



Exceptional occurrences of double, triple and quintuple tails in an Australian lizard community, with a review of supernumerary tails in natural populations of reptiles

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Abstract. For centuries, tail duplications in reptiles have attracted human curiosity, and publications on anecdotal observations of supernumerary tails have grown considerably over recent years. However, there is no recent review on the occurrence of supernumerary tails in reptiles and the consequent effects on individuals. We provide new data on the frequency of supernumerary tails, including unprecedented frequencies and observations of tail triplication and quintuplication, from our own studies in arid Australia and from literature reviews. Our observations include data for a gecko species (*Gehyra variegata*) and three species of skinks (*Eremiascincus richardsonii*, *Lerista punctatovittata*, *Morethia boulengeri*) for which supernumerary tails have not been reported so far. We assume that hyperregeneration (following injuries inflicted by predators, sharp-edged window glass, and unknown factors) was the cause for the cases observed by us. Our review spans two millennia of published works describing supernumerary tails in 146 identified species of reptiles and up to 16 unidentified species. We assess the taxonomic and geographic distributions and the microhabitats of these 146 species, while also commenting on the potential causes and effects of supernumerary tails. The identified species belong to 16 families of lizards, one of amphisbaenians, three of snakes, the tuatara (*Sphenodon punctatus*), three turtle families, and one family of crocodyles. The geographic patterns of supernumerary tails are difficult to interpret due to an imbalance in published works from the major geographic areas. The vast majority of the species affected have a terrestrial lifestyle, followed by arboreal species. The frequency of supernumerary tails is low, with multiple tails having been reported only for 59 individuals, including our new data. Little is known about the effects of supernumerary tails on their carriers. In our study, there was no indication of them affecting mobility or increasing mortality. Some authors reported handicapped movement, whereas others did not find such effects, and both males and females with tail bifurcation/duplication were able to mate successfully. Most cases of supernumerary tails are likely to be due to hyperregeneration as a reaction to injuries or incomplete breaks of vertebral fracture planes. However, only one study statistically identified the culprits as predatory mammals. In captivity, such injuries were also inflicted through attacks by conspecifics and during copulation. The few cases in natural populations that were not due to hyperregeneration were presumably caused by unknown teratogenic factors to which the individuals were exposed during ontogeny; in one case this was most likely to be radioactive contamination.

Key words. Australia, *Eremiascincus richardsonii*, *Gehyra variegata*, *Lerista punctatovittata*, *Morethia boulengeri*, Squamata, geographic distribution, herpetological history, individual effects, microhabitat, tail duplication, tail multiplication.

Introduction

For centuries, tail duplications in reptiles have attracted human curiosity (PLINIUS SECUNDUS MAJOR 77, ALDROVANDI 1642, 1645, PORTA 1644, REDI 1684, SEBA 1734, 1735, MARCHANT 1741, NEEDHAM 1750, GEOFFROY SAINT-HILAIRE 1832, 1836). Many anecdotal observations have since been reported and stimulated experimental studies of tail regeneration in lizards (PERRAULT 1721, GACHET 1834, FRAISSE 1885, TORNIER 1897, DAS 1932, BELLAIRS & BRYANT 1985, ALIBARDI 2010). Comprehensive reviews of the early literature on experimental studies and observations of nat-

ural populations have been published by GACHET (1834), LEYDIG (1872), FRAISSE (1885) and PRZIBRAM (1909). More recent experimental literature was reviewed by BELLAIRS & BRYANT (1985) who also mentioned a few observations in natural populations. In contrast to tail duplications in amphibians (HENLE et al. 2012, 2017) and axial duplication in snakes (JOHNSON 1902, SWANSON et al. 1997, WALLACH 2007, 2016, WALLACH & SALMON 2013), there are only two other more recent reviews about supernumerary tails of reptiles in natural populations (MATZ 1989, PAYEN 1991).

Whereas the literature on anecdotal observations of supernumerary tails has grown considerably over recent

years (Fig. 1), few studies have provided information about the frequency of their occurrence (for references see the review below). Likewise, very few studies have addressed the retention and effect of supernumerary tails on individuals. Assessments of the taxonomic and geographic distributions of supernumerary tails are also lacking, and there has been no recent review of supernumerary tails in natural populations of reptiles.

Here, we intend to fill these gaps from our own studies in arid Australia. Our observations include data for a gecko species and three skink species for which supernumerary tails have not before been reported. They also reveal this phenomenon to be exceptionally frequent in one species. This report also includes observations of two individuals with five tail (tips), which is an anomaly that has been recorded only once before in nature (CHAN et al. 1984); PELEGRIN & LEÃO (2016) recently found a lizard with six tails.

We furthermore provide a comprehensive review on the occurrence of tail bifurcations, duplications and multiplications in natural populations of reptiles, including an early historical perspective. We review their taxonomic, geographic and microhabitat distributions and assess their impacts on individuals. Finally, we provide a discussion of potential causes.

Methods

Terminology

Terms for supernumerary tails differ considerably among publications, especially when two tails were observed. We classified cases as bifurcation, if the splitting occurred distal to the mid-length of the longest tail, and as duplication, if the splitting was proximal to the mid-length. Published cases were allocated to these categories based on photographs and descriptive text. If the information available was insufficient, we classified cases as “no details” provided.

Study sites and sampling of lizards

Our observations stem from a long-term study that began in 1985 in the Kinchega National Park (32°28' S, 142°20' E), New South Wales, Australia, and was continued until 2016. Sampling was carried out for most years (GRIMM-SEYFARTH et al. 2019). We sampled three main study sites during 30 capture periods, each lasting approximately three weeks: the seven huts of the Kinchega Station (Station: HENLE 1990a, GRIMM-SEYFARTH et al. 2019), one site each in black box (*Eucalyptus largiflorens*), riverine woodland on grey cracking soil (RI site: HENLE 1990a, 1990b, GRIMM-SEYFARTH et al. 2019), and at the base of a red sand dune (RII site: HENLE 1989a, 1989b, GRIMM-SEYFARTH et al. 2019). We sampled two additional sites: a red sand dune with *Dodonaea attenuata* (Dune site: HENLE 1990b) and an ecotonal zone of blue bush (*Maireana* spp.) steppe and black box woodland adjacent to the old Kinchega Homestead (Homestead: HENLE 1989a) during ten capture periods, another site (Lunette) on the southern lunette of Lake Cawndilla during four capture periods, and a further site within a stand of *Casuarina pauper* trees near the kangaroo enclosure south of Lake Cawndilla (Casuarina) during one capture period. Furthermore, cursorial sampling was carried out adjacent to the main study sites. While RI, RII, the Station and the Dune were adjacent sites harbouring subpopulations that probably belonged to a metapopulation with individuals dispersing occasionally among sites, the Homestead was 2.4 km distant and was therefore considered to be home to a separate population.

We caught reptiles by hand on all sites, except at Lunette and Casuarina. On these latter sites, we sampled individuals using pitfall traps (11l-aluminium ice-cream containers). On the dune, RI and RII sites, we also sampled individuals using 25, 25 and 24 pitfall traps, respectively (only September 1985 to January 1986 at site RI). We measured all individuals and identified their sexes if species were sexually dimorphic. We marked individuals by photo-identifi-

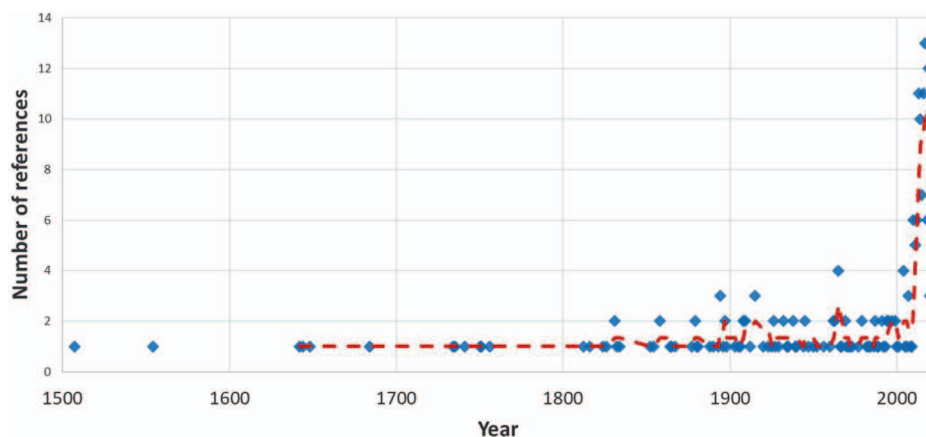


Figure 1. Annual distribution of the number of cases of tail multiplications reported. Dates refer to the year of publication and not the year of observation (which is rarely specified). The red dashed line refers to the change in averages over 5 years.

cation or toe-clipping (if photo-identification was not feasible) for long-term identification and with paint marks for short-term individual identification. We released all captured individuals at the location of their capture on the same day.

