



Evolution of Limblessness

Early on in life, many people learn that lizards have four limbs whereas snakes have none. This dichotomy not only is inaccurate but also hides an exciting story of repeated evolution that is only now beginning to be understood. In fact, snakes represent only one of many natural evolutionary experiments in lizard limblessness. A similar story is also played out, though to a much smaller extent, in amphibians. The repeated evolution of snakelike tetrapods is one of the most striking examples of parallel evolution in animals. This entry discusses the evolution of limblessness in both reptiles and amphibians, with an emphasis on the living reptiles.

Reptiles

Based on current evidence (Wiens, Brandley, and Reeder 2006), an elongate, limb-reduced, snakelike morphology has evolved at least twenty-five times in squamates (the group containing lizards and snakes), with snakes representing only one such origin. These origins are scattered across the evolutionary tree of squamates, but they seem especially frequent in certain families. In particular, the skinks (Scincidae) contain at least half of all known origins of snakelike squamates. But many more origins within the skink family will likely be revealed as the branches of their evolutionary tree are fully resolved, given that many genera contain a range of body forms (from fully limbed to limbless) and may include multiple origins of snakelike morphology as yet unknown.

These multiple origins of snakelike morphology are superficially similar in having reduced limbs and an elongate body form, but many are surprisingly different in their ecology and morphology. This multitude of snakelike lineages can be divided into two ecomorphs (a

are surprisingly different in their ecology and morphology. This multitude of snakelike lineages can be divided into two ecomorphs (a type of morphology or body form that is associated with a particular ecology or habitat type). One ecomorph is the short-tailed burrower (burrowing morph hereafter), which has evolved at least twenty times. In these species, the body length (the distance from the tip of the snout to the beginning of the tail, or vent) is elongate, and the tail is (on average) only about half of the body length. This contrasts with more typical lizards, in which the tail is around 1.5 times the body length (Wiens, Brandley, and Reeder 2006). Species of the burrowing morph spend much of their time underground, and include the worm lizards (amphisbaenians), the California legless lizard (*Anniella pulchra*), and many different lineages of skinks. They also include the snakes, but this requires some explanation (see below). Species with the burrowing morph also tend to have reduced eyes, no external ear openings, and well-ossified skulls, which are used in tunneling.

The other snakelike ecomorph is the long-tailed surface dweller (long-tailed morph hereafter), which has evolved only five times. In these species, the body is also somewhat elongate, but the tail is remarkably so, up to 2.3 times the body length (on average). In at least some groups, the overall elongation is quite similar in both ecomorphs, but is made up by these very different proportions of tail versus body (e.g., Wiens and Slingluff 2001). Many of these species occur in dense vegetation, and they are often referred to as grass swimmers. Members of this ecomorph include the anguid glass lizards (genus *Ophisaurus*), some African plated lizards (cordylids [*Chamaesaura*] and gerrhosaurids [*Tetradactylus*]), and most of the Australian snake lizards (pygopods), which are a specialized group of geckos (Gekkonidae).

Why do surface dwellers evolve unusually long tails and burrowers evolve unusually short tails? The reasons for this dichotomy are still very uncertain. However, tails of many long-tailed surface dwellers can break easily and regrow. This breakability has earned the nickname of glass lizards for the most widespread genus of the long-tailed morph (*Ophisaurus*). The ability to easily lose and regrow parts of the tail is an antipredator adaptation that is widespread in surface-dwelling lizards (Pough et al. 2004). In the long-tailed morph, the retention of a breakable tail may represent a response to higher predation on the surface relative to underground (Wiens and Slingluff 2001). Furthermore, extreme tail elongation has been noted in other grass-dwelling lizards, even those with fully

(Wiens and Slingluff 2001). Furthermore, extreme tail elongation has been noted in other grass-dwelling lizards, even those with fully developed limbs (e.g., some *Anolis* and *Takydromus*).

Conversely, one might ask why the length of the tail should be reduced in burrowers. One hypothesis suggests that because many species of the burrowing morph have relatively small body size, reducing the size of the tail may allow them to increase the size of the body cavity, making more room for developing eggs in gravid females (Wiens and Slingluff 2001). In summary, although hypotheses have been proposed to explain differences in body proportions between these ecomorphs, no studies have tested these hypotheses so far.

