebrae of all members that have been examined of the following families: Dibamidae, Anelytropsidae, Lacertidae, Cordylidae, Xantusiidae and Anniellidae. In the case of the Lacertidae, I have been able to confirm this for all genera and 130 species. No vertebral fracture planes or autotomy are found in the Platynota (Varanidae, Lanthanotidae and Helodermatidae) or in the Chamaeleonidae. Other families, in which autotomy may be present or absent, are discussed below.

Gekkonidae. Most species have functional autotomy planes throughout the post-pygal region and the only species believed to lack vertebral fracture planes completely is the very short-tailed diplodactyline, *Nephrurus asper* (Holder 1960). However, a number of forms have functional autotomy planes restricted to a small number of vertebrae just distal to the pygal series, the other vertebral planes being wholly or partly fused. In some other species fracture planes occur in most vertebrae but autotomy is usually restricted to the basal region of the tail because, distal to this, the skin is tough without areas of weakness and the axial muscle segments do not separate easily from the myosepta.

Eublepharinae. Functional autotomy planes are restricted to the most basal post-pygal vertebrae in *Holodactylus*. Fracture planes are found in most vertebrae of

other forms but in *Aeluroscalobotes* the skin and musculature lack obvious areas of weakness, except at the tail base. This is not so in *Eublepharis* and *Hemitheconyx* but here too breakage is usually basal. Autotomy appears to occur throughout the tail in *Coleonyx*.

Diplodactylinae. Functional autotomy planes are restricted to the most basal post-pygal vertebrae in *Carphodactylus*, at least some *Diplodactylus* (observed in *D. stenodactylus*, *D. strophurus* and *D. vittatus*), *Heteropholis*, *Naultinus*, *Nephrurus* (*N. laevis*), some *Oedura* (*O. castelnaui*, *O. marmorata*), *Phyllurus* and *Underwoodisaurus*. Functional planes were found throughout the tail in *Bavaya*, *Crenadactylus*, *Eurydactylodes*, *Hoplodactylus*, *Oedura lesueurii* and *O. tryoni*.

Gekkoninae. Functional autotomy planes are restricted to the most basal post-pygal vertebrae in *Colopus*, *Kaokogecko*, *Geckonia*, at least one species of *Pachydactylus* (*P. mariquensis*), *Palmatogecko*, *Paroedura* (confirmed in *P. bastardi*, *P. gracilis*, *P. picta* and *P. stumpffi*), most *Stenodactylus* (*S. affinis*, *S. doriae*, *S. grandiceps*, *S. leptocosymbotes*, *S. petrii*, *S. slevini*, *S. sthenodactylus* and *S. yemenicus*—Arnold 1980 a), *Teratolepis fasciata*, and *Uroplates*. In *Teratoscincus bedriagai*, but not other species of the genus, the neural arches of the post-pygal vertebrae are fused across the autotomy planes. Werner (1964) reports that similar fusion is found in the most distal caudal vertebrae of *Alsophylax blanfordii* (= *Bunopus tuberculatus*). *Crossobamon eversmanni* and *Pristurus carteri* have fracture planes in most of the post-pygal vertebrae but the soft tissues break easily only at the tail base. In some forms like *Chondrodactylus* and *Ptenopus* autotomy planes occur throughout the tail but fracture still usually occurs at the base (Haacke 1975, 1976 c).

Functional autotomy planes were found throughout most or all the post-pygal tail in at least some members of the following genera: *Aeluronyx*, *Afroedura*, *Agamura*, *Alsophylax*, *Aristelliger*, *Bunopus*, *Calodactylodes*, *Chondrodactylus*, *Cnemaspis*, *Cosymbotes*, *Cyrtodactylus*, *Gehyra*, *Gekko*, *Gymnodactylus*, *Hemiphyllodactylus*, *Heteronotia*, *Homonota*, *Homopholis*, *Lepidodactylus*, *Lygodactylus*, *Narudasia*, many *Pachydactylus*, *Perochirus*, *Phyllodactylus*, *Phyllopezus*, most *Pristurus*, *Ptychozoon*, *Ptyodactylus*, *Quedenfeldtia*, *Rhoptropus*, *Saurodactylus*, some *Stenodactylus* (*S. arabicus*, *S. khobarensis*, and *S. pulcher*—Arnold 1980 a), *Tarentola*, *Thecadactylus*, *Teratoscincus* (most species) and *Tropiocolotes*.

Sphaerodactylinae. Fracture planes are found throughout the post-pygal tail in all genera.

Pygopodidae. Autotomy planes appear to be well developed and are present throughout the post-pygal tail in most forms but are strongly reduced in *Pletholax gracilis* (Moffat 1972).

Agamidae. All agamids that have been examined lack autotomy planes in their caudal vertebrae but intervertebral breakage takes place in some forms. Harris (1964) and Etheridge (1967) record it in some *Agama* sens. lat., Hardy and Hardy (1977) in *Physignathus lesueurii* and Bustard (1970) in *Diporophora bilineata*. I have encountered it in some *Amphibolurus* species, *Lophognathus temporalis*, *Otocryptis wiegmanni*, *Sitana ponticeriana*, *Psammophilus dorsalis* and in members of the following subgenera of *Agama* sens. lat. †: *Agama* sens. strict., *Pseudotrappelus*, *Stellio*

† Moody (1980) divided *Agama* as presently understood into a number of separate genera. As these form a holophyletic assemblage, apparently containing all the modern descendants of a single ancestral species, I prefer to take a conservative course and avoid new and unfamiliar name combinations by treating Moody's genera as subgenera.

and *Xenagama*, but not *Trapelus*. Siebenrock (1895) suggests that breakage takes place across the central part of the more distal vertebrae, which is narrow in many species, but all fresh breaks that I have examined are intervertebral. Siebenrock's impression probably arose because, in my experience, the last vertebra remaining after autotomy undergoes some ablation, a third to three-quarters of it disappearing. As the distal part of the vertebra initially projects from the stump of the broken tail, this ablation allows the wound to heal cleanly. Nothing further happens in *Diporophora*, *Otocryptis*, *Sitana* and *Psammophilus* but in *Lophognathus temporalis*, *Physignathus lesueurii* (Hardy and Hardy 1977), all *Agama* (*Stellio*), many *Agama* (*Agama*) and in the sole species of *Agama* (*Pseudotrapelus*) a regenerate is often produced, as may also happen in *Amphibolurus caudicinctus*. This is similar in structure to regenerated tails found in other lizards and, contrary to Etheridge's statement about *Agama*, the vertebrae are replaced by a cartilaginous tube which often becomes calcified. Although no cases were encountered in which the whole original tail had been completely replaced, regenerates are often quite extensive and can be up to 80 mm long in *Agama* (*Stellio*). Details of breakage and regeneration frequencies of agamids preserved in the British Museum (Natural History) are given in table 1.

Iguanidae. Iguanines. Vertebral autotomy planes are completely absent in *Amblyrhynchus*, *Brachylophus*, *Conolophus* and *Iguana delicatissima*. They are lost, or very reduced, during ontogeny in *Iguana iguana*, some *Cyclura* species, *Ctenosaura acanthura* (personal observations) and in *Sauromalus*.

Sceloporines and their relatives. Vertebral autotomy planes are present in all sceloporines (as defined by Etheridge 1964) but are absent in the related *Phrynosoma* and in *Crotaphytus*.

Tropidurines. Vertebral autotomy planes are absent in *Uracentron* and some species of *Ophryoscoptes*.

Basiliscines. Vertebral autotomy planes are completely absent in *Corythophanes* and *Laemanctus* and are lost ontogenetically in *Basiliscus*.

Anolines. Vertebral autotomy planes are absent in *Anisolepis*, *Aptycholaemus*, *Chamaeleolis*, *Chamaelinorops*, *Phenacosaurus*, *Polychrus*, *Polychroides* and *Urostrophus*. According to Etheridge (1959) planes are present throughout the post-pygial tail of most species of *Anolis* but are completely absent in *A. darlingtoni* [= *A. etheridgei*]. They are lost ontogenetically in most members of the *A. latifrons* series but not in *A. agassizi*, *A. bonniensis*, *A. richardi* and *A. roquet* (they are however fused in the one *A. richardi* examined by me). Autotomy planes are also restricted to the more basal parts of the tail in some members of the *A. fuscoauratus* series and in *A. petersi*. Cox (1969a) indicates that planes are absent distally in adult *A. carolinensis* but that breakage can still occur. Autotomy planes are also absent distally some in *A. equestris*.

Iguanids of uncertain affinity. Vertebral autotomy planes are completely absent in *Enyalius*, *Hoplocercus* and some *Leiosaurus* and are lost ontogenetically in some *Enyalioides*.

Scincidae. In the great majority of species, autotomy planes are well developed throughout the post-pygial vertebral series, the only known exceptions being in the *Egernia* generic group which is made up of *Egernia*, *Tiliqua* (including *Omolepida* and *Trachydosaurus*), *Corucia* and *Triblonotus*—Greer, 1979). Within this assemblage, Etheridge (1967) observed that autotomy planes were absent in *Egernia depressa*. This is probably true of the very similar *E. stokesii* and is certainly so in

Table 1. Agama lizards: incidence of broken tails and regenerated tails among adults and sub-adults in museum material.

Broken tails include ones that have regenerated; they also include a proportion of post-mortem breakages but nevertheless give a good indication of relative tail fragility. Entries under Best-developed regenerate show snout to vent length, length of original tail remaining and length of regenerate, the latter being in bold type.

	<i>n</i>	Broken tails (%)	Regenerates (%)	Best-developed regenerate (mm)
<i>Agama (Agama)</i>				
<i>aculeata</i>	67	19.4	0	
<i>agama</i>	111	48.6	11.7	120 + 67 + 35
<i>anchietae</i>	31	6.5	0	
<i>atra</i>	43	35	4.7	122 + 65 + 12
<i>benueensis</i>	34	70.6	3	75 + 46 + 5
<i>bibronii</i>	86	61.6	5.8	92 + 75 + 26
<i>boueti</i>	4	50	25	102 + 51 + 22
<i>caudospinosa</i>	14	100	7.1	128 + 65 + 22
<i>distanti</i>	42	9.5	0	
<i>doriae</i>	61	45.9	8.1	79 + 33 + 9
<i>gracilimembris</i>	15	46.7	0	
<i>hartmanni</i>	4	75	0	
<i>hispida</i>	54	14.8	0	
<i>kirki</i>	20	11	0	
<i>mossambica</i>	44	43.2	0	
<i>mwanzae</i>	11	18.2	0	
<i>paragama</i>	24	50	4	79 + 26 + 25
<i>persimilis</i>	12	25	0	
<i>planiceps</i>	43	65	21	123 + 80 + 51
<i>robecchii</i>	5	0	0	
<i>rueppelli</i>	32	63	3	85 + 33 + 5
<i>sankaranika</i>	25	68	4	65 + 52 + 4
<i>spinosa</i>	63	74.6	13	110 + 70 + 40
<i>sylvanus</i>	9	11	11	105 + 105 + 2
<i>weidholzi</i>	14	93	0	
<i>Agama (Pseudotrapelus)</i>				
<i>sinaita</i>	106	54	6	
<i>Agama (Stellio)</i>				
<i>adramitana</i>	22	73	23	125 + 75 + 37
<i>agrorensis</i>	4	75	75	87 + 64 + 55
<i>annectans</i>	25	44	16	130 + 90 + 55
<i>atricollis</i>	182	28	3	77 + 63 + 44
<i>caucasica</i>	42	56	10	115 + 88 + 18
<i>cyanogaster</i>	52	39	15	112 + 50 + 40
<i>himalayana</i>	14	29	21	136 + 45 + 80
<i>lehmanni</i>	6	17	0	
<i>melanura</i>	8	50	38	114 + 60 + 75
<i>nupta</i>	41	51	27	147 + 70 + 42
<i>phillipsii</i>	44	52	23	112 + 37 + 48
<i>stellio</i>	82	57	9	117 + 100 + 11
<i>stoliczkana</i>	5	60	40	90 + 126 + 7
<i>tuberculata</i>	55	47	25	72 + 71 + 40
<i>yemenensis</i>	30	53	20	93 + 42 + 26

Table 1 (continued)

	<i>n</i>	Broken tails (%)	Regenerates (%)	Best-developed regenerate (mm)
<i>Agama</i> (<i>Xenagama</i>) <i>battilifera</i>	10	40	0	
<i>Amphibolurus</i> (s. lat.) <i>caudicinctus</i>	31	16	3	62 + 65 + 11
<i>cristatus</i>	6	17	0	
<i>isolepis</i>	14	21	0	
<i>maculatus</i>	9	11	0	
<i>pictus</i>	22	18	0	
<i>Diporophora</i> <i>bilineata</i>	14	21	0	
<i>Lophognathus</i> <i>temporalis</i>	23	43.5	15	100 + 192 + 14
<i>Psammophilus</i> <i>dorsalis</i>	21	67	0	
<i>Otocryptis</i> <i>wiegmanni</i>	8	75	0	
<i>Sitana</i> <i>ponticeriana</i>	5	40	0	

† Subba Rao and Rujabai 1972. note that 30% of adults in a wild population had lost the end of the tail.