Taxonomy for the Australian species follows COGGER (2014), except for *L. aericeps*, which GREER (1990) showed to be a synonym of *L. xanthura*. To calculate the frequency of individuals with supernumerary tails, we counted each individual as having a supernumerary tail if it had one on any capture occasion even if on other occasions it had not. We used the same method to calculate the frequency of individuals with regenerated tails. [Note, that sample sizes may marginally differ because data were recorded incompletely for a few individuals.] We compared these frequencies with the Spearman rank correlation accounting for ties in ranks (SACHS 1982). We calculated body condition by using the scaled mass index to account for growth (PEIG & GREEN 2009), following the protocol described by GRIMM-SEYFARTH et al. (2018). We only included first-time captures of individuals per capture period to calculate body condition.

Review methods

Starting in 1987, we collected any publication that mentions supernumerary tails for natural populations of reptiles. Searches in literature databases, such as Web-of-Science and even Zoological Record, retrieved only a small number of relevant publications. Therefore, our literature compilation relied mainly on the snowball system of tracing any potentially relevant cited publication. However, we only included those publications in our review that we could check ourselves. For comparisons, we extracted the annual number of publications referring to the keyword “Reptilia” from the Zoological Record and all databases accessible through the Web-of-Science until December 2019 [last accessed 05.03.2020]. We then compared the slope of increase in the number of publications per year that mention a supernumerary tail (Supplementary document S1) with that of all reptiles in Zoological Record and Web of Science.

We only considered data that were provided at least at genus level and that explicitly originated from natural populations or for which this was likely, as either the authors indicated that other specimens were captive animals, or because museum series were examined (even if data provided were only for the specimens with supernumerary tails). We relaxed these criteria for pre-1900 publications and also included individuals without identification and data that were not explicitly stated as applying to wild individuals if such an origin was plausible. We extracted the following data (if available): species name, number of individuals with supernumerary tails (broken down by number of tips), sample size, country, microhabitat, and the year of publication (Supplementary document S1).

Unless otherwise stated, nomenclature follows COGGER (2014) for Australian reptiles and UETZ et al. (2019) for other species regarding generic names, name changes due to priorities and synonymies, and for subspecies identified in the source reference that were later granted full species rank. Name changes due to the splitting of taxa into several species were made only if allocation of the data to the new species was obvious from morphological or geographic information provided by the assessed source reference or if this had already been done by other authors. Subspecies names were added if provided by the source publication.

We classified species into microhabitat categories (aquatic, arboreal, saxicolous, semi-aquatic, subterranean, terrestrial) based on references provided in Supplementary document S2. We allocated species that use more than one of these microhabitat categories to the category most frequently used.

The individual in the Natural History Museum Vienna (NMV) examined by us and the one deposited by us in the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, (ZFMK) are listed in Appendix 1.

Results

Field observations

In total, we caught 5,976 different individuals of 16 lizard species at the five study sites (Table 1). Nine species had sample sizes of at least 50 individuals. In six of these species (*Diplodactylus tessellatus*, *Heteronotia binoei*, *Lucasium damaeum*, *Ctenotus regius*, *Lerista xanthura*, and *Tiliqua rugosa*), no individual with a supernumerary tail was observed. Of these, *L. xanthura* is a fossorial species, and the remaining ones are terrestrial species (HENLE 1991); *D. tessellatus* has a specialized tail for fat storage (GREER 1989), which is used as a lever to liberate itself from a firm grip (KH, unpubl. observations). Supernumerary tails were observed in four species: *Eremiascincus richardsonii*, *Lerista punctatovittata*, *Morethia boulengeri*, and *Gehyra variegata*. Details are given below.

Across all species with a sample size of at least 50 individuals, the frequency of individuals with supernumerary tails was marginally significantly correlated to the frequency of individuals with regenerated tails (Spearman rank correlation: $r = 0.57$, $a = 0.09$) (Table 2a). For *M. boulengeri*, the ranking was the same, but it differed for *G. variegata*, with the RII subpopulation being an outlier in terms of individuals with regenerated tails (Table 2b, c). However, the number of (sub-)populations with sufficient sample sizes ($n = 3$ per species) was too small to assess significance.

Eremiascincus richardsonii with tail bifurcation

We caught an adult individual [SVL (snout–vent length): 83 mm, TL (tail length): 107 mm] with a tail bifurcation at the Kinchega Station on 1 March 2014. The tail had regenerated at 67 mm anterior to the bifurcation, with one

Table 1. Number of individuals with supernumerary tails and sample sizes for lizard species caught in Kinchega (1985–2016). N: sample size; #: Number of individuals with supernumerary tails. Not all species were found on each site.

Species	Site	N	# duplication or bifurcation	# multiplications
<i>Ctenophorus pictus</i>	All	4	0	0
<i>Pogona vitticeps</i>	All	19	0	0
<i>Diplodactylus tessellatus</i>	RI	446	0	0
<i>Lucasium byrnei</i>	All	2	0	0
<i>Lucasium damaeum</i>	All	159	0	0
<i>Rhynchoedura angusta</i>	RII	3	0	0
<i>Gehyra variegata</i>	Station (Hilton Hut)	487	11	3
<i>Gehyra variegata</i>	Station (all other huts)	1692	19	1
<i>Gehyra variegata</i>	RI	1052	8	0
<i>Gehyra variegata</i>	RII	74	0	0
<i>Gehyra variegata</i>	All other study sites	28	1	0
<i>Heteronotia binoei</i>	All	201	0	0
<i>Ctenotus regius</i>	All	160	0	0
<i>Eremiascincus richardsonii</i>	All	92	1	0
<i>Lerista punctatovittata</i>	All	198	2	0
<i>Lerista xanthura</i>	All	57	0	0
<i>Menetia greyii</i>	All	13	0	0
<i>Morethia boulengeri</i>	RII	891	2	0
<i>Morethia boulengeri</i>	Homestead	245	1	0
<i>Morethia boulengeri</i>	All other sites	99	0	0
<i>Tiliqua rugosa</i>	All	50	0	0
<i>Varanus gouldii</i>	All	4	0	0

branch measuring 15 mm and the other one 13 mm (Fig. 2). During the 2014 capture period and over the entire study period, we caught four and 92 individuals, respectively. The latter amounts to 1.1% of the individuals with tail bifurcations.

We observed the individual with tail bifurcation several times throughout the capture period in 2014, usually moving about and hunting normally, but it was not seen again in 2015 or 2016. That said, no *E. richardsonii* was observed in 2015/2016 at this study site at all, suggesting the possibility of other reasons for its disappearance than the bifurcated tail. During the entire study, we caught one individual in which ants had recently nibbled off parts of its tail, but we never recaptured it. Another individual showed a buckled regenerated tail. We observed no other tail anomalies.

Lerista punctatovittata with tail bifurcation

We caught two adult individuals (SVL: 87 mm, TL: 55 mm; SVL: 85 mm, TL: 59 mm) with bifurcated tails at the old Kinchega Homestead on 8 and 24 September 1986, respectively. For the latter individual, the distal 8 mm of the tail were bifurcated, whereas the former individual only had a short lateral supernumerary tail bud. During that capture period, we caught 27 different individuals. With a sample size of 198 different individuals captured throughout the



Figure 2. Tail bifurcation in an adult *Eremiascincus richardsonii*, Kinchega National Park, 1 March 2014 (Photo: K. HENLE).

Table 2. Percentage of individuals with regenerated tails and with supernumerary tails in species sampled in Kinchega National Park for sample sizes ≥ 50 ; a) all populations of a species pooled, b) for *Gehyra variegata* subpopulations and c) *Morethia boulengeri* (sub-)populations.

a) All species, (sub-)populations pooled		
Species	Regenerated tails	Supernumerary tails
<i>Diplodactylus tessellatus</i>	31.6	0
<i>Gehyra variegata</i>	53.6	1.29
<i>Heteronotia binoei</i>	55.4	0
<i>Lucasium damaeum</i>	14.4	0
<i>Ctenotus regius</i>	10.5	0
<i>Eremiascincus richardsonii</i>	50.5	1.09
<i>Lerista punctatovittata</i>	48	1.01
<i>Lerista xanthura</i>	45.6	0
<i>Morethia boulengeri</i>	45.4	0.24
<i>Tiliqua rugosa</i>	0	0

b) <i>Gehyra variegata</i> subpopulations		
Population	Tail loss	Supernumerary tails
RI	52.9	0.76
RII	60.8	0
Station	53.5	1.56

c) <i>Morethia boulengeri</i> (sub-)populations		
Population	Tail loss	Supernumerary tails
Homestead	59.9	0.41
RII	42.7	0.22
All other sites combined	33.7	0

entire study period at all study sites, the frequency of tail bifurcation amounts to 1%. We did not observe these individuals again on any of the consecutive sampling days in 1986 or in the following years. We captured another individual with an injured tail but did not recapture it. We did not observe any further individual with a tail anomaly.