Natural selection is a major driving force for evolutionary change, and most likely was important in the origin of each limb-reduced ecomorph. Direct evidence for this conclusion is limited, however, and many questions remain unanswered. The importance of natural selection is indirectly supported by the repeated association found between the morphology and ecology of the limb-reduced species (Wiens, Brandley, and Reeder 2006). In general, repeated evolution of the same morphology in similar habitats or (in this case) microhabitats is an important line of evidence supporting the role of natural selection in the evolution of that morphology. Furthermore, ecological niches for both of these morphs are present in every major continental region (i.e., Africa, Asia, Australia, Europe, North America, and South America), and it is illustrative that both morphs occur in each region.

Why should natural selection favor evolution of these ecomorphs? Limb-reduced species are likely able to use microhabitats not regularly used by lizards with a normal (fully limbed) body plan. Most lizards that are active underground are limb-reduced (with a few exceptions, such as the limbed, sand-swimming skink [*Scincus scincus*]). Limbs would probably only impede locomotion while burrowing or moving through narrow tunnels underground (Gans 1975). Although the advantages of snakelike morphology for the long-tailed morph are less clear, reduced limbs and an elongate body may facilitate movement through dense vegetation (Gans 1975). Hence, members of this ecomorph are often called grass swimmers. Unfortunately, detailed functional studies are still lacking that demonstrate the advantages of a limb-reduced, elongate body form for locomotion in dense vegetation or underground. In summary, the morphology of these ecomorphs may allow them to better exploit

morphology of these ecomorphs may allow them to better exploit microhabitats not used by other lizard species. In general, competition for finite resources (such as food) is thought to favor evolution of novel traits that allow species to better use resources not used by their close relatives (Schluter 2000), and competition is thought to drive the evolution of ecomorphs in other lizards (e.g., *Anolis* in the West Indies; see Losos et al. 1998).

Natural selection alone does not provide a direct answer for why morphs evolve so frequently. To explain this pattern, the geography of relevant species must also be considered (Wiens, Brandley, and Reeder 2006). With just a few exceptions (see below), the origin of each ecomorph is confined to only a single continent or part of a continent. Furthermore, many continents have multiple origins for an ecomorph, particularly for the burrowing morph (which has evolved at least twenty times across squamates, compared to only five times for the long-tailed morph; Wiens, Brandley, and Reeder 2006). Many of these origins are geographically isolated from each other within a continent. For example, the burrowing morph arose twice in North America—one found only in coastal California and adjacent Mexico (the California legless lizard [*Anniella pulchra*]), the other only in Florida (the Florida sand skink [*Plestiodon reynoldsi*]).

Why should the burrowing morph evolve so frequently? The burrowing morph often seems to evolve in association with sandy habitats and patches of these sandy habitats are often geographically isolated from each other. As one striking example, some species of the burrowing genus *Calyptommatus* are found only in sand dunes near the São Francisco River in Brazil (Rodrigues 1991). The basic idea is that species of the normal morph are widespread around the world, but when they encounter an isolated area of microhabitats that can be used by the burrowing ecomorph (e.g., sand dunes), this ecomorph will often evolve from an ancestor of the normal morphology to fill and exploit this empty niche.

In contrast, the long-tailed morph seems to disperse far more readily within and between continents. For example, the genus *Ophisaurus* ranges through North America, Mexico, Europe, and Asia. Intriguingly, the long-tailed morph has not arisen again in any of the regions where *Ophisaurus* occurs. In regions where *Ophisaurus* does not occur (South America, sub-Saharan Africa, and Australia), there have been one or more independent origins of the long-tailed morph, including the anguid genus *Ophiodes* in South America, the plated

including the anguid genus *Ophiodes* in South America, the plated lizards *Chamaesaura* and *Tetradactylus* in Africa, and pygopodid geckos in Australia (Wiens, Brandley, and Reeder 2006). Thus, the geographic isolation of each origin may also be important because the presence of an ecomorph in a region may prevent this same ecomorph from evolving again in that same region (Wiens, Brandley, and Reeder 2006). Given this, the fewer origins of the long-tailed morph may be explained (at least in part) by the seemingly greater dispersal ability of species with this morphology, relative to the many narrowly distributed species of the burrowing morph.