In addition, 565 specimens of *Agama* (*Trapelus*) were examined. Damaged tails were very rare and in no case seemed to represent autotomy; no regenerated tails were found. The species investigated and the number of adults and sub-adults examined are as follows: *A. agilis* (59), *A. blanfordi* (42), *A. flavimaculata* (149), *A. megalonyx* (1), *A. mutabilis* (150), *A. pallida* (102), *A. rubrigularis* (4), *A. ruderata* (39) and *A. sanguinolenta* (19).

non-juvenile *Corucia zebrata*. Hoffstetter and Gasc (1969) also note that autotomy planes tend to disappear in adult *Trachydosaurus* (= *Tiliqua*) *rugosus* and I have been able to confirm this. In addition, autotomy planes are absent in two adult *Tiliqua scincoides* examined by me but not in examples of *T. nigroluteus* or *T. gigas*.

Teiidae (including microteiids). Autotomy planes are well developed throughout the post-pygal vertebral series in the great majority of species that have been examined. Krause (1978) however notes that they may be largely obliterated in adult *Tupinambis teguixin*. In the one specimen examined by me fusion was restricted to the dorsal part of the neural arch. This condition was also found in a large *T. nigropunctatus* but was absent in a second individual.

Anguidae. Etheridge (1967) found well developed autotomy planes in all the forms that he examined except *Ophisaurus apodus* and *O. compressus*.

Xenosauridae. Etheridge (1967) states that autotomy planes are absent in both *Shinosaurus* and *Xenosaurus*. Hoffstetter and Gasc (1969) agree they are absent in the latter, and this is certainly true for a specimen of *Xenosaurus grandis* in the British Museum (Natural History), but say they occur in *Shinosaurus*.

Amphisbaenians and snakes

Intravertebral autotomy occurs in at least some members of all amphisbaenian families except the Trogonophidae. It is confined to a single vertebra and regeneration does not occur (Gans 1978).

Caudal autotomy has been reported in very few snakes but is present in some colubrids. Thus it has been recorded in the sybinophines *Scaphiodontophis* (Taylor 1954) and *Sybinophis* (Taylor and Elbel 1958) and in *Pliocercus* (Liner 1960). Wilson (1968) suggests that breakage is intravertebral in *Pliocercus* and perhaps *Scaphiodontophis* as well, taking place along grooves that run outwards on the expanded transverse processes. Etheridge (1967) on the other hand states that autotomy in all three genera with fragile tails takes place between vertebrae and my examination of preserved material and radiographs supports this view. No regeneration of the tail occurs but the last remaining vertebra typically undergoes some remodelling. In some cases the final vertebra is merely shortened but in others that I have seen the more posterior parts of the vertebra expand to produce a swelling with a rounded surface posteriorly and an anteriorly directed face on which the last portions of the axial musculature insert. All these autotomizing snakes have very long tails, their length often being more than 50% of the distance from snout to vent.

Tail fragility may well be more widespread in snakes than is generally realized. In addition to the three genera just discussed, it is found in *Rhadinaea decorata*. Again breakage is intervertebral, the last remaining vertebra may be remodelled and the tail is very long.

The likely history of autotomy mechanisms

The tails of modern lepidosaurians exhibit three main conditions regarding their autotomic propensities. These are autotomy intravertebral, autotomy intervertebral and autotomy absent. Is it possible to say anything about the likely historical relationship of the three states? More precisely, which is the primitive condition and are the other two states independent derivatives of it, or stages in a single sequence? Approaches to this sort of problem are discussed elsewhere, for instance by Hecht and Edwards (1977). Methods and terminology used here follow Arnold (1981).

With many characters it is feasible to suggest the sequence of states in a transformation series on morphological grounds. This is not so in the present case, but the distribution of states among closely related species gives some indication. Thus, intravertebral fracture planes and reduction or complete absence of autotomy occur together in such genera as *Pachydactylus*, *Stenodactylus*, *Anolis*, *Iguana*, *Ophryoesoides*, *Tiliqua*, *Ophisaurus* and *Amphisbaena* (where the two conditions may be present in the same species, Gans and Diefenbach 1972), indeed they sometimes occur successively during ontogeny. Similarly, easy intervertebral breakage of the tail and absence of autotomy exist together in *Agama* s. lat.,

Diporophora and *Lophognathus*. On the other hand, intra- and inter-vertebral autotomy are not known to occur in close relatives. It seems likely therefore that the sequence of evolutionary change is: intravertebral autotomy—no autotomy—intervertebral autotomy, the process either being a simple progression with intravertebral or intervertebral autotomy primitive, or absence of autotomy is primitive and the other two states are independent derivatives of this condition.

Is intravertebral autotomy more primitive than absence of autotomy?

1. Although it is highly probable that the Squamata and the Rhynchocephalia are sister groups, the interrelationships of the squamate suborders are not clear. Snakes and amphisbaenians appear to be holophyletic units but it is uncertain if modern lizards are. Furthermore, it is not known precisely how the snakes and amphisbaenians are related to lizards, or indeed to each other. Some authors consider snakes to be derived from platynotan lizards (McDowell and Bogert 1954, McDowell 1972) while Underwood (1970) suggests they share a common ancestor with lizards as a whole. Rieppel (1980) has criticized the former hypothesis but does not dismiss it entirely. Rage (1982) puts forward a case for regarding amphisbaenians as the sister group of snakes, on the other hand Böhme (1981) feels that they may be more closely related to teiid lizards. Whichever version is considered, it seems possible that either intravertebral autotomy is primitive and has been lost several times (including a number within the lizards themselves), or it has been developed independently about the same number of times. On balance, it seems more probable that a complex mechanism like intravertebral autotomy, involving modifications of all organ systems in the tail, would have undergone multiple loss rather than be developed in virtually the same form more than once, or redeveloped after it was lost.

2. Distribution of intravertebral autotomy and its absence can be compared with phylogenies of lizard groups based on other characters. For instance, a phylogeny of macroteiids (Presch 1974) suggests that reduction of the intravertebral autotomy mechanism found in *Tupinambis* is secondary. Similar results are given in the gecko genus *Pristurus*.

3. Where detailed phylogenies have not been proposed, outgroup comparison can often be used to assign polarity. This method indicates that loss of autotomy is secondary in both the *Egernia* generic group and in *Ophisaurus* (using the rest of the Scincidae and the rest of the Anguidae as the respective outgroups). It also suggests the same conclusion in the case of restriction of autotomy to the tail base in numerous gecko genera and generic groups.

4. Although exceptions are frequent, it is probable that widespread character states are more likely to be primitive than those with a restricted distribution. In all lizard families where intravertebral autotomy and absence of autotomy coexist, the former is the commoner condition.

5. Like the previous polarity indicator, the generalization that conditions appearing earlier in ontogeny are primitive appears to be subject to numerous exceptions. Nevertheless, in all known cases where the autotomic propensities of the tail change during the post-embryonic life of lizards, the alteration is from widespread intravertebral autotomy to reduction or complete loss of fracture planes.

So, all available indicators of polarity (comparison with phylogenies based on other characters, likely direction of multiple change based on morphological complexity, outgroup comparison, frequency of character states, ontogeny) suggest

that intravertebral autotomy is more primitive than its absence in the Squamata. Absences in many apparently holophyletic families indicates that it has been lost a number of times. In many instances loss of intravertebral autotomy may be relatively recent, when for instance only some members of a genus or even of a species lack it. On the other hand, its absence from whole superfamilial groupings like the Platyntota or the Agamidae plus Chamaeleonidae, indicate that its loss may be very long standing.

The derived nature of intervertebral autotomy

Moody (1980) provides a phylogeny for the Agamidae based on features other than autotomy mechanisms. This suggests that intervertebral autotomy is derived compared with absence of autotomy and may have arisen as many as eight times: in *Physignathus*, *Diporophora*, the lineage containing *Amphibolurus* and *Lophognathus*, *Psammophilus*, the *Otocryptis-Sitana* lineage and in three subgeneric groupings of *Agama* s. lat. (*Agama* s. strict., *Pseudotrapelus* and *Stellio-Xenagama*). Outgroup comparison and frequency also indicate the condition is derived, as they do for colubrid snakes where no convincing detailed phylogeny has been proposed. Complexity is of little help in estimating the direction of change as intervertebral autotomy involves far less morphological modification than intravertebral autotomy. Indeed, morphological change is apparently so slight that occasional reversal, so that intervertebral autotomy is secondarily lost, would not be unexpected.

Moody's scheme also suggests that ability to regenerate the tail may have developed, or at least been re-activated, five times in the agamids: in *Physignathus*, the *Amphibolurus-Lophognathus* lineage and in the subgenera *Agama* s. str., *Pseudotrapelus* and *Stellio*.

The fact that intervertebral autotomy appears to be derived from a non-autotomous condition adds further weight to the view that intravertebral autotomy is primitive in the Squamata. It indicates that development of autotomy can take more than one form, making it more unlikely that the intravertebral mechanism would have been developed a number of times in precisely the same way, the alternative to regarding it as primitive.

Factors determining ease of autotomy: costs, benefits and history

If natural selection acted without constraint on totally plastic phenotypes, variations in the ease with which caudal autotomy takes place, or whether it takes place at all, would represent adaptations to different situations that maximized fitness in them. This would apply to differences between taxa and between ontogenetic stages, and to short term changes within the same individual. Autotomy would be retained where it increased the chances of a lizard or other reptile approaching its full reproductive potential but lost when it reduced such chances. In autotomizing forms the facility with which the tail is shed should be determined by similar considerations. Whether caudal autotomy is worthwhile would depend essentially on the balance of its costs and benefits; only when the latter exceeded the former would it be selectively advantageous. Presence or absence of autotomy is frequently explained mainly in terms of variations in cost. Thus, loss or reduction of the ability to autotomize is often attributed to the tail being of especial survival value in other ways (see for example Woodland 1920, Boring, Chang and Chang 1948). But variation in benefits must also be taken into account. It is possible to envisage situations where the advantages of autotomy are so great that they make

the sacrifice of even a very valuable tail worthwhile and, conversely, ones where benefits are so low that even the shedding of a tail with little positive function produces no enhancement of survival.

In actuality, phenotypes are not totally plastic, so variations in the autotomy mechanism may not always represent precise adaptations to different situations. In rapidly altering environments the phenotype might not be capable of changing swiftly enough to become fully adapted to conditions prevailing at any one time. Also some kinds of phenotypic change may be less likely to occur than others. As we have seen, the mechanism of intravertebral autotomy appears to have been lost independently many times, yet there is no evidence that it has ever been redeveloped in its original form. Functionally analogous intervertebral autotomy appears to have evolved in stocks that previously lost the intravertebral mechanism but even this has not happened in many groups. There could well be a difference between the facility with which the ability to autotomize and regenerate the tail is lost and regained. If this is so, absence of autotomy may sometimes be the result of the phylogenetic history of a taxon rather than because autotomy is on balance disadvantageous in the present environment. Therefore, it would be expected that species without autotomy would not always show the predicted excess of likely costs over likely benefits. Consequently, the correlation of loss of autotomy with cost excess should be less precise than that between presence of autotomy and benefit excess. As the environments in which animals and their descendants live probably change substantially through time, the longer a stock has lost autotomy the less precise the correlation should be. Because of this, better correlation should be expected at low taxonomic levels than at higher ones.

