

Catalogue of American Amphibians and Reptiles.

Hunt, L.E. 2008. *Anniella*.

Anniella Gray
North American Legless Lizards

Anniella Gray 1852:440. Type species, *Anniella pulchra* Gray, 1852, by monotypy.

Anniella: Larsell 1926:cover of reprint. *Lapsus*.

Anniella: Baker 1987:236. *Lapsus*.

• **CONTENT.** Two species are currently recognized: *Anniella pulchra* and *A. geronimensis* (see **Comment** herein and in the *Anniella pulchra* account).

• **DEFINITION.** These are small, fossorial, limbless lizards (adult SVL 90–170 mm, tail length 34–103 mm (30%–42% of total length)). Both species are viviparous. Size differences, dichromatism, or other external sexual dimorphism is absent. This lizard exhibits a number of morphological specializations for burrowing, including: an elongate, subcylindrical body, slightly concave ventral surface, a cylindrical tail that tapers to a blunt tip, diminutive eyes with a movable, semi-transparent lower lid, no external limbs, no external ear openings, a wedge-shaped head in profile, a shovel-shaped snout, a strongly countersunk lower jaw, smooth, cycloid dorsal and ventral body scales, roughly uniform in size, and caudal scales larger than body scales. The head is covered with large, irregular scutes. The interclavicle element of the pectoral girdle is vestigial or lost entirely in adults (see **Comment**). The pelvic girdle is vestigial, consisting of a pair of rod-shaped ilia. The left lung and left oviduct are vestigial. The tongue is bilobed, villose, and attached medially along its entire length. The lateral nasal gland is greatly developed and the configuration of the walls of the vestibule and nasal valve permit complete occlusion of the nares while burrowing. Dorsal color varies significantly within and between species, ranging from jet black and dark brown in some coastal populations to copper, tan, olive, grey, and metallic silver in other coastal populations and interior populations (see species accounts). Ventral color varies from pale yellow to bright yellow to grey-violet. A black or brown vertebral stripe and one or more lateral stripes are present in most populations. The lateral stripes coalesce along the sides of the head to form an eye stripe in some populations. Brown or brownish-black pigment surrounds the ventral scales on the tail, forming faint or distinct zigzag stripes between the scale rows.

There are 68–81 procoelous presacral (dorsal) vertebrae, 3–4 (typically 3) sacral vertebrae, and 36–59 postsacral (caudal) vertebrae. The caudal chevrons are fused to the centra, and the branches unite to form a common stem. The first 3–4 caudal vertebrae lack the chevron bones and fracture planes that are present in more distal vertebral elements. The cranium is adapted for burrowing and is characterized by thickened, closely knit, or fused elements, a short snout, and expanded occipital and temporal regions