Multiple origins of the ecomorphs may also be facilitated by their relatively recent origins. Almost all origins of these ecomorphs are less than 100 million years old (Wiens, Brandley, and Reeder 2006). Given scientists' knowledge of the timing of continental drift, these morphs must have originated after the major breakup of continents, an event that doubtless contributed to their geographic isolation.

In addition to *Ophisaurus*, three other lineages of limb-reduced squamates are relatively widespread and occur on multiple continents. Surprisingly, these species are members of the burrowing morph. These are the blind lizards (dibamids), worm lizards (amphisbaenians), and snakes. Dibamids are a primarily Asian group that also includes a species in Mexico (*Anelytropsis*) that is sometimes recognized as a distinct family. Amphisbaenians are a widespread group of burrowing reptiles found in warm or tropical areas of the New World, as well as parts of Africa, Europe, and the Middle East. Within the amphisbaenians are a number of remarkable adaptations associated with their burrowing lifestyle, including a novel element associated with the ear that attaches to the lower jaw (the extracolumella), interlocking skull elements, and a diversity of bizarre head shapes associated with different modes of digging (Kearney 2003; Kearney and Stuart 2004). Intriguingly, these three widespread lineages (amphisbaenians, dibamids, and snakes) also differ from the other limb-reduced lineages of the burrowing morph in being substantially older (all three appear to be more than 100 million years old; Wiens, Brandley, and Reeder 2006).

Snakes are the best known of the limb-reduced squamates. The reason for this seems obvious. Snakes have been wildly successful, making up about 3,000 of the roughly 8,000 species of squamates (Pough et al. 2004).

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Why might snakes be so successful relative to other groups of limb-reduced squamates? Snakes are older than many other groups with reduced limbs (more than 120 million years old), but this is not the only factor, as amphisbaenians are of similar age but have far fewer species. Instead, the success of snakes may be more likely explained by their ability to use resources not used by most other squamates. Snakes differ from other squamates in several respects, and one of the most important may be in the remarkable flexibility of their jaws and skulls that characterizes most species (Pough et al. 2004). This flexibility seemingly allows them to open their jaws to eat larger prey than would be possible for most other lizards to eat (at least without dramatically increasing their body mass). Thus, whereas most lizard species feed on insects and other small invertebrates, snakes typically feed on other vertebrates, including birds, mammals, fish, amphibians, and other reptiles, including other snakes (Pough et al. 2004). Along with their use of larger prey items, snakes have evolved novel mechanisms (such as constriction and venom) to subdue or kill oversized prey before swallowing them, in contrast to lizards, which typically swallow their prey alive.

Paradoxically, although the morphology of snakes places most species within the burrowing ecomorph (i.e., relatively elongate bodies and a relatively short tail), most snake species are not burrowers (Pough et al. 2004). Why do so many species have the burrowing morphology but not the lifestyle? The phylogeny within snakes may offer a clue. The earliest branch in snake phylogeny is a group of burrowers (the scolecophidians, or blind snakes), and many other early branches are burrowers as well (such as aniliids, uropeltids, and xenopeltids; Pough et al. 2004). Many snakes appear to have become secondarily surface dwelling, and have maintained their relatively short tails through this transition (Wiens, Brandley, and Reeder 2006). Many other aspects of snake morphology may be a remnant of their underground origin, such as the loss of external ear openings. Despite their subterranean ancestry, snakes have diversified to occupy a range of habitats and microhabitats that is at least as wide as that of all other lizards combined, including arboreal species in tropical rain forests (one of which even glides), many surface-dwelling terrestrial species, a large number of freshwater species, and the most diverse group of living marine reptiles, the highly venomous sea snakes (Pough et al. 2004).

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Some authors have suggested that snakes evolved limblessness in association with aquatic habitat use rather than a subterranean lifestyle (e.g., Lee, Bell, and Caldwell 1999). However, the hypothesis of a terrestrial, subterranean origin for snakes was solidified by the reported discovery in 2006 of a fossil snake (*Najash rionegrina*), a species that is clearly the earliest lineage within snakes and that occurred in a terrestrial (and possibly subterranean) environment (Apesteguía and Zaher 2006). This study also found that all of the earliest branching lineages within snakes are terrestrial if not burrowing.