Benefits of autotomy

Caudal autotomy seems able to benefit lizards and other reptiles in two quite distinct ways: it lets them break away from a predator that has seized them by the tail and it allows the tail to be used as a distraction, engaging the attention of a predator while the lizard escapes. In distraction the tail is sometimes 'offered' to a predator while still attached to the lizard thus diverting attack from the unexpendable head and body and various tail movements and markings can be interpreted as displays enhancing this process (p.155). Once a tail is shed, whether after such a display or after a predator has grasped the tail of a fleeing lizard, it may act to distract the attacker from further pursuit of the rest of the potential prey. Shed tails usually move for some time and seem able to attract the attention of a predator. Indeed, movement is increased by the tail being touched and it may well elicit the same responses as an animal capable of escape. Eating the shed tail may in fact be a more beneficial course for the predator than pursuing the lizard further. The tail is usually a poorer potential meal than the rest of the lizard but has the advantage of being already secured while the rest of the lizard may well evade capture (the tail is like the proverbial bird in the hand worth two in the bush). Furthermore, there is the risk that, if temporarily abandoned, the moving tail will attract the attention of some other animal that will eat it. Movement probably also increases the time that must be spent subduing and swallowing the tail, allowing the lizard more time to escape. The two strategies are, of course, not necessarily complete alternatives: some species use one or the other according to circumstance (see, for instance, Bustard 1968, on *Gehyra variegata*).

The benefits of the escape strategies involving caudal autotomy are likely to vary in different situations.

1. Benefits will be slight if predation is very rare.
2. Simply breaking away from a predator is only beneficial if the lizard is fast enough to elude further pursuit by speed and agility or to reach a secure refuge. Distraction techniques probably demand less speed but even here the lizard still has to get away from the vicinity of the predator before it disposes of the shed tail and to deny it the choice between this and the rest of the prey. The problem may be aggravated, as tail loss itself can reduce the speed of a lizard (p. 139). It seems probable from this that the benefits of autotomy to very slow-moving lizards may be slight.
3. Autotomy will be of less importance if the lizard has other means of deterring predators. For instance, a large species may often be able to fight off attacks with teeth and claws without having to incur the costs of autotomy.
4. Conversely, autotomy is likely to be more beneficial to small species and use of the tail to divert attack from the head and body will be more important for delicately constructed forms with limited ability to fight back than for more robust species.
5. The efficiency of the tail as a distraction depends on its being an acceptable item of diet, or apparently so. Therefore, tails or tail fragments that are very small, or spiny, or that do not move much are likely to have little effect.

Costs of autotomy

In most lizards, tails have survival value in areas other than predator evasion by autotomy. Indeed, these other uses are so widespread that the simple division of tails by Vitt *et al.* (1977) into actively and passively functional types may be inappropriate. (In this division, actively functional tails include those with obvious non-autotomic functions such as swimming, climbing, defence and balance, while passively functional tails include those without a specific function other than autotomy for predator escape.) Nevertheless the aggregate selective value of the tail varies substantially between taxa, and probably between ontogenetic stages; consequently the cost of losing it is variable. Apart from transient loss of alternative functions, this cost also often includes the price of replacing the original tail by regeneration.

Locomotion and balance

1. *Use as a counterpoise in running.* In many cursorial lizards, the tail is raised during running and acts as a counterpoise to the head and body so that weight is concentrated over the hind limbs which are often the main source of forward propulsion. This is particularly so in bipedal forms and Snyder (1949) has shown that loss of only the distal third of the tail is enough to prevent the iguanid, *Basiliscus*, running on its hind legs. The tail is also important as a counterpoise in quadrupedal species such as the lacertid, *Podarcis sicula*. If this lizard is persuaded to run over fine, rolled sand, it leaves deep hind footprints with distinct posterior ridges caused by the backwardly directed force created as the lizard thrusts its body away from the foot. In contrast, the fore feet make shallower prints without posterior pressure ridges, indicating that they take less of the weight of the lizard and that their contribution to forward locomotion is small. Spacing of the prints of the fore feet also shows that these are both off the ground for a substantial part of the stride, so the hind limbs must be providing total support at this time. In animals where much of

the tail has been autotomized deeper footprints indicate that the forelegs support more weight and are not both simultaneously taken off the ground.

2. *Use as an inertial damper.* The tail also appears to function as an inertial damper in reducing lateral swing of the hindquarters. In most cursorial lizards the legs move in more or less horizontal arcs and there is a consequent tendency for the rump to oscillate from side to side; the presence of a large tail with substantial inertia limits this.

I tried to get experimental evidence of the importance of the tail in locomotion by comparing the running performance of intact *Podarcis sicula* with those in which a large proportion of the tail had been removed (Arnold 1970). Sixteen male lizards of similar size (75–80 mm from snout to vent) were collected near Trogir, Yugoslavia and divided into two groups, one containing eight lizards with intact tails, the other eight lizards with about two-thirds to three-quarters of the tail missing. Four of the latter were caught in this state, the others underwent breakage at capture. The last four had all lost part of their tail before and had regenerated it. These were chosen because they must have had previous experience of running with a truncated tail, so any poor performance in running trials would be less likely to be due to their possible need to learn new running techniques. To reduce the effect of recent injury, these lizards and the others were kept in a large cage for one week before the trials. They were also allowed to run some distance on open ground the day before observations were made. In the trials, each lizard was chased over open, sandy ground, its course which was measured afterwards, being marked by scratching the ground with a stick. The lizard was pursued until it began to tire (in all cases for less than 35 m) and timed with a stop watch. Results for tailed and tailless individuals were paired according to similarity in the distance covered and in body temperature (table 2). The overall significance of differences in speed of fully tailed and partly tailed specimens was assessed using the Wilcoxon Matched Pairs Test (Siegel 1956). Despite considerable variation in performance within both groups it is apparent that the lizards with broken tails are slower than fully tailed ones over roughly equivalent distances ($P=0.01$).

Ballinger, Nietfeldt and Krupa (1979) found that the speed of the teiid *Cnemidophorus sexlineatus* is reduced by 36% over distances of 3 m when the tail was removed and Ponzo (1982) got similar results with *Cophosaurus texanus* and *Uma*

Table 2. Effect of tail breakage on speed in *Podarcis sicula*.

Pair no.	Body temperature at start of run (°C)		Distance run (m)		Speed (cm per s)	
	Intact	Broken	Intact	Broken	Intact	Broken
1	31	31	27	23.8	259	198
2	31	31	29.2	27.3	203	152
3	31	31	34.5	32	164	120
4	33.5	33.2	22.5	19.5	225	203
5	34	33.4	22.3	18	309	171
6	34	34	15.7	11	270	190
7	33.5	34	33.4	27	282	215
8	34.4	34	21	16.2	302	227

notata. Pond (1981) discovered that running in the iguanid *Dipsosaurus dorsalis* is impaired by removing a substantial part of the tail.

3. *Use as a counterpoise in climbing.* Cott (1926) observed that *Polychrus marmoratus* can stand erect on a branch when reaching upwards to grasp a twig because the long tail hanging downwards keeps it stable. Ballinger (1973) produces evidence that the tail is also important in balancing *Anolis carolinensis* and that tail loss reduces ability to perch in unstable situations.

4. *Use in swimming.* Many kinds of lizards use the tail in swimming and in the more regularly aquatic forms it is laterally compressed. These include the iguanids *Amblyrhynchus* and *Basiliscus*, the agamids *Lophosaurus* and *Physignathus*, the teiids *Crocodylurus* and *Dracaena*, some *Varanus* species and *Lanthanotus*.

5. *Use as a stabilizer and provider of lift in gliding.* Arboreal lizards that can glide, such as the agamid *Draco*, the gecko *Ptychozoon* (Cantor 1847, Tweedie 1950) and the lacertid *Holaspis guentheri* (Schlotz and Volsøe, 1959), are probably all stable gliders. Stability occurs in most relatively primitive gliding or flying animals that do not have the highly evolved nervous and sensory system necessary to cope with aerodynamic instability; it is ensured by the presence of an adequate horizontal surface behind the centre of gravity (Maynard Smith 1952). In *Ptychozoon* and *Holaspis* the flattened tail probably provides a large proportion of such a surface and certainly contributes to the total area providing lift, so its loss may well reduce gliding ability.

Weight spreading

Lizards that climb in flimsy vegetation or travel across its surface often distribute their weight over as large an area as possible via a long, often slender tail. Among lacertids this occurs in such forms as *Lacerta viridis* and *Psammodromus algirus* and especially among the east Asian Grass runners, *Takydromus*.

Prehensibility and adhesion

Tails may be coiled spirally around twigs or stems to maintain position in vegetation. This is best known and particularly developed in chameleons but occurs in other forms such as the iguanids *Polychrus* (Cott 1926), *Phenacosaurus* (Schmidt and Inger 1957) and *Chamaeleolis* and the geckoes *Nephrurus*, *Heteropholis* and *Aeluroscolobotes*. The gecko, *Lygodactylus* has an adhesive pad on the tail tip, similar in structure to those on the digits, that is used as a fifth point of attachment, for instance when jumping (see e.g. Vitt and Ballinger 1982).

Use as a weapon

In some lizards the tail is used as a weapon in intraspecific combat. Thus males of *Agama agama* strike each other about the head with their tails (Harris 1964). This sort of behaviour may also be directed at potential predators, as occurs in the iguanids *Iguana* (Schmidt and Inger 1957) and *Ctenosaura*, in a number of *Varanus* species and in some forms with thick spiny, club-shaped tails such as several species of the agamid genus *Uromastyx*.

Production of deterrent exudates

A few geckoes of the genus *Diplodactylus* can expel a very viscous exudate from subcutaneous glands in the tail that probably deters predators (Bustard 1970, Rosenburg and Russell 1980).

Use as a burrow plug

The agamid *Uromastyx thomasi* has a disc-shaped tail with a spiny upper surface. When it enters burrows, this tail is turned downwards so that any predator following the lizard will be presented with an effective blockage that prevents further progress (Arnold 1980 b). It is probable that *Agama battilifera* and *A. taylori* use their rather similar tails in this way and the gecko *Diplodactylus conspicillatus* which inhabits the abandoned holes of trap-door spiders, plugs the entrances with its expanded tail thereby reducing water loss (Bustard 1970).

Use in intraspecific signalling

See page 157.

Social status

Tail loss sometimes decreases social status in encounters with other lizards of the same species, as Fox and Rostker (1982) demonstrate in juvenile *Uta stansburiana*. These authors suggest that such decreases may impose a social handicap on successful home range acquisition, thereby increasing the risk of death. A similar loss of social status in tailless *Anolis carolinensis* is reported by Hennig (1979).

Storage of energy reserves

Lizards frequently have substantial caudal fat deposits, especially in forms with very plump tails such as *Heloderma*, and there is evidence that these reserves are mobilized when feeding does not occur (see for instance Avery 1970, on *Lacerta vivipara*). Viability can be reduced when lizards are deprived of caudal fat by autotomy. Bauwens (1981) found that juvenile *Lacerta vivipara* survived less well in hibernation if the tail had been lost and only partly regenerated. Clark (1971) has shown that the skink *Lygosoma* (= *Scincella*) *laterale* may survive about 35 days when starved but only 24 days if the tail has been lost.

Use in subsequent predator attacks

If a substantial proportion of it is shed, the tail cannot be used as an effective anti-predator device until regeneration takes place. This applies whether such use involves further autotomy or some other strategy (see p. 157). Tinkle (1967) discovered that a significant proportion of the short-lived iguanid *Uta stansburiana* regenerate the tail more than once, indicating that predatory attacks are probably quite frequent. So it seems that many lizards stand an appreciable risk of meeting a predator before the autotomized tail has grown again.