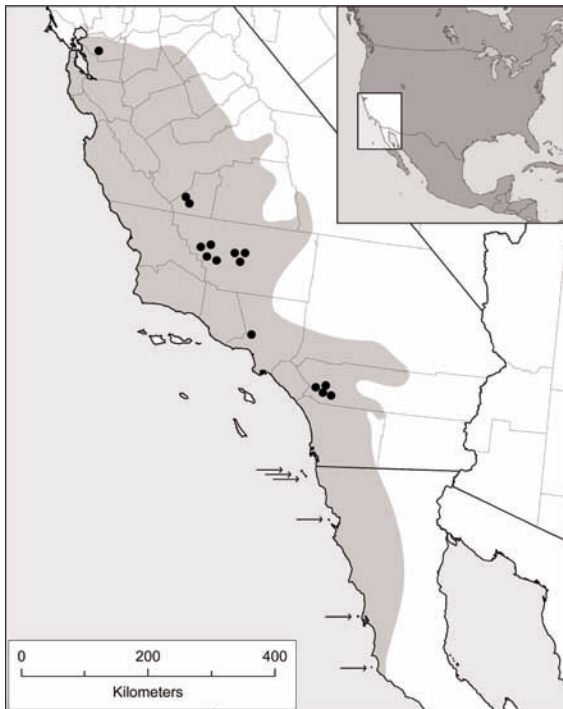
of the braincase. The frontoparietal suture provides mesokinetic flexion. The mandible is shorter than the skull and is inset. The retroarticular process of the mandible is widened posteriorly and twisted. The teeth are subpleurodont, recurved, fang-like, and have a mediodorsal groove. There are 4–5 premaxillary teeth and 4–7 (usually 7) maxillary teeth, separated by a diastema. Palatine and pterygoid teeth are absent. The mandible has five bones and supports 7–8 dentary teeth. The braincase is closed laterally by descending wings of the parietals and posteriorly by an interlocking suture between the prootic and parietal bones. The postorbital bone does not enter the orbit. The skull is streamlined by loss of the upper temporal arch, postorbital arch, and squamosal and strong reduction of the jugal with little or no angulation. An interorbital septum is present. There is no parietal foramen, but there is a cavity near the anterior edge of the fused parietals that contains the parietal eye. The frontals unite ventrally to form a complete subolfactory arch. Small, thin dorsal and ventral osteoderms are present on the body and tail, and cranial osteoderms are absent. Basipterygoid processes are present, the epipterygoids are reduced in size, and the interpterygoid vacuity is well developed. The palatine has extensive choanal grooves, the maxilla broadly overlaps a single premaxilla, and a premaxillary foramen is absent. The vomers are broad. The quadrate is short and inclined forward. There is a single hyoid arch, the hypohyals are cartilaginous and not fused to the basihyals, the ceratohyals are absent, and a geniomyoideus muscle is present. The tympanic membrane and eustachian tubes are absent and the middle ear is replaced by lymph cavities. The columella is reduced to a large footplate that occupies the entire lateral wall of the otic capsule. A cartilaginous extracolumella is firmly embedded in the quadrate. The ciliary tufts of the hair cells are bidirectionally oriented.

• **DESCRIPTIONS.** Gray (1852) provided only a cursory description when he named the genus. Most of the descriptions of the genus are based on the taxon currently known as *Anniella pulchra*. Detailed descriptions of the external morphology of one or both species can be found in Boulenger (1885b), Coe and Kunkel (1906), Dowling and Duellman (1978), Grismer (2002), Hunt (1983, 1984), Richardson (1852), Shaw (1940), Smith (1946), Stebbins (1954, 2003), Hutchins et al. (2003), and Van Denburgh (1922). Baur (1894), Coe and Kunkel (1906), and Rieppel (1978a, 1980a,b) provided detailed descriptions of the skull and other features of internal morphology.

• **ILLUSTRATIONS.** Line drawings and/or illustrations of the external morphology of one or both species are found in Coe and Kunkel (1906), Friederich (1978), Hunt (1983), Richardson (1852; reproduced in Bettelheim [2006]), Scherpner (1968), Shaw (1940), Smith (1946), Stebbins (1954, 2003), and Terent'ev (1961). Many of the references listed under **Pertinent Literature** and in the species accounts

contain line drawings and/or photographs of osteological or other internal anatomical features of *Anniella pulchra* (Bellairs and Boyd 1950; Cope 1892a,b; Edmund 1960; Filoramo 2007; Kearney 2002a; List 1966; McDowell and Bogert 1954; Rieppel 1981; Stokely 1947a; Wever 1978). **Black-and-white and/or color photographs** of one or both species can be found in Grismer (2002), Hunt (1983), Pianka and Vitt (2003), Smith (1946), and Van Denburgh (1922). Bell et al. (1995) and Bell and Whistler (1996) provided line drawings of fossils. Gorman (1973) illustrated the karyotype.

• **DISTRIBUTION.** The geographic distribution of this genus coincides closely with the California Floristic Province (Raven and Axelrod 1978; also see **Comment** in the *Anniella pulchra* account). It is found from central California (Contra Costa County) southward through southwestern California to Punta Baja and Isla San Geronimo in northwestern Baja California Norte, Mexico. Elevations range from near sea level to over 2,050 m in California (Sierra Nevada and Transverse Range). Insular populations occur on the



MAP. Distribution of *Anniella*. Arrows indicate offshore localities, and dots reported fossil localities.