Can any squamate lose its limbs? Considering the origins of limb-reduced body plans in the context of the evolutionary history of squamates suggests that almost any group of lizards can potentially evolve one or both morphs. For example, the burrowing morph has evolved in families of lizards distributed throughout the squamate tree, including amphisbaenians, anguids, dibamids, geckos, gymnophthalmids, and skinks. Although the long-tailed morph has not evolved as often, its distribution seems equally widespread on the tree, occurring in anguids, geckos, and plated lizards (cordylids and gerrhosaurids). The only major exception to this widespread pattern (or lack of pattern) appears to be the iguanians (agamids, chameleons, iguanas, and relatives), a group of over 1,400 species in which no instances of snakelike limb reduction and body elongation have been reported (Pough et al. 2004). Although some other lizard families lack limb-reduced species (e.g., Lacertidae, Teiidae, Xantusiidae, Varanidae), all of them are closely related to families that do have them. Iguanians differ from other lizards in several fundamental aspects of their behavior and morphology. Some of these may prove to be directly or indirectly associated with their failure to evolve these ecomorphs. Some unusual iguanian traits include ambush foraging (versus active foraging in most other lizards), visual prey detection (versus chemical detection), and use of the tongue (versus the jaws) in prey capture (Pough et al. 2004). Lingual prey capture may be particularly difficult or impossible for limbless lizards, which may have difficulty raising their heads well above the ground.

Evolution of limb-reduced body form occurs widely in squamates, but some families seem to be more favored for this transition than others. At least half of the origins of the burrowing morph occur in one group, the skinks. What predisposed skinks to

morph occur in one group, the skinks. What predisposed skinks to evolve this ecomorph so often? Many skink species seem to be more cryptic (e.g., found under leaf litter and other cover) than many other lizards, and so may be more inclined to evolve burrowing behavior than lizards that are more active on the surface. Another group of lizards in which the burrowing morph evolves repeatedly, the South American gymnophthalmids, also seems to have a tendency toward cryptic behavior and microhabitats (Pough et al. 2004). These trends are suggestive but require further study.

Another interesting pattern is the rarity of transitions between ecomorphs. While it might seem that the easiest way for a given ecomorph to arise in a region is for one limbless ecomorph to originate from another, this appears to have only happened once (the burrowing pygopod genus *Aprasia* evolved from long-tailed surface dwellers; Wiens, Brandley, and Reeder 2006). Intriguingly, it seems to be easier to evolve the dramatic changes in morphology associated with going from lizardlike to snakelike body form than it is to make the shift in ecology between surface dwelling and burrowing. This raises the question of how this major change in morphology actually happens.

How does the transition from lizardlike to snakelike morphology actually occur? This can be thought of in at least two ways. First, what morphological changes occur? Second, what genetic and developmental changes underlie these changes in morphology?

Analyses of a large database of phylogeny and morphology across squamates (Wiens, Brandley, and Reeder 2006; Brandley, Huelsenbeck, and Wiens 2008) suggest that the evolution of snakelike morphology typically involves three correlated changes (i.e., changes occurring more or less at the same time). First is the elongation of the body length, such that body length increases relative to the width of the body or length of the head. This seems to be associated with an increase in the number of vertebrae that lie between the head and the beginning of the tail. Second is the reduction in limb size relative to other body parts. Third is the gradual loss of digits, going from five fingers and five toes down to one or none on each limb. These trends seem to be very consistent across squamates, despite differences in ecology between the two ecomorphs, the large number of diverse squamate clades, and the huge timescale involved (over 180 million years).

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Analyses of morphology show that loss of digits from both limbs is usually correlated, as is reduction in limb size (Brandley, Huelsenbeck, and Wiens 2008). However, digits and limbs are lost from the front limbs rather more often than from the hind limbs. Many taxa retain vestigial hind limbs but have lost all vestiges of the forelimbs, including many snakes. There are also a few exceptions, including at least one (*Biporus*) that has well-developed forelimbs with five digits but lacks hind limbs entirely.