Morethia boulengeri with tail bifurcation

We caught two adult individuals (SVL: 44 mm, TL: 48 mm; SVL: 43 mm, TL: 62 mm) with bifurcated tails at the site RII on 20 February 2012 and 11 February 2016, respectively. We also caught an adult female (SVL 46 mm, TL: 48 mm) with a bifurcated tail tip at the site Homestead on 17 September 1985. For the first two individuals, one branch of the bifurcated tail measured 18 mm, the 2nd branch 16 mm (Fig. 3a) and 6 mm and 2 mm (Fig. 3b), respectively. In addition, on 13 February 2013, we caught an adult male (SVL: 40 mm, TL: 43 mm) that might have developed a tail bifurcation afterwards (Fig. 3c).

At the RII site, we captured 29, 28, and 19 different individuals in 2012, 2013, and 2016, respectively. Throughout the whole study period, we caught 891 individuals; thus, the frequency of tail bifurcations across all years was 0.2%. At the Homestead site, we caught 245 different individuals between 1985 and 1987, amounting to a frequency of tail bifurcation of 0.4%. At all other sites, we caught 99 individuals; none of them exhibited a supernumerary tail.

We did not observe the individual with the tail bifurcation in 2012 or the female from Homestead again on any of the consecutive sampling days in the same or the following years. However, the one from 2016 was observed regularly throughout the 2016 capture period.

We also observed five individuals with incompletely detached tails. Two of them were observed again during the same capture period (i.e., within less than 3 weeks) without any indication of tail bifurcation. In addition, we observed 39 individuals that had recently lost their tails, of which nine were recaptured in the following years. None of them developed tail bifurcation.

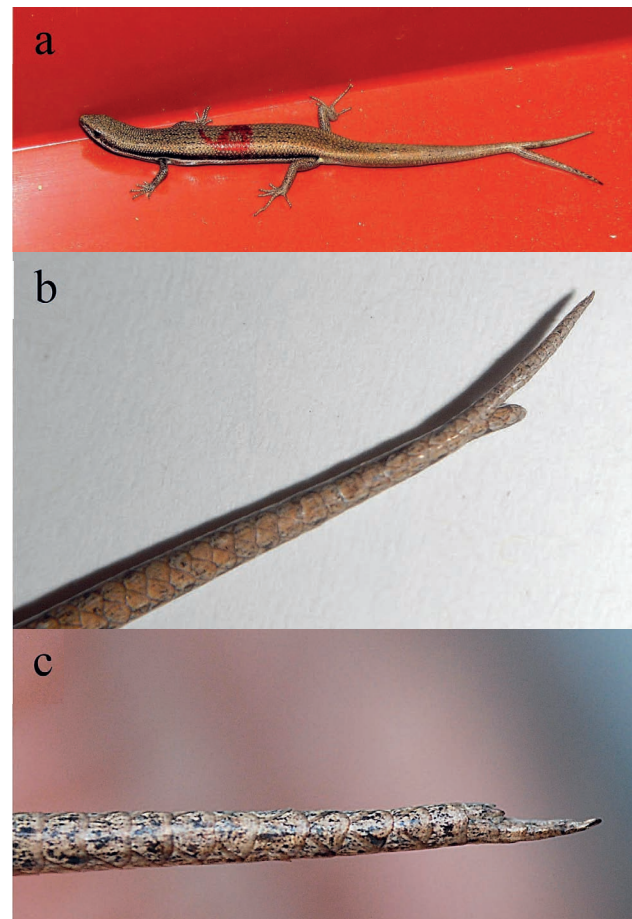


Figure 3. Tail bifurcation in two adult *Morethia boulengeri*, Kinchega National Park, a) 20 February 2012, b) 11 February 2016, and c) a possibly beginning tail bifurcation in an adult male, 13 February 2013 [Photos: K. HENLE (Fig. 3a); GRIMM-SEYFARTH (Figs 3b & c)].

Supernumerary tails in *Gehyra variegata*

In total, we captured 43 individuals with supernumerary tails, eight at the RI site, 34 at the Station, one at the Dune site, and none at the RII site (Table 1). The percentage of individuals with supernumerary tails was marginally significantly higher ($\chi^2 = 2.87$, $\alpha = 0.09$) at the Station (1.6%) than at the RI site (0.8%). At the Station, fourteen individuals (2.9%, $n = 487$) with supernumerary tails lived on one hut ("Hilton") and 20 (1.2%, $n = 1692$) on the other six huts combined (Table 1). This difference is statistically significant ($\chi^2 = 5.74$, $\alpha = 0.02$). Of the eight individuals at the RI site, six were adults and two were subadults; four were females, three were males, and one was too small for sexing. Of the 34 individuals at the Station, 29 were adults, four were subadults, and one was a juvenile; 14 were males, 17 were females, and three were too small for sexing.

At the RI site, all individuals with supernumerary tails showed bifurcation, with lengths ranging from 1 to 8 mm. At the Station, the lengths of the two tail tips for 22 individuals with tail bifurcations (Fig. 4a) ranged from 0.5 to 19 mm ($n = 8$ at the Hilton Hut, $n = 14$ for all other huts). Of the remaining 12 individuals with supernumerary tails, seven (3 on the Hilton Hut, 4 on all other huts) had tail duplications (Fig. 4b), four (3 on the Hilton Hut, 1 on all others) exhibited tail triplication (Fig. 5), and two individuals

on the Hilton Hut showed quintuplication. The individual captured at the Dune site had a supernumerary tail bud at the base of the tail (Fig. 4c). The body condition of individuals with and without tail multiplications did not differ at RI (t-test, unpaired, $t = -0.29$, $df = 22.6$, $p = 0.77$, $n = 1922$, mean scaled mass index = 2.16 and 2.17 for individuals with and without tail multiplication, respectively) or in the Station sub-population (t-test, unpaired, $t = 0.93$, $df = 87.9$, $p = 0.36$, $n = 4025$, mean scaled mass index 2.66 and 2.62 for individuals with and without tail multiplication, respectively).

Of the eight individuals with tail bifurcations at the RI site, 75% were recaptured in following capture periods and thus had survived until the next year. Two of the six recaptured individuals still possessed their tail bifurcations. From the other four individuals, two had lost their tails at the previous point of bifurcation (hence, they lost their forks) and two had autotomized their tails more proximally. Of the 29 individuals with tail bifurcations or duplications at the Station, 14 individuals were recaptured during subsequent capture periods (48.3%). While five of them still exhibited tail bifurcations/duplications, six had lost their tails at the point of the previous bifurcation/duplication, and three had lost their tail proximally. One of the individuals that had repeatedly been recaptured with tail bifurcations, again lost its tail proximally after four years.

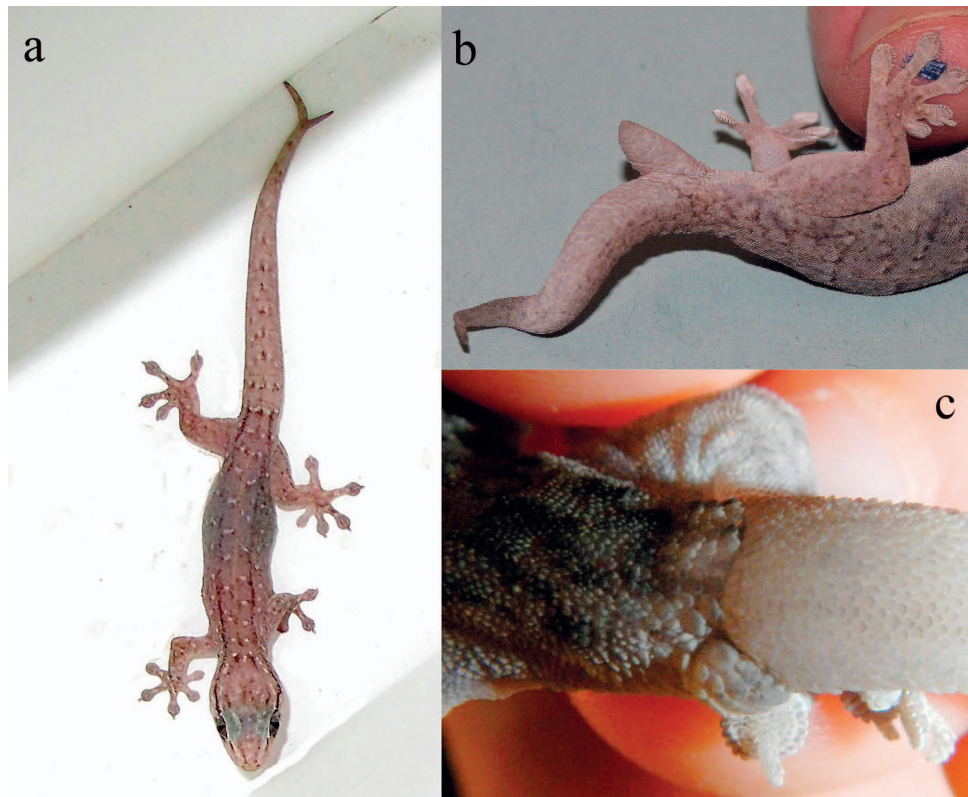


Figure 4. Various types of tail bifurcation or duplication in *Gehyra variegata*. a) adult male with a bifurcated tail tip, Kinchega Station, 20 February 2012; b) adult female with tail duplication, Kinchega Station, 3 February 2013; c) adult female with a small bud at the base of the regenerated tail, Dune study site, 19 February 2016 (Photos: A. GRIMM-SEYFARTH).