Incidental disadvantages of fragile tails

Even in the absence of predators likely to eat the whole lizard, ability to autotomize the tail, and in particular the inherent fragility that this involves, may incur costs. Fragile tails can be damaged when being used as weapons in intraspecific combats (Harris 1964 for *Agama agama*) or they may possibly be broken off by the jaws of a rival, although it is uncertain how common this is (p. 152). Similar loss may also occur by accident and there is even the possibility of tail predation by animals unable to deal with the whole lizard. In captivity at least, the lacertid *Podarcis lilfordi* often pulls the tails off similarly sized lizards including conspecifics. Finally,

any mechanism that results in an exposed surface of bone and soft tissue inevitably involves some risk of infection.

Cost of tail replacement

Regenerating a new tail diverts energy and material from other body functions. For instance, Ballinger and Tinkle (1979) demonstrate that the young of some *Sceloporus* species grow more slowly if they are replacing a shed tail and Vitt, Congdon and Dickson (1977) suggest that up to 50% of total growth energy may be allocated to tail regeneration in the skink *Eumeces gilberti*. These authors also calculate that the energy contained in a regenerated tail of the gecko *Coleonyx variegatus* is equivalent to 47% of the energy in one egg of this species, pointing out that this figure underestimates the actual cost of regeneration because it ignores metabolic energy losses. In plethodontid salamanders, Maiorana (1977) also indicates that autotomized tails are regenerated at some expense to future reproduction.

Modifications that make autotomy more effective or reduce its costs

As we have seen, caudal autotomy in reptiles is often a much more elaborate phenomenon than mere possession of a breakable tail, for there are refinements that increase its efficiency. These include the widespread properties of continued mobility of the tail after shedding and neurological control of the threshold at which autotomy is elicited. In addition, there are a number of less widely distributed modifications that seem likely to ameliorate the balance between benefits and costs in particular circumstances.

Factors that may increase efficiency

Amount of tail shed. As will be shown (p. 147) the amount of tail shed seems to be related to the kind of escape strategy employed: breaking away or distraction.

Bright colouring and conspicuous movement. Many lizards have brightly coloured tails or move them in a conspicuous way in the presence of predators, or both. This may enhance the distractive effect of the tail (p. 155).

Factors that may reduce costs

Restriction of regeneration. The cost of tail replacement can be avoided by not regenerating it, or spread by doing so only slowly. But this is only likely to be feasible if tail shedding does not involve substantial net long-term costs (see p. 163).

Consumption of shed tails. Shed tails are not always eaten by the predator that caused them to become detached. In such circumstances, individuals of some species may return and eat their tail, enabling them to recoup some of its contained material and energy. Clark (1971) reports this behaviour in *Lygosoma laterale* (= *Scincella lateralis*) and Vitt, Congdon and Dickson (1977) demonstrated it in captive *Eumeces* and *Xantusia*.

Behavioural modification. Possibly, by modifying its behaviour until the tail is at least partly regenerated, a lizard could avoid some of the likely functional costs of

autotomy. For instance, by stopping closer to cover, it could reduce the risk of being attacked by a predator at a time when caudal autotomy could not be used successfully and locomotory ability was impaired. Hennig (1979) suggests that *Anolis carolinensis* may compensate in this sort of way for tail loss.

Total loss of intravertebral autotomy

Complete absence of a functional autotomy mechanism is not always easy to recognize with certainty because, even where vertebral fracture planes are obliterated, breakage of the tail and regeneration may still occur, as in *Anolis carolinensis* (Cox 1969a) and possibly in adult *Iguana iguana* (G. Underwood, personal communication). Conversely, presence of vertebral fracture planes does not necessarily indicate that autotomy takes place with facility, since the soft tissue of the tail may not part easily (p. 133). Nevertheless, vertebral structure seems to give a good indication of autotomic propensity in most cases.

If the loss of intravertebral autotomy frequently resulted from environmental selective pressures similar to those still acting on the taxa concerned, its distribution should correlate with particular life modes in which the likely costs of autotomy exceed likely benefits. Appraising likely costs is difficult, even in an informal qualitative way, for there are numerous possible components, none of which has been fully assessed for a particular species. Variations in likely benefit are perhaps less hard to discern, as the factors liable to be significant are fewer and easier to estimate. Furthermore, benefit levels may be more important, on the whole, than cost levels in determining whether autotomy is lost. This is because benefits vary more. Costs are usually considerable because, in most cases, the tail is regenerated, requiring substantial metabolic input, and there are typically some significant losses in tail function while this occurs. On the other hand, costs may rarely be extremely high since it is probable that most lizards survive the effects of tail loss which are only transient and may be of quite short duration as regrowth is often swift and functional losses may be substantially repaired even when the tail is only partially regrown. Furthermore, behavioural modifications during this period, such as stopping closer to cover, could well reduce the risks of subsequent predation. In contrast, benefits of autotomy may be virtually non-existent, for instance in species too slow to escape from predators, or very large in allowing escape from near-certain death.

Among the families where some species retain intravertebral autotomy, the Iguanidae possess most forms that have lost fracture planes completely or do so during ontogeny. As these species do not constitute a single taxonomic assemblage within the family, they may well give a useful indication of the sorts of evolutionary situation where loss of autotomy is advantageous. The forms where autotomy is lost are listed in table 3 and fall into three main groupings on the basis of their modes of life. The first, which is made up entirely of iguanines, consists of very large lizards. They are often capable of active defence against predators by biting, clawing and tail lashing and several are found only on small islands where predation levels are likely to be low, at least for adults. Both these factors would be expected to reduce the benefits of tail shedding. The second group appear to be slow forms and are of modest size with tails that are small (*Phrynosoma*) or spiny (*Hoplocercus* and *Uracentron*). Slowness and tails that are unlikely to capture the attention of a predator for long again restrict the possible value of caudal autotomy.

The third grouping, which is by far the largest, includes a range of lizards that appear to spend all, or a substantial part of their time among small branches, twigs

Table 3. Lizards in which the ability to autotomize the tail is absent.

	Very large body size	Confined to distant small islands	Tail not very palatable	Often slow moving	Bipedal	Habitat	Sources of information on behaviour and habitat
IGUANIDAE							
Group 1							
<i>Amblyrhynchus</i>	+	+				G, and marine	
<i>Conolophus</i>	+	+				G	
<i>Ctenosaura*</i>	+					G(C)	
<i>Cyclura*</i>	+	+				G	
<i>Iguana delicatissima</i>	+	+				C, trees	
<i>Iguana iguana*</i>	+					C, trees	Cott, 1926
Group 2							
<i>Hoplocercus</i>			spiny	+		G	
<i>Leiosaurus</i>			small			G	
<i>Phrynosoma</i>			small	+		G	
<i>Uta</i>			spiny	+		G	Cott, 1926; Duellman, 1978
Group 3							
<i>Anisolepis</i>						C	
<i>Anolis etheridgei</i>						C	
<i>Anolis latifrons</i> series						C	Miyata, 1977; Williams, 1965, 1967, Williams <i>et al.</i> , 1970.
<i>Apticholaemus</i>						C	
<i>Basiliscus</i>					+	C(G)	
<i>Brachylophus</i>		+				C	
<i>Chamaeleolis</i>				+		C	
<i>Chamaeleonorops</i>				+		C	Duellman, 1963.

and leaves or other complex vegetation. To escape from predators, such as birds and snakes by speed is often difficult in such an environment, since surfaces are discontinuous and secure refuges rare. Many of these lizards are sluggish, at least at times, and frequently adopt slow gaits. Some are capable of hopping from branch to branch (for instance *Corythophanes*—Davis 1953, *Laemanctus*—McCoy 1968, *Polychrus*—Cott 1926 and Böker 1935) but even this mode of progression is not especially fast. Anti-predator mechanisms may involve aggressive displays or postures that increase apparent body size (Davis 1953) rather than immediate resort to flight. In such a habitat, where escape by speed is often hard, caudal autotomy is likely to have reduced value in enabling lizards to break away from predators or distract them, especially as tails in this grouping are often very slender and unsucculent and so unlikely to deflect the attention of an attacker. This line of explanation is less convincing in the case of the basiliscines (*Basiliscus*, *Corythophanes* and *Laemanctus*), for many species are known to descend from vegetation and are capable of bursts of fast locomotion on horizontal surfaces (Duellman 1963, McCoy 1968, Davis 1953), so it might be thought that they could benefit from autotomy. However, when running fast they are bipedal and, in *Basiliscus* at least, the tail is essential for maintaining the necessary posture (p. 138); it may therefore be retained for this reason. The same may be true of the frequently bipedal ground-dweller, *Crotaphytus*. In contrast to the forms discussed above, most other iguanids, including the great majority of fast ground dwellers and habitual climbers on rock surfaces and tree boles, retain autotomy.

Most other lizards with no autotomy, at least when adult, that belong to families where intravertebral autotomy still occurs, show similarities in morphology and often life mode to the three main groupings of non-autotomous iguanids. Thus *Tupinambis* is a large, formidable lizard, *Egernia stokesii* has a spiny tail, the species of *Tiliqua* and *Nephurus laevis* are relatively slow-moving with small tails and *Corucia zeburata* is a slow species that habitually climbs in vegetation. Non-autotomous *Ophisaurus* however have no iguanid analogues and it is not easy to see why tail-shedding ability should have been lost here.

Many Platynota, Agamidae and Chamaeleonidae are ecologically similar to species from other families that lack autotomy mechanisms. Thus many varanids are large and capable of actively deterring some predators while chameleons and some agamids generally live in vegetation and are slow moving, but numerous forms are ecologically analogous to members of other families that retain intravertebral autotomy. For instance, some of the small Australian species of *Varanus* have modes of life that are generally similar to those of some autotomizing skinks, teiids and lacertids. In the same way, the agamid *Leiolepis* is quite like the iguanid *Dipsosaurus* and the small ground-dwelling agamids, *Phrynocephalus* and *Tympanocryptis*, superficially resemble such iguanids as *Holbrookia*. This lack of correlation tends to support the view put forward on p. 137, that absence of intravertebral autotomy in the Platynota, Agamidae and Chamaeleonidae is due to loss early in the history of these groups, or to primitive absence, rather than to its being universally disadvantageous to present species.

It might be asked why intravertebral autotomy has not been lost more widely, given the apparent facility with which this mechanism disappears. This may simply be because the great majority of species retaining it do not have the sort of life mode in which loss occurs. For example, among fully autotomous geckoes, pygopodids, lacertids, teiids, xantusids, cordylids and agamids, there are few that are really large,

very slow or possess unappetizing tails; nor do many inhabit the sort of vegetation in which many non-autotomous iguanids occur.

Evolution of intervertebral autotomy in some agamid lizards and some colubrid snakes

The development of intervertebral autotomy may involve relatively slight modification of tail structure and has apparently arisen a number of times (p. 136). Even so, in the Agamidae it is by no means universal and is confined to two ecomorphological types of lizard. 1. Mainly climbing forms, the majority of which live on rock surfaces. Included are *Agama* (*Agama*), *Agama* (*Pseudotrapelus*), *Agama* (*Stellio*) and *Psammophilus*. 2. Entirely terrestrial forms and ones that climb in vegetation. They have relatively long hind legs and very long tails that become extremely slender distally. A number are known or suspected to be bipedal (Russell and Rewcastle 1979) and autotomy is usually restricted to the distal parts of the tail. They include some *Amphibolurus* species (*A. caudicinctus*, *A. cristatus*, *A. isolepis*, *A. maculatus* and *A. pictus*), *Diporophora bilineata*, *Lophognathus temporalis*, *Otocryptis*, *Physignathus lesueurii* and *Sitana*.