Genetic and developmental bases for these evolutionary changes in morphology remain poorly understood. Different genes or suites of genes are likely involved in different aspects of this transformation (i.e., body elongation, limb-size reduction, digit loss, limb loss). Based on developmental studies in other vertebrates, one set of genes is likely responsible for regulating number of vertebrae and thus may determine the patterns of body elongation (S. Carroll, Grenier, and Weatherbee 2005). Studies by Michael D. Shapiro and colleagues (Shapiro, Hanken, and Rosenthal 2003) on limb-reduced Australian skinks suggest that changes in the duration of expression of the *SHH* (*Sonic Hedgehog*) gene in the developing limb bud are responsible for digit loss (i.e., shortened duration of expression leads to fewer digits). As is common for many developmental genes, *SHH* seems to play different roles at different points in time during limb development.

The transition from a lizardlike morphology to a snakelike morphology is one of the most dramatic transitions in animal evolution. Yet, phylogenetic studies suggest that it has occurred dozens of different times over the evolutionary history of squamates. Furthermore, the presence of fully limbed (i.e., with five digits) and fully limbless species within some genera (e.g., the skink genera *Brachymeles* and *Lerista*) suggests that this transition may happen quite quickly. But how long exactly?

Matthew C. Brandley and colleagues attempted to quantify how long this transition might take (Brandley, Huelsenbeck, and Wiens 2008). In this study, the evolution of body form was reconstructed on an evolutionary tree in which lengths of the branches reflect ages of different species (using a type of modified molecular clock method). Based on these results, the transition from fully limbed to limbless may take roughly 15 to 25 million years. However, more detailed sampling within genera (particularly in the skinks) will most likely show that this change takes place more quickly.

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This analysis of the timing of body-form evolution showed another intriguing result. Many authors have noted that several species seem intermediate in their morphology, between having well-developed limbs and no limbs at all. For example, rather than having all five digits or losing their limbs entirely, they may retain only two to four digits. Almost all authors studying limb-reduced lizards have assumed that such morphologies represent an intermediate stage in the process of transforming from lizardlike to snakelike. But analysis of the timing of body-form evolution shows that these intermediate morphologies are retained for relatively long periods of time (roughly 10 to 60 million years, but most typically around 25 million years), at least as long as it takes for the entire transition to take place in other taxa. Perhaps these species have these intermediate morphologies not because there has not been enough time to become fully limbless, but rather because selection specifically maintains these intermediate morphologies. One interesting implication of this result is that the morphological transformation from fully limbed to fully limbless might actually be quite different from what is inferred based on studying these seemingly intermediate species.

The observation that many species retain vestigial limbs for long periods of time suggests that they serve some purpose. For example, observational studies of some skinks suggest that reduced limbs aid in balance (Bruno and Mageri 1976; Orsini and Cheylan 1981), and laboratory studies show that even very tiny limbs are used to aid locomotion on some surfaces (Gans and Fusari 1994). In some boas and pythons, tiny hind limbs are retained only in males and seem to be used in courtship and mating (Murphy et al. 1978).

Finally, phylogeny-based studies of snakes and lizards have revealed another surprising result. Several studies have found evidence suggesting limbs and digits that have been lost over evolutionary timescales can be regained. An analysis of snake phylogeny has found that two fossil genera (*Haasiophis* and *Pachyrachis*) with relatively well-developed hind limbs (including four digits) represent relatively advanced snakes, and that these well-developed limbs evolved from ancestors with either vestigial limbs or no limbs at all (Tchernov et al. 2000). Analyses of amphisbaenian phylogeny suggest that *Bipes*, a genus with well-developed forelimbs, is actually a relatively recent group nested among the limbless amphisbaenians (Kearney and Stuart 2004), and that the forelimbs

amphisbaenians (Kearney and Stuart 2004), and that the forelimbs may have reemerged after being lost (Brandley, Huelsenbeck, and Wiens 2008). Analyses of gymnophthalmid and scincid lizards suggest that lost digits may have reevolved repeatedly in these groups also (Kohlsdorf and Wagner 2006; Brandley, Huelsenbeck, and Wiens 2008). These results imply a remarkable flexibility in the genetic systems that control the loss of digits and limbs, and that limbs and other structures that are lost in evolutionary time are not necessarily lost forever. Instead, at least some species that have lost limbs and digits seem to retain some or all of the genetic machinery to develop limbs, even if limbs are not actually expressed in the adult phenotype.