Since cases of triplications and quintuplications are rare in natural populations (see review below), we will describe them in more detail. An old female (SVL: 55 mm) with a tail triplication was captured on the Hilton Hut in February 2012. It was first caught as a juvenile in 2001 and recaptured as an adult with a regenerated tail in 2003 and 2005. The tail had regenerated at the tail base, which was unusually thick. The triplication started 5 mm further distal and the two smaller supernumerary tails measured 12 and 13 mm from the triplication point, respectively. The longest tail was 37 mm in total and exhibited a second regeneration point 9 mm distal to the tail base (Fig. 5a). This individual with a triplication was recaptured several times during the 2012 capture period. It had lost its tail at the point of multiplication with a single 27 mm long regenerate in 2013, which had grown to 30 mm when it was recaptured in 2016. Another adult female (SVL: 55 mm) marked in February 2000 on the Hilton Hut had developed a tail triplication when she was recaptured in March 2002, with the three tips measuring 25, 8 and 1 mm, respectively. The same individual exhibited a kink at the point of triplication. It was never recaptured again.

Most exciting are the cases of two adult females on the Hilton Hut. The first one (SVL: 58 mm) had a fully regenerated tail when it was first marked in March 1986, recaptured in November 1986 with no change to the tail, but exhibited a tail triplication in November 1991. This individual was recaptured in January 1992 when it was still displaying tail triplication. When it was recaptured again in January 1994, its tail had quintuplicated, with the longest supernumerary tail now measuring 9 mm. The individual was recaptured during the same capture period, but not in any of the following years. Another female (SVL: 52 mm) with a short regenerating tail (19 mm length) was first marked in November 1985. It was already adult, presumably at the end of its second year of life. After several recaptures in January and March 1986 with the regenerating tail having grown to 26 and 31 mm, respectively, it was recaptured again, now with a tail quintuplication, in November 1986. Three main tails originated at the base of the tail, the longest being 17 mm in length, and two of the three tails being bifurcated. It displayed tail multiplication throughout Novem-

ber and December 1986, but had lost its tail completely by January 1987. Until March 1987, it had been growing three new tails, all originating at the base of the tail (Fig. 5b). The three branches measured 17, 13 and 8 mm, respectively. This individual was later collected (ZFMK 49409).

We captured 39 individuals with injured or partly broken tails throughout the study, with 18 of them being recaptured during later capture periods. None of these injuries showed indications of developing into tail bifurcation, but one developed a kink at the point of the injury. It has already been observed by DUGÈS (1829) and WOODLAND (1920) that partially broken tails are usually completely detached before regeneration begins.

Three adult individuals with tail bifurcations at the Station exhibited kinked tails at the same time. Another adult male was noted for his having a large bulge laterally on the tail. As this did not classify as a supernumerary tail, we did not include it as an instance of tail duplication.

Review

Our review returned 231 primary publications that reported supernumerary tails in 455 individuals from 293 natural populations of reptiles representing 146 identified species (Supplementary document S1). PAYEN (1991) listed specimens from museum collections of which only some had been identified to species level and without information about their origins (specifically as to whether from captivity or natural populations). Therefore, we did not include these in our review data.

An early historical perspective

Two millennia ago, PLINIUS SECUNDUS MAJOR (77) mentioned tail duplications in lizards. According to ARNAULT DE NOBLEVILLE & SALERNE (1756) and TOFOHR (1905), ARISTOTLE (4th century BC) had also been aware of such cases, but our understanding of his writing is that he only knew that lizards and snakes (!) were able to regenerate their tails. (Note, these authors did not quote the exact



Figure 5. Two female *Gehyra variegata* with different types of triple tails, Kinchega Station; (a) 22 February 2012 (Photo: A. GRIMM-SEYFARTH); (b) 13 March 1987 (Photo: K. HENLE).

source of Aristotle that they were referring to.) It then took more than a thousand years before further observations of supernumerary tails were published: VESPUCCI (1507) reported lizards with bifurcated tails living on some oceanic islands “a 1000 leagues [≈ 5555 km] from Lisbon”. Later, GESNER (1554) wrote that he had received a sketch of a lizard with a tail duplication from a medical doctor from Meissen, Germany.

A century thereafter, ALDROVANDI (1642, 1645) summarized the knowledge about supernumerary tails in lizards. He supposed that lizards “born” with two or three tails were not rare. ALDROVANDI (1642) published drawings of five individuals, three with tail bifurcations, one with triplication at the tail base, and one with four tail tips. In the latter specimen, one tail was bifurcated twice. Presumably, these were the first illustrations of lizards with supernumerary tails. Two of the specimens with tail bifurcations were named “*Lacertus viridis*”. Under current taxonomy, one specimen, which was presumably from Liguria, Italy, but possibly both were *Lacerta bilineata*. Later on, JONSTON (1657) copied three of these illustrations (without quoting ALDROVANDI).

PORTA (1644) remarked that he had seen many lizards with duplicated or triplicated tails (without providing further details), and MARCGRAV (1648) even described a new species based on a lizard with a bifurcated tail as “*Ameiva brasiliensibus*”, which, according to CUVIER et al. (1831), is a species of *Polychrus*. Later, SEBA (1734) published a drawing of the same “species” with a bifurcated tail, but it remains unclear as to whether he was referring to the same specimen. A relatively short time after MARCGRAV, REDI (1684) also became aware of lizards with two tails and provided a sketch of one with three tails (twice bifurcated; possibly a species of *Podarcis*). Furthermore, he is one of the few authors who personally observed two snakes with two tails each.

In the 18th century, SEBA (1734, 1735) included drawings of six lizard species with bifurcated tails, but not all of them can be taxonomically identified. Subsequently, MARCHANT (1741) caught one *Podarcis muralis* with a triplicated tail – with the third tail being very small. NEEDHAM (1750) wrote that lizards with bifurcated tails were occasionally found in Portugal, and VALMONT DE BOMARE (1791) stated that lizards (presumably *P. muralis*) with two or three tails were not uncommon in France.

From 1863 (the year to which the Zoological Record dates back) until 1944, interest in reptiles with supernumerary tails grew significantly (linear model, scaled increase per year (slope) = 0.04, $p < 0.001$; Fig. 1) with an average of 0.5 publications per year (min = 0, max = 3). In comparison, the total number of publications about reptiles mentioned in the Zoological Record increased much less (linear model, scaled slope = 0.001, $p < 0.001$). From 1945 to 2000, the average number of publications mentioning supernumerary tails levelled off at one publication per year (min = 0, max = 4) with no further increase during the 20th century (linear model, scaled slope = 0.005, $p = 0.116$; Fig. 1). However, there was an increase in the number of

publications about reptiles in general based on the Web-of-Science (linear model, scaled slope = 0.03, $p < 0.001$) and the Zoological Record (linear model, scaled slope = 0.04, $p < 0.001$). In the 21st century, the increase became exponential with the relative increase in publications mentioning supernumerary tails in reptiles (linear model, scaled slope = 0.30, $p < 0.001$; Fig. 1) being three times greater than publications about reptiles in general based on the Web-of-Science (linear model, scaled slope = 0.11, $p = 0.001$) and 7.5 times greater based on the Zoological Record (linear model, scaled slope = 0.04, $p < 0.001$).

Taxonomic distribution

This review identified 146 species, for which supernumerary tails have been reported. They belong to 16 families of lizards, one of amphisbaenians (*Trogonophis wiegmanni*), three of snakes, the tuatara (*Sphenodon punctatus*), three testudinal families, and one crocodilian family (Supplementary document S1).

Most observations of supernumerary tails apply to individuals belonging to Lacertidae (162), Gekkonidae (89 cases), Scincidae (49), Teiidae (41), and Iguanidae (27) (Fig. 6). Within these families, many but not all species liberally autotomize their tails (BELLAIRS & BRYANT 1985). These numbers contrast with the opinion of TOFOHR (1903) who stated that geckos are less prone to developing bifurcation because of their outstanding ability to autotomize tails. Tail bifurcations and triplications have also been observed in at least eight species of agamids, which lack intra-vertebral fracture planes (BAIG et al. 2012). Nevertheless, the family Agamidae includes species in which tail breakage occurs frequently (BELLAIRS & BRYANT 1985, BATEMAN & FLEMING 2009, WAGNER et al. 2009).