Thus although apparently quite easily evolved, intervertebral autotomy has not developed in a variety of fast, ground-dwelling agamids that, by analogy with intervertebrally autotomizing iguanids (p. 146), might be expected to have it. One possible reason for this is that the evolution of autotomy and of regenerative ability in agamids may be independent events. Forms like *Diporophora*, *Otocryptis*, *Psammophilus* and *Sitana* can only autotomize and do not regenerate, whereas most of the other agamids listed above do both. If intervertebral autotomy usually evolves before the ability to regenerate, it will only become established in situations where permanent loss of much of the tail does not carry heavy penalties, or if loss can usefully be limited to a small portion of it. Such situations may be rather rare.

As we shall see (p' 153), there is circumstantial evidence that the tail is often less important to rock-dwelling species than to those in other habitats, so tail loss here may be survivable even without regeneration. In the case of long-tailed, frequently bipedal agamids where autotomy is usually restricted to the distal part of the organ, such modest loss may not reduce the balancing function of the tail very much. It might be thought that, if this were true, analogous bipedal forms, such as the basiliscine iguanids, might also have distal autotomy but they do not. This may be due to the way in which the ability to shed the tail has been lost in groups such as iguanids which were originally intravertebral autotomizers. Both in ontogeny and phylogeny the fracture planes in the vertebrae fuse from the tail tip forwards (p. 129). Consequently, if there is selection pressure to retain the greater part of the tail for balancing purposes in bipedal forms, the whole organ must become non-autotomous.

It is difficult to think what factors might have caused the development of intervertebral autotomy in the few species of snakes known to possess it. The rarity of the condition suggests that it has arisen only in rather special circumstances, but what these are is still a matter for conjecture.

Restriction of autotomy to the tail base

This occurs quite widely in geckoes and is also reported in some iguanids, particularly species of *Anolis*. But in this genus, although the distal vertebrae lack fracture planes, they can still autotomize in some cases (p. 143). Because of this, discussion here will be limited to the geckoes.

Table 4. Geckoes in which autotomy usually occurs at the tail base.

	Believed to be relatively slow	Habitat	Source of information on behaviour and habitat	Fast close relatives with autotomy throughout the tail
Eublepharinae				
<i>Achrosalobotes*</i>		C, twigs, leaves etc.	Inger and Greenberg, 1966; Taylor, 1963	
<i>Holodactylus</i>	+		Neumann, 1905	
Diplodactylinae				
<i>Carphodactylus</i>		G/C, low vegetation and debris	Cogger, 1975	
<i>Diplodactylus stenodactylus</i> ,				
<i>D. strophurus</i> , <i>D. vittatus</i>		G, A	Cogger, 1975	
<i>Heteropholis</i>		C, twigs, leaves etc.	McCann, 1955; Robb, 1980	
<i>Naultinus</i>	+	C, twigs, leaves etc.	McCann, 1955; Robb, 1980	
<i>Nephurus</i>	+	G, A	Cogger, 1975	
<i>Oedura castelnaui</i>		C, standing and fallen trees	Cogger, 1975	
<i>Oedura marmorata</i>		C, standing and fallen trees, also rocks	Cogger, 1975	
<i>Phyllurus cornutus</i>		C, tree trunks	Bustard, 1970; Cogger, 1975	
<i>Phyllurus platurus</i>		C, caves etc.	Cogger, 1975	
<i>Underwoodisaurus milii</i>		G, arid to moist places	Cogger, 1975	

Gekkoninae					
<i>Colopus</i>		G, A	FitzSimons, 1943	<i>Pachydactylus</i> spp.	
<i>Crossobamon eversmanni</i> *	+	G, A	Terent'ev and Chernov, 1949	Palearctic <i>Cyrtodactylus</i> spp.	
<i>Gekkonina</i>		G, A	observation of captives	<i>Tarentola</i> spp.	
<i>Kaokoagecko</i>	+	G, A	Haake, 1976a	<i>Pachydactylus</i> spp.	
<i>Pachydactylus mariquensis</i>		G, A	FitzSimons, 1943	<i>Pachydactylus</i> spp.	
<i>Palmatogecko</i>	+	G, A	FitzSimons, 1943; Haake, 1976	<i>Pachydactylus</i> spp.	
<i>Paroedura</i>		G (C), A	Angel, 1942	<i>Phyllodactylus</i> spp.	
<i>Pristurus carteri</i> *	+	G, A	field observations	<i>Pristurus</i> spp. (e.g. <i>P. rupestris</i>)	
<i>Stenodactylus</i> spp. (see p. 130)	+	G, A	Arnold, 1984	<i>Stenodactylus arabicus</i> , <i>S. khobarensis</i>	
<i>Teratolepis</i>	+	G, A	Minton, 1966	<i>Hemidactylus</i> spp.	
<i>Teratoscincus bedriagae</i>		G, A			
<i>Uroplates fimbriatus</i>	+	C, tree trunks etc.	Krapp, 1963		

*—autotomy planes present in most tail vertebrae.

C—climbing form.

G—ground dweller.

A—found in arid open habitats.

In most lizards, the tail is autotomous throughout its length distal to the pygal vertebrae and breakage often takes place just in front of the place where the tail is seized, or contracted, by a predator. This economy of autotomy minimizes costs for a lizard breaking away from the grip of a pursuer and it is consequently rather surprising at first sight that some species always shed the whole tail, especially as it often contains substantial amounts of stored fat (for example in *Underwoodisaurus milii*). But, breaking away from a predator is only likely to be successful if the lizard has the speed to evade any further pursuit or if a refuge is close by. Relatively slow species, particularly ones living in habitats where secure shelters are few, probably rely on a different strategy in which the tail is used to deflect the attention of predators from the more vulnerable head and body. Certainly, some geckoes of this type often wave the tail in a conspicuous way, rather than fleeing immediately (p. 156). However, sacrifice of the smallest portion of tail possible may not be sufficient to retain the attention of a predator and restriction of autotomy to the tail base could be a means of ensuring that a large enough 'bait' is provided to deflect an attacker. If this interpretation of basal autotomy is correct, we should expect it to occur in relatively slow geckoes and ones without easy access to secure refuges. Although no wide-ranging comparative studies of the speed of geckoes have been made, it is apparent when what is known about basal autotomizers is surveyed (table 4) that many of them do seem to be relatively slow. On the other hand, close relatives with autotomy planes throughout the tail, where they can be identified, are usually faster. This is certainly true for the two groups of which I have field experience: *Pristurus* and *Stenodactylus*. Further, many basal autotomizers occupy open arid country where refuges are likely to be sparse and most of the others climb in bushy vegetation where the same may be true (p. 146). A number of other forms have autotomy planes throughout the tail but nevertheless frequently shed the organ from the base. Among these are *Chondrodactylus* and *Ptenopus* which again are relatively slow-moving geckoes that live in arid open environments (Haacke 1975, 1976 c).

Ontogenetic shift from autotomy to non-autotomy

Some iguanids and skinks and the teiid *Tupinambis* possess well-developed autotomy mechanisms when young but these are reduced, or more often obliterated, by maturity. Presumably the change results from a shift in the balance of costs and benefits, either the former rising or the latter falling with increase in body size, or both. It seems probable that the benefits of autotomy are often greater in young animals because of their more marked vulnerability compared with adults (see p. 161). Ontogenetic loss of autotomy is commonest in quite large species where adults may frequently be able to fight off predators or produce impressive displays, strategies not available to juveniles. Another possibility, in some cases, is that young animals may be faster and more agile than adults and, because of their size, better able to find cover, so that autotomy is more likely to allow escape than in the slower, less concealable adults.

Short-term changes in the readiness with which the tail is shed within individual lizards

As stated previously, the strength of individual fracture planes determines the maximum force necessary to produce breakage of a particular part of the tail, but much smaller stimuli may initiate autotomy and the threshold for this often varies considerably within individual lizards. Such variation has undergone little formal

investigation but a number of observations indicate that it exists. 1. Conscious animals typically shed their tails more easily than unconscious ones. 2. Ease of autotomy may vary with temperature, for example in *Uta stansburiana* (Brattstrom 1965), *Podarcis sicula* (Quattrini 1952), *Stenodactylus* (Werner 1964) and *Gehyra variegata* (Bustard 1968). In most cases, autotomy occurs most easily at high temperatures, but in *Gehyra* it takes place readily at both high and low temperatures and with greater difficulty in between. 3. Captive lizards that become tame will tolerate a degree of handling of the tail that would produce immediate autotomy in wild animals. This is true of many lacertids. 4. In some species, such as the lacertids, *Podarcis sicula* and *Lacerta vivipara*, the tail is shed quite readily if grasped as the lizard runs away. But when the lizard is held by the body and the tail pulled or twisted by a predator, it can be detached only with difficulty.

These examples suggest that tail shedding is modified in response to external circumstances. If the mechanism is optimally adjusted by natural selection, autotomy should only occur easily in situations where likely benefits exceed likely costs. The likely costs of losing a given portion of the tail are probably quite constant in the short term (although they may vary seasonally, for instance if large amounts of fat are stored in the tail at certain times of year). Likely benefits on the other hand change very rapidly. The benefits of autotomizing the tail are probably low until a predator is at close quarters. They will rise further if the predator actually makes contact with the tail and would be expected to be higher still if it is of a kind that is efficient at capturing lizards.

Some at least of the known individual variation in autotomy threshold appears to be adaptive and Brattstrom (1965) and Bustard (1968) provide functional explanations of temperature correlated change in *Uta* and *Gehyra* respectively. In the case of a lizard held by the body (4, above), it may be argued that tail shedding is of little advantage since it will not aid escape. In this situation, a high autotomy threshold would make retention of the tail more probable so that, if the lizard subsequently managed to break free, it could still utilize caudal autotomy in any further pursuit.

Variation in the readiness with which the tail is shed in different species

Not only should the complete loss of autotomy mechanisms be determined by the balance of costs and benefits but also the relative readiness with which the tail is shed by different autotomizing species. Tails should be relinquished most easily in species where the likely costs of loss, in terms of future reproduction, are least. If loss of the tail is comparatively inexpensive, the lizard can 'afford' not to take high risks and autotomy can be brought into operation even in circumstances where the chances of being caught are not especially high. Conversely, if loss of the tail is likely to be very costly, autotomy should be delayed until the probability of being caught without using it approaches certainty. For example, if loss of the tail reduces future reproduction by 40% on average, then it would be appropriate to initiate autotomy when the risks of being caught and killed by the pursuing predator are also 40%. But, if the chances of failing to reproduce after tail loss are 80%, it would be better to delay autotomy until the probability of being killed by the predator rises to this level. Animals with low-cost tails should therefore tend to autotomize at earlier stages in a particular kind of predator attack and at lower levels of tactile stimulation.

That such differences in autotomy threshold exist between species is apparent to any one who has tried to catch a variety of kinds of lizard. Some species shed the tail when it is only lightly touched during pursuit while in others the organ must be very

firmly grasped before breakage takes place. Among European lacertids, tails appear to break most readily in rock-climbing species like *Lacerta oxycephala* and, in Arabian geckoes, fragility seems to be greater in climbing forms than in ground-dwellers. Such assessments are of course subjective but no satisfactory comparative measurements of tail fragility have been made. This is largely because it is difficult to deliver calibrated stimuli to lizards in natural conditions, while with captive animals habituation and restraint may alter autotomy thresholds, perhaps differentially between species. What is more, applied stimuli should mimic the kind of contacts made by predators; such devices as the attachment of weights to the tail (Quattrini 1952, Brattstrom 1965), while easy to apply and measure, are unlike anything that lizards usually encounter.

The meaning of differences in incidence of autotomy between species and populations

Differences frequently exist between species and between populations of the same species in the incidence of autotomized tails. A number of interpretations of such variations have been made. Bustard and Hughes (1966) for instance regarded them as an indicator of age differences between the populations they were studying, while Rand (1954) and Pianka (1967) considered that they reflected differences in predation level. In fact there is a variety of factors that may contribute to apparent differences in incidence between samples.