Modern reptiles with limb reduction fall into two ecomorphs, but additional ecomorphs of limb-reduced squamates may have existed in the past. For example, a recently discovered fossil from the Upper Cretaceous (approximately 95 million years old) suggests that there have also been aquatic species with reduced limbs. In *Adriosaurus microbrachis* both sets of limbs are very small, and the forelimb is reduced to only a single upper arm bone. Another group of aquatic marine squamates from the Upper Cretaceous, the dolichosaurs had limbs that were very small in proportion to their overall body size (Caldwell 2000). The specific function of limb reduction in these animals is uncertain, although reduction of some limbs is common in aquatic tetrapods (e.g., manatees, whales) and may aid in locomotion.

Amphibians

Evolution of limb-reduced elongate body forms is not confined to reptiles. Modern amphibians seem to have evolved from an ancestor that resembled a modern salamander (and by extension, a typical lizard), with four limbs and a tail. But a limb-reduced morph evolved quickly thereafter. Caecilians are a widespread and ancient group of elongate, limbless, short-tailed, burrowing amphibians. Caecilians consist of about 175 currently recognized species and are widespread in wet tropical regions in Asia, Africa, and Latin America (Pough et al. 2004). Many species resemble earthworms, which they also feed on. A few caecilian species are also aquatic. Caecilians are widely considered to be the sister group to the clade formed by the frogs and toads (anurans) and salamanders (caudates).

Elongate body form and limb reduction have also evolved repeatedly within salamanders (Wiens and Hoveman 2008). The family Amphiumidae consists of one genus with three species, each

family Amphiumidae consists of one genus with three species, each with elongate, eel-like body form, highly reduced limbs, and a variable number of digits among species (one, two, or three digits per limb). The family Sirenidae contains two genera, both with elongate body form and no hind limbs. Forelimbs are well-developed, however, with three (*Pseudobranchius*) or four (*Siren*) digits. Both amphiumids and sirenids are aquatic species that also are burrowers (Pough et al. 2004). They also have relatively short tails, and thus are consistent with the short-tailed burrowing ecomorph. As in squamates and caecilians, body elongation appears to be achieved through an increase in the number of presacral vertebrae.

Do the multiple origins of the short-tailed burrower ecomorph in amphibians show the same biogeographic pattern as in reptiles, which had separate origins in different geographic regions? The answer is both yes and no. As might be expected, both amphiumids and sirenids occur outside the range of the tropical caecilians, in temperate North America (Pough et al. 2004). Contrary to expectations, however, ranges of amphiumids and sirenids overlap broadly in the southeastern United States, to which both groups are largely confined. Furthermore, the limb-reduced ecomorph has failed to evolve in salamanders in other temperate regions where salamanders occur but caecilians do not, such as in temperate Asia, Europe, and western North America (Wiens and Hoveman 2008). It is unclear why only the southeastern United States seems favorable to the evolution of this ecomorph, and why two lineages should have evolved this ecomorph in apparent sympatry.

Outside of amphiumids and sirenids, relationships between limb reduction, digit loss, and body elongation are not as clear in other salamanders (Wiens and Hoveman 2008). For example, several other salamanders with elongate body form and relatively small limbs do not lose digits (*Lineatriton* and *Oedipina*) or lose only the fifth toe (*Batrachoseps*). Conversely, many salamanders have lost the fifth toe without body elongation and reduction in relative limb size (e.g., *Hemidactylium*). This sporadic loss of the fifth toe also occurs in some species of lizards that otherwise show no tendency toward limb reduction and body elongation. Remarkably, although body elongation in salamanders typically seems to be achieved through an increase in number of vertebrae, in the Mexican salamander *Lineatriton* elongation is achieved through lengthening of the vertebrae instead (Parra-Olea and Wake 2001).

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Evolution of limblessness not only has a geographic component (i.e., multiple origins on different continents) and a taxonomic component (i.e., origins of similar ecomorphs in different groups of reptiles and amphibians), but it may have a temporal component as well. In the Paleozoic era, an entire lineage of limbless amphibians (the aistopodans), not closely related to any modern amphibians, arose and went extinct. Some members of this lineage had more than 200 vertebrae and lacked all limbs and limb girdles, and also had a skull that bore some similarities to that of modern snakes (R. Carroll 1988). Aistopodans lived from roughly 350 million to 250 million years ago and preceded the origin of caecilians, limb-reduced salamanders, and snakelike squamates.

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