With the exception of the agamids *Hydrosaurus weberi* and *H. cf. pustulosus*, which have elaborate tail fins, the crocodile *Caiman crocodilus* and the iguanid *Amblyrhynchus cristatus*, which have laterally flattened tails that are essential for swimming (DAWSON et al. 1977, BARR et al. 2019), all species in which supernumerary tails have been observed do not possess an elaborate tail structure or a functional specialization of the tail. However, in *H. pustulosus*, only the distal part of the tail, which does not have a fin, was bifurcated (GAULKE & DEMEGILLO 2006), and in *H. weberi*, the terminal bifurcation was only 11 mm long (COLWELL 1993).

Whereas BARBOUR (1926) claimed that snakes with two tails were unknown, ALDROVANDI (1640) reliably reported on two-tailed vipers, and REDI (1684) dissected two snakes with two tails. Our review found reports of twelve individuals with tail bifurcations or duplications in at least eight snake species from natural populations. In his review of axial duplication in snakes, WALLACH (2007) stated that 6.2% of 505 snakes from which axial duplication was known involved the duplication of tails. However, it remains unclear as to which of the specimens were captive-born or from the wild and which species were involved. He also published

a photographic atlas (WALLACH 2016) that contains photos of tail duplications in snakes of five species, but again it remains unclear as to which of them were from natural populations.

Reports are also available for other taxonomic groups that usually do not autotomize their tails: the amphisbaenian *Trogonophis wiegmanni* (BRINDLEY 1894), the crocodile *Caiman crocodilus*, and the turtles *Chelydra serpentina* (RAHMAN 2011), *Pseudemys peninsularis* (HILDEBRAND 1938), *Emydura* aff. *australis* (KUCHLING 2005), and *Phrynops tuberosus* (MOTA RODRIGUES & FEITOSA SILVA 2013).

Geographic distribution

Most reports of supernumerary tails stem from Europe (113 individuals). This is followed by 71 individuals from Oceania, including our own 48 observations from Australia, by 50 individuals from South America, 48 individuals from Asia, 46 individuals from North America, and 44 individuals from Central America (including the Caribbean, the Bahamas, and the Bermuda Islands). Only 14 individuals have thus far been reported from Africa. This biased geographic distribution of cases of supernumerary tails more likely reflects the long history, number of naturalists, and fieldwork carried out in the different continents rather

than the true distribution of supernumerary tails in nature. To assess the true distribution, systematic reporting as to whether supernumerary tails were observed or not, would be essential for all large-scale field studies.

Microhabitat distribution

All 146 identified species for which supernumerary tails have been reported could be assigned to one of our microhabitat categories (terrestrial, arboreal, saxicolous, subterranean, aquatic and semi-aquatic). Of those, 86 are primarily terrestrial, 29 are primarily arboreal, 13 primarily saxicolous, seven primarily subterranean, six primarily aquatic, and five are primarily semi-aquatic (Supplementary document S2). From our own observations at Kinchega NP in Australia, the frequency of supernumerary tails was lowest in the terrestrial skink *M. boulengeri* (0.2%) (Table 2a), followed by the arboreal gecko *G. variegata* in its natural habitat (0.7%) (sample sizes in Table 1) and the subterranean skinks *L. punctatovittata* (1%) and *E. richardsonii* (1.1%) (Table 2a). The highest rate of supernumerary tails was observed in the *G. variegata* living on the huts at Kinchega Station (mean all huts: 1.6%) (Table 2b).

Tail break frequency is related to the microhabitat in some lizard assemblages but not others (reviewed by BATEMAN & FLEMING 2009). For example, PIANKA & PIANKA

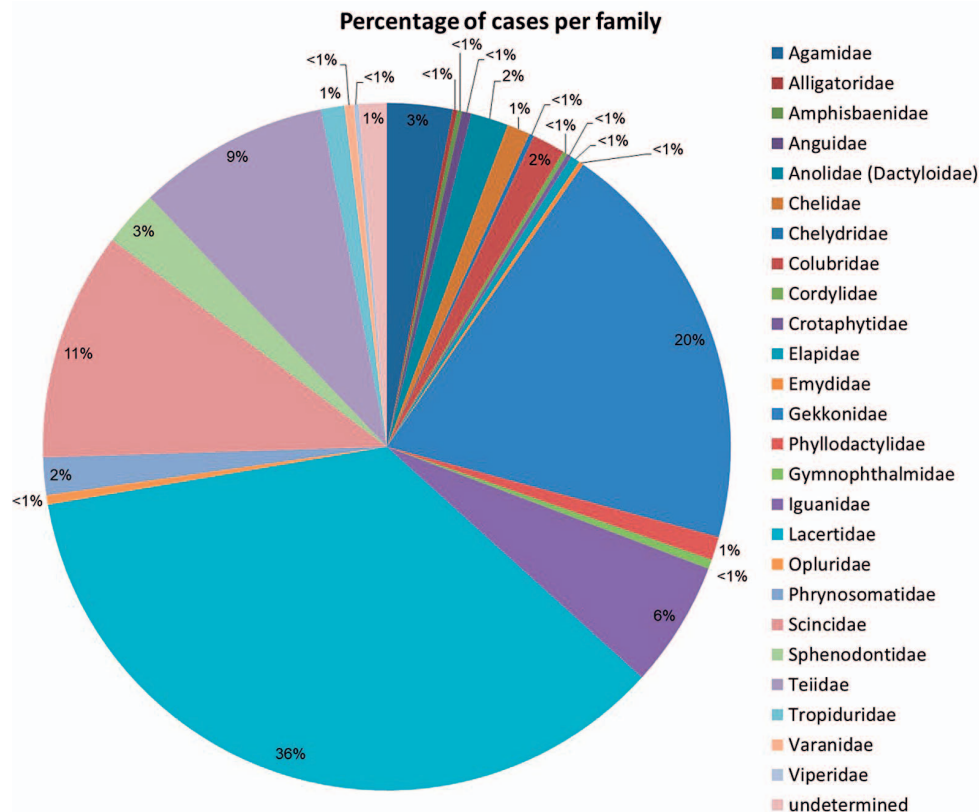


Figure 6. Overview of families from which tail multiplications were reported from natural populations. Percentage refers to percentage of cases. For detailed information, see Supplementary document S1.

(1976), PIANKA & HUEY (1978), and JAKSIĆ & FUENTES (1980) recorded higher autotomy frequencies in species assemblages for those species that utilised more exposed or higher microhabitats (e.g., trees or rocks). Conversely, GARCÍA-MUÑOS et al. (2011) found that individuals of the terrestrial lizard *Podarcis bocagei* with autotomized tails preferably occupied more closed habitats compared to individuals with original tails in order to avoid predators.

In line with these observations, we found that across all publications with a sample size ≥ 50 individuals, mean percentages of individuals with supernumerary tails in a population were higher for arboreal and saxicolous species compared to terrestrial and fossorial ones (1.4% in five populations of five species versus 0.8% in 35 populations of 26 species, respectively, Table 3); this difference is statistically significant (Mann-Whitney U-Test, $U = 129$, $\alpha = 0.04$). Too few data are available for the other microhabitat categories for comparison. Notwithstanding, across all the 455 reported individuals with supernumerary tails, averages of 3.4 and 3.2 individuals were reported per arboreal and terrestrial species, respectively, 4 per semi-aquatic, 1.7 per saxicolous, and 1.3 individuals per aquatic species. Only 1.3 cases per species were reported for fossorial species. This might also suggest a slightly higher rate of individuals with supernumerary tails in arboreal species than in terrestrial ones, but a reporting bias caused by anecdotal observations cannot be excluded.

Frequency of tail bifurcations, duplications, and multiplications

Of the 455 published cases of supernumerary tails found in the literature (including our own observations in the Kincheva National Park), most involve bifurcations (256) and duplications of tails (109). Trifurcations of tails have been reported only in rare cases (51). More than three tails or tail tips were only found in eight individuals: four quad-

uplications, three quintuplications, and one hexaplication (Table 4). [PAYEN (1991) lists three other specimens with three, four, and five tails, respectively, for which no origins (captive or wild) are provided]. Tail quadruplications were found in only four lacertid and one teiid species. ALDROVANDI (1642) described one lizard (presumably *Podarcis muralis*) with a doubly bifurcated tail, and MÜLLER (1852, 1864–1865) found one *Lacerta bilineata* with an externally visible tail duplication that turned out to be a quadruplication when X-rayed. PAYEN (1991) mentioned an adult *L. trilineata* (NMW 19489) that exhibited tail duplication, where one branch showed two tips and a bulb on the duplication point, adding up to four tails (Fig. 7). Lastly, TRAUTH et al. (2014) observed three *Aspidoscelis sexlineata sexlineata* (Teiidae) with tail multiplications, among them one individual with four tails that had been collected in Alabama, USA.

Besides the two *Gehyra variegata* with five tails observed by ourselves, CHAN et al. (1984) found one individual of *Lepidodactylus lugubris* with a tail shorter than half of its normal length and with five distinct tips among 319 geckos of four different species captured on buildings throughout the island of Hawaii, USA. Recently, PELEGRIN & LEÃO (2016) described a young *Salvator merianae* (Teiidae), which had a dorsal injury along its entire tail from which were growing six separate tail tips of variable length.