1. *Collecting bias.* Museum curators and reptile collectors in general tend to prefer intact animals, so museum material and other non-random samples may be somewhat misleading in exaggerating the proportion of undamaged tails. This bias is liable to act differentially, autotomy being more fully eliminated in samples from species or populations where it is relatively rare, since fewer damaged animals have to be rejected and replaced by perfect ones. However, catching lizards is rarely so easy that many are discarded and, although such bias may change apparent absolute frequencies of autotomy, the order of autotomy incidence among a group of samples is probably not greatly changed. The problem can of course be eliminated by collecting random samples.

2. *Misidentification.* In many species, regenerated tails are conspicuously different from the originals and consequently easy to recognize. This is not always the case and it is sometimes possible to underestimate the number of regenerates present if they resemble original tails closely. However, as vertebrae are replaced by a cartilaginous tube in regenerated tails, they can always be identified by radiography.

3. *Intraspecific conflict.* Tails, or portions of tails, may be lost in fights between members of the same species. Harris (1964) reports such damage in *Agama agama*, where males strike each other with their tails, and Vitt *et al.* (1974) believe that the higher tail breakage frequency in males of the iguanid *Sceloporus magister* stems partly from territorial fighting. Zweifel and Lowe (1966) apply a similar interpretation in the case of *Xantusia vigilis*, although this is disputed by Vitt *et al.* (1977). In some groups, such as lacertid lizards, tail loss rarely seems to result from intraspecific conflicts, even in captivity. The importance of this factor in increasing natural incidence of broken tails can only be properly assessed by field observation of the species concerned.

4. *Age structure of populations.* The probability of an individual lizard losing its tail and regenerating a new one increases with time, although the increase is often not

uniform, young animals frequently being more prone to caudal autotomy than adults (see, for instance, data given by Cook 1979, and Blair 1960).

All other things being equal, long-lived species will tend to have higher aggregate levels of tail breakage than short-lived ones. This effect can be countered by comparing samples of known age, either recognized by relative size or by previous individual marking.

5. *Incidence of unsuccessful predation.* Incidence of broken tails will be higher in species and populations where encounters with predators and subsequent escape after autotomy are frequent.

6. *Ability of lizards to elude predators after autotomy.* The frequency of autotomized tails in a population will only increase if tail shedding significantly improves the chances of a lizard escaping. If animals are very often caught after autotomy, broken tails may remain rare in samples even though predation levels are high.

7. *Differences in the ease with which autotomy takes place.* See page 151.

In principle, it is possible to assess all these factors, but substantial ecological knowledge of the species concerned is necessary and rarely available. In particular, predator pressure is hard to estimate without extensive collateral studies of other animals in the communities in which the lizards live. Also, as already noted, the readiness with which autotomy takes place is difficult to measure realistically. Because of these problems it is usually not possible to unravel the contributions of intraspecific conflict, age, predation and ease of autotomy to the incidence of broken tails. This means that the use of tail damage as an indirect source of information about any of these factors is generally not feasible, although there are possible exceptions. Schoener (1979) and Schoener and Schoener (1980) explore a method of estimating predation parameters from tail break data in *Anolis*. Again, when comparing geographically close populations of the same species, it is likely that many behavioural traits and inherent longevity are similar, in which case predation level is the most probable cause of substantial differences in frequency of breakage. The same assumptions can be made, but with less confidence, when dealing with widely separated populations of the same species or with closely related species. For instance Huey and Pianka (1977) attribute the low level of tail breakage found in juvenile *Eremias* (= *Heliobolus*) *lugubris*, compared with the young of congeneric forms in the same area, to reduced predator pressure arising from mimicry of noxious beetles. This is not unreasonable since the samples are alike in age and are quite similar in many aspects of behaviour and environment.

It might be thought that tail break incidence does at least give an indication of the relative success of autotomy in enabling lizards of different species to evade predators. This would be so if each lizard with a broken tail had only survived a predator attack thanks to autotomy. But, as we have seen, species in which autotomy does not incur great costs may shed the tail at a time when the risks of a predator successfully catching them are still relatively low. In such cases, each shed tail is unlikely to represent a lizard saved by autotomy from certain death, whereas in species in which tails are given up less willingly this may be more nearly so.

Autotomy levels do often show a broad correlation with particular ecological circumstances. Thus Werner (1968) notes that among geckoes occurring in Israel, broken tails are commoner in climbing species than among ground dwelling ones and Jaksić and Fuentes (1980) found this to be true among Chilean *Liolaemus*. A similar correlation exists among European lacertids of the genera *Lacerta* and *Podarcis* (fig. 1), as it does in communities of lizards in eastern Arabia (fig. 2) and in species of

Agama in Africa (fig. 3). The cause of this correlation is uncertain, largely because many of the ecological data likely to be relevant are lacking. Nevertheless, at present, there are no indications that most factors likely to increase the incidence of broken tails act more strongly on climbing species. Thus, they are not more obviously prone to intraspecific combat, or to longer life or predation. On the other hand, subjective impressions suggest that climbing species relinquish their tails more easily than ground dwellers (p. 152). If this is really so, it could indicate that tail loss is less costly in these forms. One reason for this may be that the tail is less important in the locomotion of forms that climb habitually. Here, the body is not counter-balanced by the tail, as is possible and necessary in cursorial forms where the hindlimbs provide most forward propulsion (p. 138). Also, because the feet are firmly attached to the substrate when climbing, lateral oscillation of the hindquarters is less of a problem.

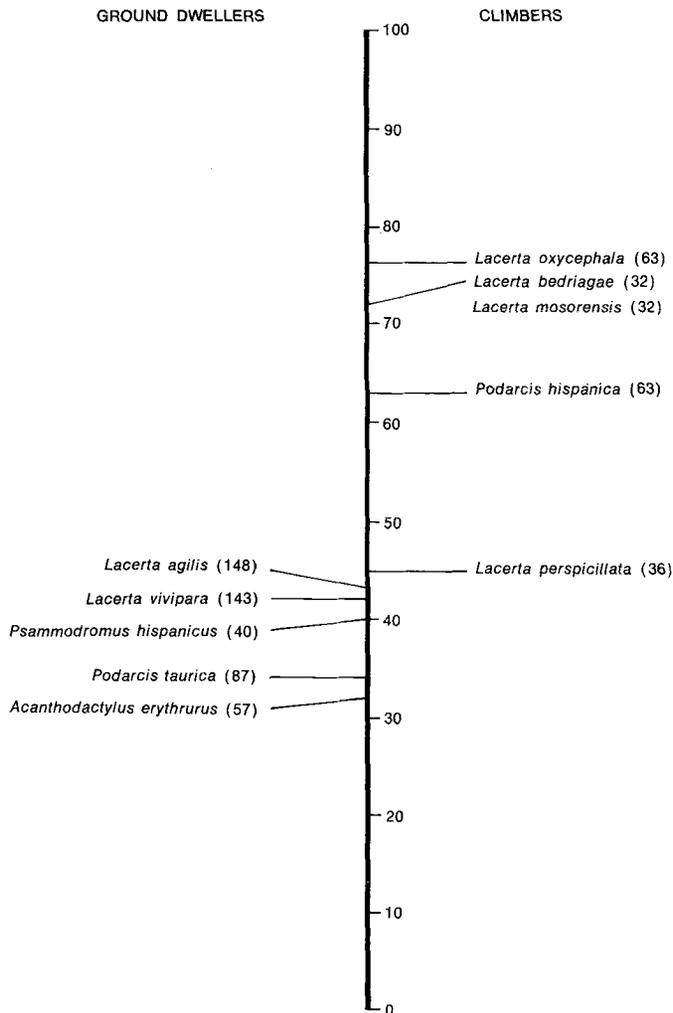


FIG. 1. European lacertids: percentage of museum specimens with naturally autotomized tails. Figures in parentheses indicate sample sizes. Based on material in collection of British Museum (Natural History).

Colouring and behaviour that may divert attention from the head and body to the tail

Many lizards have tail colouring that contrasts with the rest of the body. Often the tail, or at least its more distal parts, is conspicuously marked while the head and body are cryptic, matching the usual surroundings of the species concerned. It seems possible in many cases that such tail colouring enhances the distractive effect of the tail, so that predator attention is more likely to be directed towards it rather than to the head and body. A similar function may be served by tail movements made in the

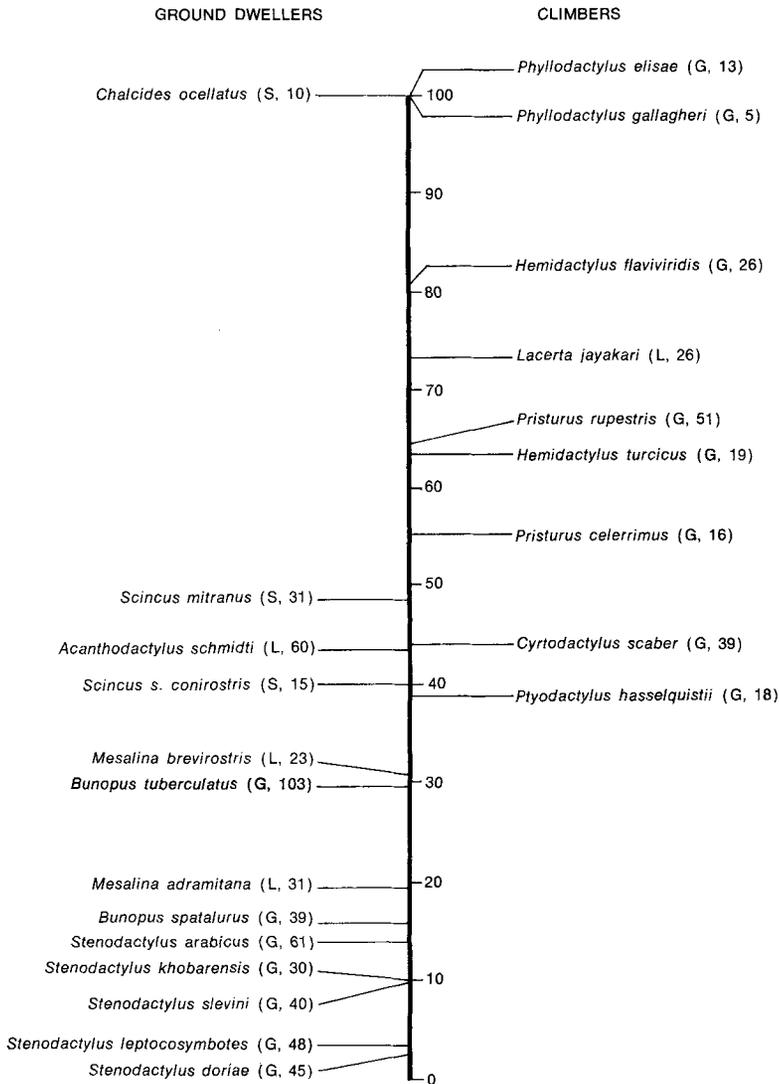


FIG. 2. Lizards from the United Arab Emirates, eastern Arabia: percentage of museum specimens with naturally autotomized tails. Letters in parentheses indicate families, G-Gekkonidae, L-Lacertidae, S-Scincidae; figures indicate sample sizes. Division into ground dwellers and climbers is based on information in Arnold 1980 b, 1984 and Arnold and Gallagher 1977. Data from material in collection of British Museum (Natural History).

presence of potential predators. These are often seen in species with conspicuously marked tails but also occur in some forms where the body and tail are not contrastingly coloured. In some geckoes, such as young *Stenodactylus leptocosymbotes* and *S. slevini*, sinusoidal waves pass slowly along the extended tail; in others, including *Chondrodactylus* and *Palmatogecko*, the tail may be raised above the body (Haacke 1976 a, c) and *Teratolepis* often brings the tail towards an attacker (Minton 1966). Many lacertids wave the distal part of the tail in the presence of possible predators and, when these are at close quarters, *Lacerta oxycephala* will switch it