Including our own study, sample sizes were at least 50 individuals for 42 natural populations, allowing the frequencies of occurrence of supernumerary tails to be calculated (Table 3), with the highest frequency (6.3%) reported for *Sphenodon punctatus* (SELIGMANN et al. 2008). It remains unclear, however, as to whether all these individuals were preserved soon after collecting them in the wild or whether they subsequently obtained their supernumerary tails in captivity. This is followed by a population of *Hemidactylus frenatus* with 5.4% (GARCÍA-VINALAY 2017), *Cyclura rileyi* with 5.3% (HAYES et al. 2012), and a population of *Hemidactylus agrius* (ANDRADE et al. 2015) with 3.2%. In all oth-



Figure 7. Adult *Lacerta trilineata* (NMW 19489) collected in Dalmatia in 1893 (see PAYEN 1991) exhibiting tail duplication where one branch terminated in two tips and a bulb on the duplication point summing up to four tails. a) entire individual dorsally; b) tails ventrally (Photos: H. GRILLITSCH).

Supernumerary tails in reptiles

Table 3. Sample sizes (N) of reptile populations examined for supernumerary tails (# cases: number of cases), their origin and their microhabitat; only studies with N ≥ 50 were included that observed at least one case of supernumerary tails.

Species	Country	Lifestyle	Reference	# cases	N	Frequency
Rhynchocephalia						
<i>Sphenodon punctatus</i>	New Zealand	terrestrial	DAWBIN 1962	2	750	0.0027
<i>Sphenodon punctatus</i>	New Zealand	terrestrial	SELIGMAN et al. 2008	9	143	0.0629
Squamata - Gekkota						
<i>Gehyra variegata</i>	Australia, Kinchega	arboreal	this study	43	3333	0.013
<i>Hemidactylus mabouia</i>	East Africa (whole sample); Tanzania (duplication)	arboreal	LOVERIDGE 1920, 1947	1	72	0.0139
<i>Hemidactylus agrius</i>	Brazil	saxicolous	ANDRADE et al. 2015	2	63	0.0317
<i>Hemidactylus frenatus</i>	Mexico	arboreal	GARCÍA-VINALAY 2017	4	74	0.0541
<i>Homonota uruguayensis</i>	Brazil	saxicolous	ABEGG et al. 2014	1	1000	0.0010
Squamata - Iguania						
<i>Cyclura carinata</i>	Bahamian Archipelago, Caicos	terrestrial	IVERSON 1979, HAYES et al. 2012	4	390	0.0103
<i>Cyclura cyclura</i>	Bahamian Archipelago, Gaulin Cay	terrestrial	HAYES et al. 2012	2	310	0.0065
<i>Cyclura cyclura</i>	Bahamian Archipelago, White Bay Cay	terrestrial	HAYES et al. 2012	1	99	0.0101
<i>Cyclura cyclura</i>	Bahamian Archipelago, Bitter Guana Cay	terrestrial	HAYES et al. 2012	1	59	0.0169
<i>Cyclura rileyi</i>	Bahamian Archipelago, Fish Cay	terrestrial	HAYES et al. 2012	1	57	0.0175
<i>Cyclura rileyi</i>	Bahamian Archipelago, Bush Hill Cay	terrestrial	HAYES et al. 2012	8	328	0.0244
<i>Cyclura rileyi</i>	Bahamian Archipelago, White Cay	terrestrial	HAYES et al. 2012	4	75	0.0533
<i>Uta stansburiana</i>	USA	terrestrial	TINKLE 1965	4	3729	0.0011
Squamata - Scincomorpha						
<i>Ablepharus kitaibelii</i>	Bulgaria	terrestrial	VERGILOV & NATCHEV 2017	4	415	0.0096
<i>Acanthodactylus aegyptius</i>	Israel	terrestrial	STARK et al. 2018	1	76	0.0132
<i>Ameivula ocellifera</i>	Brazil	terrestrial	DANTAS SALES & XAVIER FREIRE 2019	1	127	0.0079
<i>Aspidoscelis sexlineata sexlineata</i>	USA	terrestrial	TRAUTH et al. 2014	2	2001	0.0010
<i>Aspidoscelis velox</i>	USA	terrestrial	CORDES & WALKER 2013	1	> 200	0.0050
<i>Chalcides ocellatus</i>	unknown	terrestrial	TERNI 1915	1	1000	0.0010
<i>Eremiascincus richardsonii</i>	Australia	subterranean	this study	1	92	0.0109
<i>Lacerta agilis</i>	Netherlands	terrestrial	STRIJBOSCH 1999	3	3539	0.0008
<i>Lacerta agilis</i>	Poland	terrestrial	DUDEK & EKNER-GRZYB 2014	1	> 500	0.0020
<i>Lacerta agilis</i>	Germany	terrestrial	YOU 2010, WILLIGALLA et al. 2011	1	168	0.0060
<i>Lerista punctatovittata</i>	Australia	subterranean	this study	2	198	0.0102
<i>Liopholis whitii</i>	Australia	terrestrial	HICKMAN 1960	1	350	0.0029
<i>Morethia boulengeri</i>	Australia, Kinchega, RII site	terrestrial	this study	2	891	0.0022
<i>Morethia boulengeri</i>	Australia, Kinchega, Homestead	terrestrial	this study	1	245	0.0041
<i>Notomabuya frenata</i>	Brazil	terrestrial	VRCIBRADIC & NIEMEYER 2013	3	216	0.0139
<i>Ophisops elegans</i>	Israel	terrestrial	TAMAR et al. 2013b	1	> 360	0.0028
<i>Plestiodon anthracinus</i>	USA	terrestrial	WALLEY 1997	1	350	0.0029
<i>Plestiodon longirostris</i>	Bermuda, Castle Island	terrestrial	TURNER et al. 2017	2	238	0.0084
<i>Plestiodon longirostris</i>	Bermuda, Southampton Island	terrestrial	TURNER et al. 2017	5	268	0.0187
<i>Podarcis melisellensis</i>	Croatia	terrestrial	BAECKENS et al. 2018	1	72	0.0139
<i>Psychosaura macrorhyncha</i>	Brazil	terrestrial	VRCIBRADIC & NIEMEYER 2013	1	106	0.0094
<i>Takydromus tachydromoides</i>	Japan	terrestrial	TELFORD 1997	1	1275	0.0008
<i>Teius teyou</i>	Bolivia	terrestrial	CASAS et al. 2016	1	640	0.0016
<i>Timon lepidus</i>	France	terrestrial	RENET 2013	2	approx. 630	0.0032
<i>Zootoca vivipara</i>	Netherlands	terrestrial	STRIJBOSCH 1999	3	7580	0.0004
<i>Zootoca vivipara</i>	Poland	terrestrial	DUDEK & EKNER-GRZYB 2014	1	> 500	0.0020
Squamata - Serpentes						
<i>Coluber constrictor</i>	USA	terrestrial	MITCHILL 1826	1	120	0.0083

Table 4. Summary of the number of individuals with supernumerary tails reported from natural populations of reptiles. For detailed information, see Supplementary document S1.

	Bifurcation	Duplication	Trifurcation/ triplication	Quadruplication	Quintuplication	Hexaplication	No details	# cases
Rhynchocephalia								
Sphenodontia	5	5	0	0	0	0	2	12
Squamata								
Amphisbaenia	1	0	0	0	0	0	0	1
Anguimorpha	2	2	0	0	0	0	0	4
Gekkota	53	22	11	0	3	0	5	94
Iguania	50	4	10	0	0	0	1	65
Scincomorpha	136	63	29	4	0	1	23	256
Serpentes	0	12	0	0	0	0	0	12
without identification	2	0	1	0	0	0	0	3
Testudinata								
Cryptodira	1	1	0	0	0	0	0	2
Pleurodira	5	0	0	0	0	0	0	5
Crocodylia								
Alligatorioidea	1	0	0	0	0	0	0	1
Total	256	109	51	4	3	1	31	455

er populations, the frequency was below 2.5% and usually well below 1% (24 populations, Table 3; see also Tables 1&5 for populations without supernumerary tails), and very low when the sample size was more than 1000 individuals (0.04–0.15%, five populations excluding our *G. variegata* subpopulations at the RI and Station study sites; Tables 1&2b). These data indicate that the frequency of supernumerary tails will usually be below 0.2% in large natural populations, but the absence of individuals with supernumerary tails is rarely specifically stated (Table 5). They also show that the frequency of supernumerary tails in our two large *G. variegata* subpopulations were well above that of any other population with sample sizes of more than 1000 individuals. For *M. boulengeri* and *L. punctatovittata*, the frequency was at the upper range limit reported in other studies with similar sample sizes, and there is apparently no other study that reported supernumerary tails for several species from the same or adjacent study sites.

Retention of supernumerary tails, impacts on individuals, and survival

Numerous studies have addressed the effects of tail loss on lizards (e.g. ARNOLD 1988, HARRIS 1989, HENLE et al. 1989a, 1990b, BATEMAN & FLEMING 2009). The costs of tail loss may include loss of social status, loss of stored energy, change in behaviour, reduced chance of survival, as well as fewer and smaller offspring (HARRIS 1989, PIANKA & VITT 2003, BATEMAN & FLEMING 2009), but may also be negligible (BATEMAN & FLEMING 2009, PIANKA & VITT 2003) or even lead to higher survival rates (NIEWIAROWSKI et al. 1997).

In contrast, almost nothing is known about the effects of supernumerary tails on their carrier, whether they may lose them again, and if so, whether they regenerate a single normal tail or whether they regenerate supernumerary tails again. RAHMAN (2011) captured a common snapping turtle (*Chelydra serpentina*) with a bifurcated tail several times between 2007 and 2009, while TURNER et al. (2017) recaptured three *Plestiodon longirostris* with bifurcated tails within 1–2 months. PASSOS et al. (2014) captured an adult female *Tropidurus semitaeniatus* with a regenerated bifid tail (approx. ½ tail length) multiple times over 17 months. During this period, this female grew and became gravid despite her unusual locomotion. MOSER (2000) also observed a pregnant female *Lacerta agilis* with a tail duplication. Similarly, a captive male *Podarcis siculus* with a supernumerary lateral tail springing from close to the tail base that was approximately 1/3 of the length of the main regenerated tail repeatedly mated successfully with a female with a tail bifurcation at approximately the beginning of the last third of the tail despite impaired movement capabilities (TOFOHR 1905). One of the *M. boulengeri* with a bifid tail was observed on a regular basis by us throughout the survey month without any indication of its movement being impaired and without moulting problems.

Tail loss usually incurs survival costs, but this is not true for all cases (reviewed by BATEMAN & FLEMING 2009). Whereas we cannot say anything about the between-year survival of *M. boulengeri*, *L. punctatovittata* or *E. richardsonii* with a bifid tail, we have frequently recaptured *G. variegata* specimens that had maintained their multiple tails across study years. In natural habitats, 75% of the *G. variegata* individuals with bifid tails definitely survived until the next year, which matches the constant adult survival rate

Table 5. Sample sizes (N) of lizards examined for supernumerary tails with negative results; only studies with $N \geq 50$ were included; for our Australian data, see Table 1.

Species	Country	N	Reference
<i>Acanthodactylus</i> species	? (Collection of Tel-Aviv University)	> 1000	TAMAR et al. 2013a
<i>Acanthodactylus boskianus</i>	? (Collection of Tel-Aviv University)	391	TAMAR et al. 2013a
<i>Cyclura cyclura</i>	Bahamian Archipelago, Leaf Cay	1210	HAYES et al. 2012
<i>Cyclura cyclura</i>	Bahamian Archipelago, U Cay	561	HAYES et al. 2012
<i>Cyclura cyclura</i>	Bahamian Archipelago, Noddy Cay	60	HAYES et al. 2012
<i>Cyclura cyclura</i>	Bahamian Archipelago, No. Adderly Cay	96	HAYES et al. 2012
<i>Cyclura rileyi</i>	Bahamian Archipelago, Green Cay	86	HAYES et al. 2012
<i>Cyclura rileyi</i>	Bahamian Archipelago, North Cay	87	HAYES et al. 2012

of 0.75 for this site (GRIMM-SEYFARTH et al. 2018). Thus, tail bifurcation does not seem to have a negative impact on survival in this subpopulation. In the *G. variegata* subpopulation at the Station, the recapture rates for individuals with tail bifurcations/duplications and multiplications were 48.3 and 50%, respectively. Annual survival rates at the Huts depended strongly on environmental conditions, varying between 39.7 and 79.8 % (GRIMM-SEYFARTH et al., unpubl. data). Hence, we cannot say much about the influence of supernumerary tails on survival, except that they do not seem to decrease survival rates substantially.

In any case, we observed an adult female with a duplicated tail hunting on a window in 2014. When other geckos approached, the female defended her foraging site snapping at the other individuals in the manner adult *G. variegata* usually display. This behaviour implies that tail duplication does not interfere with these individuals' abilities to defend their foraging sites with aggressive behaviour. In line with this, the body conditions of individuals with and without tail multiplications did not differ in the RI or in the Station subpopulations. Likewise, TURNER et al. (2017) caught seven *Plestiodon longirostris* with bifurcated tails on Bermuda that did not differ in body mass or SVL from skinks with normal tails. The weighted mean rate of supernumerary tails (1.4%) in the two subpopulations studied by them was very similar to the weighted mean rate in *G. variegata* in our study. OFER et al. (2020) caught an adult female *Stenodactylus sthenodactylus* with a tail duplication that was the 9th largest ($n = 54$) and 5th heaviest ($n = 48$) measured by them throughout the distribution range of this species in Israel. In addition, WÖSS (2010) observed a male *L. agilis* with a tail triplication in excellent physical condition and remarkably bright breeding colours. These observations suggest that individuals with tail multiplications are just as successful in hunting as individuals with normal tails.

Causes of supernumerary tails

Early scholars suggested various causes for supernumerary tails, ranging from congenital, an inert disposition, the divine hand, a superabundance of material, injuries of

various kinds, to hyperregeneration (reviewed by GACHET 1834). While supernumerary tails have different causes, including congenital ones, hyperregeneration after trauma is most frequently considered to be the cause. Early on, PLINIUS SECUNDUS MAJOR (77) knew that lizards may develop tail duplications if their tails were amputated. Experiments and the anatomical examination of regenerating tails in the 17th and 18th centuries by PERRAULT (1721) and others (reviewed by GACHET 1834) and GACHET's (1834) own studies demonstrated that regenerating tails contain only cartilage but no vertebrae. In addition, the shape, size, colour and the size and shape of scales of regenerated (portions of) tails usually differ from the conditions present in the original tail. These conditions are also observed in most supernumerary tails. Therefore, GACHET (1834) concluded that hyperregeneration is the cause of supernumerary tails. Note that the externally distinguishing characteristics between original and regenerated tails may disappear with increasing lengths of regenerated tails in some species, such as *M. boulengeri*, or become subtle in some individuals but not in others, such as in the *G. variegata* of our study. Most, but not all, later authors followed the explanation provided by GACHET (1834) that supernumerary tails are the result of abnormal regeneration.

TORNIER (1897) seems to have been the first who understood why autotomized or cut tails may lead to tail duplication. He observed that either cuts have to be at an oblique angle, tails have to be incompletely broken off, or that vertebrae have to become injured. However, if the injury is too great, the tail that is initially still attached will later be autotomized.

Later, WOODLAND (1920) and DAS (1932) discovered that relatively superficial injuries confined to the muscles and overlying tissue can also result in small extra tails growing from them. For example, a *Tupinambis nigropunctatus* that bruised its tail in a cage developed six additional tails, three grew rapidly but only one of them soon reached a size similar to the original tail (QUELCH 1890). [Note that the title of the paper is misleading as it mentions four tails; this presumably caused subsequent authors to incorrectly quote this number of tails.] Likewise, another teiid, *Salvator merianae* from Argentina, with a severe injury to the entire dorsal part of the tail developed six tails along the

injury (PELEGRIN & LEÃO 2016). These authors claimed that the injury must have been inflicted with a sharp object cutting off the tissue and described that the injury looked dried up rather than regenerated.

Superficial injury, such as the loss of single scales from the tail, does not seem to result in the development of a supernumerary tail by default (BELLAIRS & BRYANT 1985). Differences in the type and degree of injury may also explain why tail bifurcation developed in one of three adult *Acanthodactylus boskianus asper* when the tail tips were cut off (TAMAR et al. 2013a) whereas this did not happen in any of the *G. variegata* studied by us that had incompletely detached or injured tails or in which tail tips were removed.

Triplicate tails can also be obtained experimentally if the tail tip is broken off and two independent injuries are inflicted on tail vertebrae (TORNIER 1897). If the injuries are located close together, the regenerating tail tips may be enveloped in a single skin sheath and thus be recognizable only when using radiography (BUGUET 1898). Externally, they may appear as bifurcated or as a single tail, as was the case in one *Lacerta bilineata* dissected by MÜLLER (1852, 1864–1865).

For most instances from natural populations, it remains unclear as to what caused the tail injuries that resulted in the growth of supernumerary tails. In insular *Cyclura* populations, supernumerary tails only occurred on islands where the lizards coexisted with invasive mammalian predators but not on islands without them (HAYES et al. 2012).