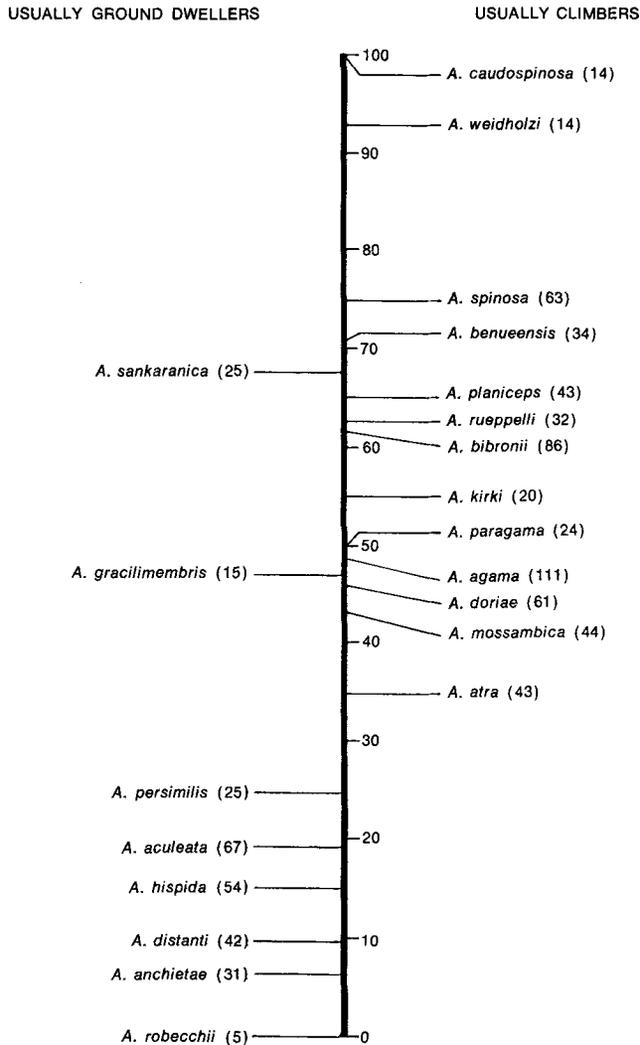


FIG. 3. African *Agama* (subgenus *Agama*): percentage of museum specimens with broken tails. Both pre- and post-mortem damage is included but figures probably give a good indication of natural fragility. Division into usually ground dwellers and usually climbers is based on information on labels attached to specimens and comments by Broadley (1971), FitzSimons (1943), Grandison (1968, 1969), Loveridge (1936, 1953), MacDonald (1981), Parker (1942) and de Witte (1953).

vigorously from side to side. Mertens (1946) describes a variety of other tail movements in lizards.

Alternative interpretations of conspicuous tail markings and movements are of course possible.

1. *Crypsis*. Markings, such as bold transverse bars, may be disruptive, breaking up the outline of the tail.

2. *Intraspecific signals*. Tail movements, especially when combined with bright markings, may be intraspecific signals. For instance, geckoes assigned to the genus *Pristurus* frequently move their sometimes boldly marked tails in response to the presence of conspecifics and often such behaviour is reciprocated. Clark and Hall (1970) suggest that the brilliantly coloured tails found in the young of many north American *Eumeces* deter adults of the same species from attacking them and Peters (1964) believes that the bright colour on the tail and thighs of immature individuals of some *Eremias* species stops adult males from treating them as potential rivals or mates.

3. *Aposematic colouring*. Bright tail colouring could be aposematic, indicating that the lizard concerned is unpalatable.

4. *Mimicry*. Curling the tail upwards has been interpreted as scorpion mimicry in the agamid *Phrynocephalus* and in the geckoes *Chondrodactylus* (FitzSimons and Brain 1958) and *Coleonyx variegatus* (Parker and Pianka 1974). In juveniles of the lacertid *Eremias lugubris*, tail and body contrast in colour, apparently because the body mimics distasteful carabid beetles of the genus *Anthia* while the tail is cryptic, matching the usual substrate of this lizard (Huey and Pianka 1977).

5. *Flash coloration*. Tail colouring and movement may contribute to antipredator devices not involving autotomy. For instance, bright markings may be 'flash colours': in lizards where the underside of the tail is conspicuously marked, exposure and then sudden concealment of this pattern by a running animal may fix the attention of a predator on the spot where the bright colouring was last seen, even though the otherwise cryptically coloured prey has moved on.

6. *Warning of expensive pursuit*. Alternatively, a conspicuous tail signal when a predator is seen may be advantageous in deterring it by advertising the fact that the potential prey is aware of its predicament, so pursuit may be costly (Arnold 1980 b).

None of the available explanations of conspicuous tail markings and movement necessarily rule out the others and, in many species, not enough is known about behaviour and ecology to completely exclude all the alternatives to distracting attention from the head and body. The case for this particular function is stronger if the species concerned is known to actively display the tail in the presence of a predator. It would be enhanced further if experiment showed that attack was often diverted by these movements but such information is rarely available. Conversely, extension of bright colour on to the hind legs and posterior body suggests that distraction of attention to the tail is not its sole function.

Conspicuous tail markings occur in some non-autotomic species, although not as commonly as elsewhere. For instance, certain *Varanus* species, such as *V. varius* have the tail clearly banded and in the agamid *Phrynocephalus* it is often strongly barred beneath. In many such cases the main function is probably not to direct attention to the tail but, even here, this explanation cannot be completely excluded since diversion of attack from more vital areas to the tail may be advantageous even though it cannot be shed. Greene (1973) makes a case for such usage in some snakes with bright, non-autotomic tails.

Table 5. Distribution of conspicuous tail colouring among the lizards of the United Arab Emirates and Sultanate of Oman, eastern Arabia. Asterisks indicate species that do not autotomize. Geckoes and agamids can change colour quite rapidly, so bright tail colouring may not always be visible in some of the species that possess it.

	Conspicuous tail colouring		Tail colouring more intense distally	Main activity period: nocturnal—n, or diurnal—d	Mainly climbing—c, or ground dwelling—g	Frequently found in open microhabitats
	young	adults				
GEKKONIDAE						
<i>Bunopus spatulatus</i>				n	g(c)	+ rocky ground
<i>Bunopus tuberculatus</i>				n	g	in and among plants
<i>Cyrtodactylus scaber</i>	black and white bars	reduced	+	n	g/c	often near vegetation
<i>Hemidactylus flaviviridis</i>	very weak light and dark bars	absent	+	n	c	+ walls, trees
<i>Hemidactylus homoeolepis</i>	black and white bars	reduced	+	n	c(g)	+ rocks, stony ground
<i>Hemidactylus lemurinus</i>	very weak light and dark bars	absent	+	n	c	+ large boulders
<i>Hemidactylus persicus</i>	weak light and dark bars	reduced	+	n	c	+ rocks, walls
<i>Hemidactylus turcicus</i>	black and white bars or yellowish	reduced	+	n	c(g)	+ walls, trees
<i>Hemidactylus yerburii</i>	black and white bars	reduced	+	n	c	+ rock faces
<i>Phyllodactylus elisae</i>	black bars on white ground	as young	+	n	c	+ large boulders etc.
<i>Phyllodactylus gallagheri</i>	black and white bars	as young	+	n	c	+ rock faces
females	black and white bars	as young				
males	light and dark bars	yellow				
<i>Pristurus carteri</i>	light and dark bars	reduced	uniform	d/n	g	+ stony or sandy ground
<i>Pristurus celerrimus</i>	black and white bars	as young	+	d	c	+ rock faces
<i>Pristurus cf. flavipunctatus</i>	black and white bars	as young		d	c	tree trunks
<i>Pristurus minimus</i>	white beneath in some regions	as young		d	g	close to plants
<i>Pristurus rufpestris</i>	moderate light and dark bars	reduced	+	d	c	small rocks etc.
<i>Phydactylus hasselquistii</i>	strong light and dark bars	rather reduced		n/d	c	+ rock faces
<i>Stenodactylus arabicus</i>	light and dark bars	as young	uniform	n	g	+ sand
<i>Stenodactylus doriae</i>	light and dark bars	as young	uniform	n	g	+ soft sand
<i>Stenodactylus khobarensis</i>	light and dark bars	as young	uniform	n	g	+ salt flat

<i>Stenodactylus leptosymbotes</i>	black with white tip	reduced	no	n	g	+ firm sand etc.
<i>Stenodactylus slevini</i>	strong light and dark bars	reduced	uniform	n	g	+ firm sand etc.
<i>Teratoscincus scincus</i>			?	n	g	+ sand
LACERTIDAE						
<i>Acanthodactylus boskianus</i>	blue	absent	+	d	g	+ sand
<i>Acanthodactylus felcis</i>	blue	absent	+	d	g	
<i>Acanthodactylus felcis</i>	blue	absent	+	d	g	
<i>Acanthodactylus masirae</i>	red	absent	+	d	g	
<i>Acanthodactylus ophiodurus</i>	blue	absent	+	d	g	
<i>Lacerta cyanura</i>	blue	rather less intense	+	d	c	+ rock surfaces
<i>Lacerta jayakari</i>	blackish	absent		d	g/c	rocks and vegetation
<i>Mesalina adramitana</i>	bluish in some regions	absent	+	d	g	+ hard ground
<i>Mesalina ayunensis</i>	blue	rather less intense	+	d	g	+ rocky ground
<i>Mesalina brevirostris</i>				d	g	close to plant cover
SCINCIDAE						
<i>Ablepharus pannonicus</i>				d	g	litter etc.
<i>Chalcides ocellatus</i>				d	g	litter etc.
<i>Mabuya aurata</i>				d	g/c	stones with vegetation
<i>Mabuya brevicollis</i>				d	g/c	vegetation
<i>Mabuya tessellata</i>	?	yellowish or reddish		d	c	rocks, often with vegetation
<i>Scincus mitranus</i>	blue	absent	+	d	g	+ sand
<i>Scincus s. conirostris</i>	?	absent	?	d	g	+ sand
AGAMIDAE						
<i>Agama adramitana</i> , males		red		d	c	+ boulders etc.
<i>Agama flavimaculata</i> *, males		red		d	g/c	scrub etc.
<i>Agama sinaita</i>				d	c	+ boulders etc.
<i>Phrynocephalus arabicus</i> *	dark tip, black and white bars below	as young		d	g	+ sand
<i>Phrynocephalus maculatus</i> *	dark tip, black and white bars below	as young		d	g	+ salt flat etc.
<i>Uromastyx microlepis</i> *				d	g	+
<i>Uromastyx thomasi</i> *				d	g	+

Table 6. Lizards with conspicuous tail colouring in Europe west of the U.S.S.R.

	Conspicuous tail colouring		Tail colouring more intense distally	Main activity period: nocturnal—n, or diurnal—d	Mainly climbing—c, or ground dwelling—g	Frequently found in open microhabitats
	young	adults				
Gekkoniidae						
<i>Cyrtodactylus kotschaji</i>	light and dark bars	reduced	+	n/d	c	
<i>Hemidactylus turcicus</i>	light and dark bars	reduced	+	n	c	+
<i>Phyllodactylus euroaesus</i>	light and dark bars	reduced	+	n	c	
<i>Tarentola mauritanica</i>	light and dark bars	reduced	+	n	c	+
Lacertidae						
<i>Acanthodactylus erythrurus</i>	red	absent	+	d	g	+
<i>Lacerta bedriagae</i>	blue	reduced or absent	+	d	c	+
<i>Lacerta horvathi</i>	pale blue-green	absent	+	d	c	+
<i>Lacerta monticola</i>	blue	absent	+	d	c	+
<i>Lacerta ocycephala</i>	blue and black bars	rather less bright	+	d	c	+
<i>Lacerta perspicillata</i>	blue	reduced	+	d	c	+
<i>Lacerta schreiberi</i>	orange or yellowish	absent	?	d	g(c)	+
<i>Podarcis hispanica</i> (some populations)	blue	absent	+	d	c	+
<i>Podarcis tilfordi</i> (some populations)	blue	reduced or absent	+	d	c	
<i>Podarcis muralis</i> (some populations)	greyish	absent	+	d	c	+
<i>Podarcis peloponnesiaca</i> (some populations)	blue	absent	+	d	c	+
<i>Psammotromus alpinus</i>	orangish	absent	?	d	(c)	dense vegetation
Scincidae						
<i>Ophiomorus punctatissimus</i>	stronger spotting	reduced	+	—	g	subterranean

The possibility that conspicuous tails divert attention from the head and body will be explored further by examining their distribution in two lizard communities: those of eastern Arabia and Europe west of the U.S.S.R. They have been chosen because I have personal experience of them in the field, so relevant information is fuller. Thus life colours that disappear in preserved specimens have been noted and some tail displays observed and assessed under natural conditions. Notes on the ecology of the species concerned may be found elsewhere (Arnold and Gallagher 1977, Arnold *et al.* 1978, Arnold 1980 b, 1984). The known occurrence of bright tails in these communities is set out in tables 5 and 6. A number of regularities are apparent and are discussed below.