In captivity, biting among conspecifics (TORNIER 1897) and during copulation (ZAWADZKI 2003) were observed causes of supernumerary tails. For a natural population of *Podarcis muralis*, in which all eleven observed males but none of the females had bifid tails, FUNKE (2001) assumed that bifurcation was due to attacks from other males. Lizards whose tails had been incompletely bitten off in fights with rivals or incompletely removed experimentally attempted to autotomize their tails by biting and tearing off the semi-detached tail (DUGÈS 1829, WOODLAND 1920, WEYRAUCH 1999). According to DELMORE et al. (2012), this self-inflicted amputation is not detrimental to tail regeneration. They experimentally found out that in the leopard gecko (*Eublepharis macularius*), neither the duration nor the process of tail regeneration are related to the location and the mode of detachment (autotomy at a fracture plane vs. amputation outside a fracture plane). These processes may explain why none of the *M. boulengeri* and *G. variegata* individuals with semi-detached tails observed by us developed a supernumerary tail and may contribute to the rarity of supernumerary tails in natural populations.

Not all duplications of tails can be ascribed to regeneration phenomena. As was already observed by PERRAULT (1721) and MARCHANT (1741), regenerated tails lack vertebrae and instead contain only cartilage [see BELLAIRS & BRYANT (1985) for a more recent account]. Thus, the presence of cartilage versus vertebrae may facilitate a differentiation of cases due to hyperregeneration from those due to abnormal congenital development, but note that based on radiographs, PAULIAN & RAHARIJAONA (1950) report-

ed that in a specimen of *Oplurus cuvieri* with tail triplication, the longest regenerated tail contained ossified axial elements. Moreover, the internal morphology of regenerated tails has only been studied in a small range of species and some, such as the skink *M. boulengeri*, regenerate tails that are indistinguishable externally from original tails (own unpublished observations). It is not known whether vertebrae regenerate in the tail of this species. Only PEIRCE (1972) and SRINIVASACHAR (1956) reported a vertebral column in both tails of a juvenile lizard: in a single individual of the skink *Afroablepharus wahlbergi* and *Eutropis carinata*, respectively. Notwithstanding the caveats, these cases were presumably due to a developmental anomaly. In addition, PAYEN (1991) suggested that tail duplication in an adult *Gonatodes albogularis albogularis* collected in Venezuela was also due to abnormal development but did not provide any supporting data.

According to BELLAIRS & BRYANT (1985), the *Trogonophis wiegmanni* specimen described by BRINDLEY (1898) may be a further case of abnormal development, as this genus is not known to be capable of caudal autotomy and tail regeneration is not known in trogonophid amphisbaenians (GANS 1978). While turtles do not autotomize their tails either, and regeneration of lost parts of the tail remains largely unstudied, KUCHLING (2005) did happen to clarify that the supernumerary tail of an *Emydura* aff. *australis* lacked ossification and was thus presumably due to regeneration. Therefore, the abovementioned case of *T. wiegmanni* could also be due to hyperregeneration. Because the tail tip only showed a short bifurcation in a *Chelydra serpentina*, RAHMAN (2001) assumed that this case was likewise due to hyperregeneration.

Congenital anomalies of embryos, among them conjoined twins that were fused at the head and/or thorax but with separate posterior bodies, each with a complete tail, appeared among abnormal embryos produced by the parthenogenetic Caucasian rock lizard (*Darevskia saxicola*) (DAREVSKY 1966). Congenital tail duplications may also result from external teratogenic factors to which lizards were exposed during ontogeny. This was probably the case in an embryo of *Zootoca vivipara* from the highly contaminated East Uralian radioactive trace, which additionally exhibited polydactyly (SEMENOV & IVANOVA 1995). Likewise, in snakes, which are in general incapable of autotomy (although pseudoautotomy is known to occur in more than 30 genera: CRNOBRNJA-ISAILOVIC 2016), most, if not all cases of tail duplication are most likely due to abnormal embryonic development. WALLACH (2007) summarised the causes of abnormal embryonic development and proposed that most cases of duplications arise because of an incomplete division of single embryos or the partial fusion of two embryos. However, he also found indications of genetic causes like inbreeding or hybridization as well as environmental and chemical influences during incubation or gestation, such as temperature changes, anoxia, toxins, pollution, or radiation. Additionally, regeneration after embryonic lesion might play a role.

While we do not know the causes of supernumerary tails in the specimens observed by us, colours and scalation

of the supernumerary tails – which usually differ between original and regenerating tails (GACHET 1834) – suggested that most of them had emerged due to hyperregeneration. Predators might have contributed to the exceptionally high frequency of supernumerary tails in the *G. variegata* observed by us at the Hilton Hut in Kinchega, as was the case in insular populations of *Cyclura* (HAYES et al. 2012). The strong correlation between the prevalence of both regenerated and supernumerary tails across species in our study also suggests that the frequency of individuals with supernumerary tails is related to the risk of (partial) tail loss in a population/species. The Hilton Hut is used as a kitchen and for storing food, with domestic mice (*Mus musculus*) being more common there than in any other hut or in the surrounding natural habitat. In addition, this hut is more frequently used in the evenings compared to other huts, which attracts large praying mantis to the light. However, it is unlikely that individuals had repeatedly escaped predation attempts and suffered injuries that were great enough to cause caudal bifurcation and multiplication but not serious enough to lose the tail. Supernumerary tails could also occur more often due to increased competition between individuals on the food-rich Hilton Hut, which harbours more than twice as many individuals than any other hut. In the geckos *Mediodactylus kotschy* and *Hemidactylus turcicus*, defence mechanisms as a response to intraspecific interactions in populations with high densities and competition levels were the main background for autotomy (ITESCU et al. 2016). This could be the case on the Hilton Hut, although severe biting between conspecifics was not observed by us.

Nevertheless, the exceptionally high frequency of individuals with multiple tails at the Hilton Hut suggests the existence of some additional causes besides high predator pressures and competition. One possible reason could be that tail injuries also occurred because the individuals often pass over the very sharp-edged panes of glass covering the windows, which might result in cuts similar to experimentally induced tail multiplications. Sharp-edged glass and metal litter are also scattered underneath the huts and at the RII and Homestead sites and might likewise have contributed to tail bifurcation at those sites. On the other hand, the frequent occurrence of other tail anomalies, such as bent tails (HENLE & GRIMM-SEYFARTH, in prep.) and the occurrence of two individuals with five tails on the Hilton Hut, with only two other lizards ever having been found with five or more tails in nature, indicate reasons for the high frequency at the Station other than injuries alone.

One additional reason could be the exposure of individuals to chemicals, as the Hilton Hut was subjected to chemical termite control in most years, including chlordane. However, while this caused the death of several skinks and frogs at the hut (HENLE 1988), we can only speculate whether exposure to chemicals might also affect the complex process of tail regeneration. While the molecular mechanisms underlying the processes of regeneration that lead to tail duplications have apparently not yet been investigated, HUTCHINS et al. (2014) found that tail regeneration

in lizards involves mechanisms other than regeneration in anamniote vertebrates. They identified 326 genes that were involved in tail regeneration in *Anolis carolinensis*, which outlines the complexity of the process. Thus, it appears probable that the exposure to chemicals could indeed have a trigger effect on tail regeneration.

Conclusions

Published anecdotal observations of supernumerary tails have rapidly proliferated over recent years, but in the absence of a detailed review covering the last 100 years, knowledge has remained rather fragmentary. Despite a long history of interest, only a handful of in-depth observations from natural populations are available. Our study in Australia, which is the only larger lizard community assessed, shows that substantial differences in the prevalence of supernumerary tails may occur among species within a lizard community, among populations of the same species in different habitats, and even among subpopulations. Our review indicates that primarily terrestrial and arboreal species may acquire supernumerary tails, but our study in Australia shows that fossorial species may also develop them. Whereas supernumerary tails have also been observed in species from taxonomic groups that generally lack autotomization, only five cases of bifurcation of the tail tip are known in species with specialized tails.

Differences between original and regenerated tails in scalation, colour, and shape allow most observed cases of supernumerary tails to be referred to hyperregeneration. However, those factors that inflicted the trauma in the first place have only been established in very few cases and include predators and artificial structures. In our Australian study, semi-detached tails never induced the development of supernumerary tails.

Almost nothing is known about the effects of supernumerary tails on their carriers. So far, no negative effects on body condition (TURNER et al. 2017, our study), survival (our study), or reproduction (McCANN 1940) have been reported for natural populations. In our study from Australia, this may be due to the abundance of food for the subpopulation (GRIMM-SEYFARTH et al. 2019) that had the highest rate of supernumerary tails.

In summary, further studies to assess the occurrence and absence of supernumerary tails within whole reptile communities and across different populations are required to advance our understanding of their ecological and biological causes and consequences. Dedicated long-term field studies and the collaborative efforts of scientists who share their data for joint analyses are essential to understand rare phenomena such as supernumerary tails.

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Appendix 1

Collection material examined

Gehyra variegata: Kinchea National Park, Hilton Hut: ZFMK 49409. *Lacerta trilineata*: Dalmatia: NMW 19489.

Supplementary data

The following data are available online:

Supplementary document: supporting databases;

S1: Database of supernumerary tails in natural populations of reptiles;

S2: Microhabitat data and their references for the species covered in S1.