1. In nearly all cases where it is present, conspicuous tail colouring is substantially exposed in the living lizard. It typically occurs on the dorsal surface and is most intense here, although it may extend beneath the tail as well. The main exceptions to this are the two Arabian species of *Phrynocephalus* where, although the tail is only dark-tipped above, it is strongly barred black and white beneath. Observations in the field suggest that this colouring is often not exposed when lizards are in immediate danger of capture. Instead, the tail is raised and curled in response to lizards of the same species and sometimes on the appearance of other, larger animals, possibly as an indication that capture may be expensive in terms of effort.

Permanently exposed bright tail colouring is likely sometimes to draw the attention of predators to lizards that might otherwise have gone undetected. At first sight, a better strategy would be to have conspicuous colouring concealed, for instance beneath the tail, and exposed only when a predator is at close quarters. This however would require the predator to be detected quite early in its approach, to give time for the tail colouring to be deployed. Most lizards may not be able to afford the high degree of vigilance involved, especially at times when their attention is largely devoted to hunting. In these circumstances, the risk inherent in permanently exposed bright colouring, of sometimes attracting a predator that otherwise might have passed the lizard by, may be offset by the advantage of predator attention being constantly directed towards the tail.

2. In species where it is present, conspicuous tail colouring is better developed in young than in adults and, in many cases, disappears entirely before maturity. This could reflect the generally greater vulnerability of juveniles to predation. Being small, they can be tackled by a greater range of predators. They are also frequently more delicately built than equivalent-sized adult lizards, for example ossification of the skull is often incomplete. In addition to this, newly hatched or dispersing juveniles are unfamiliar with their immediate surroundings and cannot flee to refuges or otherwise evade capture with the speed and facility that detailed knowledge of a home range gives.

3. Conspicuous tail colouring is typically associated with open environments where vegetation and the shadows it throws are relatively sparse. Thus in Arabia contrastingly coloured tails are found in ground-dwelling forms from open sand and harder substrates, such as members of the genera *Acanthodactylus*, *Scincus*, *Stenodactylus* and *Teratoscincus* and in *Mesalina ayunensis*. They also occur in species climbing on continuous open surfaces, especially rock faces. These include *Lacerta cyanura* and the geckoes *Hemidactylus turcicus*, *H. yerburi*, *Phyllodactylus elisae*, *P. gallagheri* and *Pristurus celerrimus*. In contrast, bright tails are absent in lizards that habitually occur in litter, dense vegetation or on rocky surfaces with good plant cover; among these are *Bunopus tuberculatus*, *Pristurus minimus*,

Mesalina brevirostris, *Ablepharus pannonicus*, *Chalcides ocellatus*, *Mabuya aurata*, *M. brevicollis* and *M. tessellata*. In Europe, where most lizard habitats are more enclosed than in Arabia, bright tail colour is uncommon and really distinct examples occur mainly in species that frequently climb on open surfaces. It occurs in a variety of rock dwelling species but, even among these, it is absent from forms like *Lacerta graeca* and *L. mosorensis* that are most frequently found quite close to cover or in shade. *Acanthodactylus erythrurus*, an open ground dweller in southwestern Europe also has a brightly coloured tail when young.

Lizards living in such open, uniform habitats are often quite easily seen. Even when dorsal colouring matches their background, outlines and the characteristic shadows that lizards throw are often poorly concealed.

4. Most of the species with conspicuous tails listed in tables 5 and 6 are active forms. Many, like the lacertids and skinks, are wide-ranging foragers that move continuously as they hunt. A number of geckoes are also quite mobile when feeding; these include *Hemidactylus homoeolepis*, *H. yerburii*, *Phyllodactylus elisae* and *Stenodactylus* species. Whether there is a real correlation between bright dorsal colour that attracts attention to an autotomizable tail and activity cannot really be checked on the Arabian and European lizard communities as inactive species are not very numerous and most of them are agamids lacking a caudal autotomy mechanism. However, among the lizards of the United States that are capable of shedding their tails, conspicuous colouring is much commoner in actively hunting groups like teiids (*Cnemidophorus*) and skinks (*Eumeces*) than among the iguanids which are largely 'sit and wait' hunters.

5. Nocturnal species with conspicuous tails, which in the communities considered here are all members of the family Gekkonidae, nearly always have the tail patterned with dark and light areas, frequently forming transverse bands. In contrast, most diurnal forms have bright colours of which by far the commonest are blue and blue-green. This difference correlates with the usual visual capacity of nocturnal and diurnal predators. Night operating hunters have poor colour vision and probably the most conspicuous objects to them are ones where light and dark areas are juxtaposed; many diurnal hunters on the other hand can distinguish colours.

The predominance of blue and blue-green colouring in diurnal lizards may be adaptive in that, to human eyes at least, blues and blue-greens are conspicuous close to but much less arresting at a distance when compared to reds and yellows. If natural predators of day-active lizards have the same differential colour sensitivity, blue would have the advantage of making the tail stand out at close quarters but would be less likely than reds and yellows to attract predators from a distance. In Arabia, *Pristurus celerrimus* and *Phrynocephalus* are exceptional in being diurnal but having black and white tail markings. In both cases, the tail appears to be used in intraspecific signalling (Arnold and Gallagher 1977, Arnold 1984) and perhaps its greater conspicuousness is advantageous in this context. Whether predation is incidentally increased is unknown. In *Phrynocephalus* the black and white markings are beneath the tail and concealed for most of the time while *Pristurus celerrimus* is very fast and agile.

Variation in rate and extent of tail regeneration

Most lizards that autotomize the tail regenerate the shed portion and, in the majority of cases, the greater part of it is replaced quite rapidly. For instance,

Lacerta dugesii may produce a regenerate 90% the length of the original portion lost in twelve weeks (Bryant and Bellairs 1976). In contrast, a number of forms regenerate very slowly, if at all. Leaving aside the agamids that have intervertebral autotomy but do not reproduce the shed portion of the tail, very low or nil regeneration rates appear to be most frequent in elongate, usually legless lepidosaurs that burrow in earth or live cryptically close to the earth-vegetation interface or under objects. Thus, *Anguis fragilis* typically produces less than a 5 mm long regenerate in 14 weeks (Bryant and Bellairs 1976) and growth rate in the skink *Ophiomorus streeti* may be slower still (Rathor 1971). Similarly, Miller (1944) reports that a captive *Anniella pulchra* developed a regenerate of only 4.1 mm in eleven months. Detailed information on regeneration rates is not available for other lizards with this general life mode but only small regenerates are found in museum material of many of them, suggesting that tail replacement is very incomplete, or at least extremely slow. This appears to be true of the anguids, *Ophisaurus* and *Ophiodes* and such skinks as *Acontias*, *Melanoseps*, *Ophiomorus* species in addition to *O. streeti*, *Parachalcides*, *Scelotes* and *Sphenops*. As previously noted, there is no caudal regeneration at all in autotomizing amphisbaenians or in the few colubrid snakes that shed portions of the tail.

It seems probable in the lizards listed above, which have the ability to regenerate albeit slowly, that rate and extent of tail replacement is determined by the balance of present costs and benefits rather than by historical factors. Possible benefits of regeneration include the wide range of tail uses listed on p. 138. Costs on the other hand may involve the energetic and material expense of replacing the tail and that of maintaining it subsequently. In fact benefits may not be high in these lizards for few of the potential advantages of possessing a tail seem likely to be important to them. It may contribute to locomotion but, in forms employing serpentine progression amongst herbage or in loose soil, additional length may not increase locomotion rate once a critical total is exceeded. The tail may also be less important as an anti-predator device in these largely cryptic forms. Nevertheless, in at least some of them, it seems to allow breaking away from predators and may do so more than once, in spite of poor regenerative capacity. In *Anguis*, for instance, although many animals have damaged tails these are rarely broken close to the vent and often most of the organ is still present. This suggests that losses are often small and that the tail may be able to function in a number of predator encounters, even though there is little regrowth between them. Costs of regeneration may be considerable and possibly they are important in dictating very restricted replacement in slow growing forms like *Anguis*. In such cases, the loss of a portion of the tail may even have advantages in allowing more energy to be devoted to reproduction.

Summary

The ability to shed (autotomize) all or part of the tail, usually in response to predator attack, and often to subsequently regenerate it is widespread in lizards and amphisbaenians and also occurs in a few snakes and in the tuatara. Most species possess a sophisticated intravertebral autotomy mechanism which seems to be primitive in the Squamata. This appears to have been independently lost in members of many groups, but some agamids and snakes have regained the ability to shed their tails by a simpler intervertebral means and a number of agamids have also re-developed tail regeneration as well.

Breakable tails are used to evade capture in two main ways: by enabling reptiles to break away from predators that have grasped them by the tail and by providing a distraction which deflects the attention of the attacker away from the vulnerable head and body. It is argued that loss of caudal autotomy has occurred when the costs of tail shedding outweigh its benefits. Likely costs include the expense of regrowing the tail and the loss of a variety of possible tail functions that may cause partial incapacitation, at least until the tail regenerates. Benefits of autotomy are liable to be low if predation is rare, if the animal is able to protect itself effectively in other ways, if it is too slow to evade further pursuit after the tail is shed, or if the tail is small or unpalatable and consequently not likely to distract a predator. Benefit variation may well be greater than cost variation and therefore more important in initiating the loss of autotomy mechanisms. Many taxa that do not shed the tail appear to conform to the above interpretation, but in some cases, such as the *Platynota*, *Agamidae* and *Chamaeleonidae*, lack of intravertebral autotomy may reflect the history of these groups rather than being a direct result of present ecological pressures. The distribution of intervertebral autotomy in the *Agamidae* suggests that it may have evolved only in rather special circumstances where tail fragility is advantageous even in the absence of the ability to regenerate.

Restriction of autotomy planes to the tail-base, so that the whole organ is lost, a condition found in a number of relatively slow-moving geckoes, is interpreted as a means of ensuring that enough of the tail is shed to distract a predator from further pursuit. The stimulus necessary to induce autotomy can vary rapidly in individual lizards and at least some of these changes probably maximize the effectiveness of the tail-shedding mechanism. Differences in the readiness with which all or part of the tail is shed exist between species and are likely to reflect the balance of costs and benefits in particular cases. Variations in incidence of broken tails between species and populations may be due to such differences in fragility but many other factors may play a part, including the age structure of samples, incidence of unsuccessful attacks by predators and ability to evade predators after autotomy. There is a clear tendency for climbing lizards, especially those living on rock surfaces, to have higher incidences of broken tails than ground-dwelling species, perhaps because the tail is usually less important in locomotion in the first group. Many lizards possess conspicuously coloured tails and tail movements that seem likely to help distract attention from the head and body. Conspicuous tail colouring is more frequent and often better developed in young animals, which tend to be more vulnerable than adults, and in active species from open habitats where crypsis may not always be very effective. Conspicuous tails usually have contrasting light and dark areas in nocturnal forms but are often a single bright colour in diurnal ones, probably reflecting the visual capacities of their respective predators. The predominance of blue tails in day-active species may be because this colour is striking close to but not very arresting at a distance, so it may not attract predators from far away while still drawing their attention at close quarters.

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