Baja California Norte islands of Los Coronados (north, east, and south islands), Todos Santos (north and south islands), San Martin, and San Geronimo.

• **FOSSIL RECORD.** The oldest known fossils referable to *Anniella* are from Upper Miocene deposits in Contra Costa County, California (Gauthier 1980). Pliocene and Pleistocene fossils identified as *Anniella* have been described from localities in Los Angeles, Kern, Kings, and Riverside counties, California (Bell 1993, Bell et al. 1995, Bell and Whistler 1996, Reynolds et al. 1990, 1991). All of the California fos-

sil localities are within the modern geographic distribution of *A. pulchra*. Gauthier (1982) described the annielline, *Apodosauriscus minutus*, from Lower Eocene deposits in Sweetwater County, Wyoming.

• **PERTINENT LITERATURE.** Most of the published work on the genus is based on the wide-ranging species, *Anniella pulchra* (see species account). References are listed by topic: **anatomy and morphology** (Baur 1894, 1895; Beuchat 1986; Coe and Kunkel 1906; Cope 1892a,c, 1896a,b; Filoramo 2007; Fitch 1981; Fox 1977; Frazzetta 1962; Fürbringer 1870, 1922; Gabe and Saint-Girons 1965, 1967, 1969, 1970a,b, 1971, 1972; Gabe et al. 1964; Gans 1975; Gans and Fusari 1994; Gasc 1967, 1981; Gomes 1974; Greer 1985, 1991; Hunt 1984; Jullien and Renous-Lécuru 1973; Kochva 1978; Luppa 1977; Lynn 1970; Lynn and Colorigh 1967; Lynn and Walsh 1957; Meylan 1982; Mullen 1967; Perrier 1928; Ralph 1975; Raynaud and Pieau 1985; Rieppel 1978a, 1980a,b; Saint-Girons 1967, 1970, 1972, 1976; Schwenk 1985; Smith et al. 1983; Tanner and Avery 1982; Weston 1936; Wiens and Slingluff 2001), **behavior** (Ferguson 1977; Greene et al. 2006; Miller 1944; Van Denburgh 1922), **biogeography** (Barrett et al. 2003; Brown 1904; Dunn 1931; Grismer 2002; Murphy 1983; Pianka 1989; Savage 1960; Van Denburgh 1895), **brain** (Hilton 1955; Larsell 1926; Northcutt 1978; Senn 1969; Senn and Northcutt 1973; Schwab 1979; ten Donkelaar and Bangma 1992), **blood cells** (Saint Girons 1970; Saint-Girons and Saint-Girons 1969), **caudal autotomy** (Arnold 1984a,b, 1988; Bellairs and Bryant 1985; Etheridge 1967; Miller 1944), **checklists** (Angel 1949; Casas A. and McCoy 1979; Flores-Villela and Canseco-Márquez 2004; Frank and Ramus 1995; Liner 1994, 2007), **classification and phylogeny** (Baur 1894; Bellairs 1949a,b, 1950, 1969; Bellairs and Kamal 1981; Bellairs and Underwood 1951; Boulenger 1884, 1885b; Bush et al. 1990; Caldwell 2000; Camp 1923; Caprette et al. 2004; Clark 2003; Conrad 2004; Cope 1864, [1870] 1871, 1875, 1885, 1887, 1889, 1892a,b, 1897; Dowling and Duellman 1978; Duellman 1982; Duméril et al. 1870; Estes 1983, 1970; Estes et al. 1988; Etheridge 1961; Evans et al. 2006; Gans 1978; Gao and Norell 1998; Gauthier 1982; Gill 1886; Gilmore 1928; Good 1987; Hallermann 1998; Harris 1985; Hoffmann 1890; Hoffstetter 1962; Hoffstetter and Gasc 1969; Jollie 1960; Kearney 2002a,b, 2003; Kiembara 2008; Lee 1997; Macey et al. 1999; McDowell 1967; McDowell and Bogert 1954; Mertens 1971; Piskurek et al. 2006; Presch 1988; Renous 1985; Rest et al. 2003; Rieppel 1978a, 1980a,b, 1981; Rieppel and Zaher 2000; Rieppel et al. 2008; Romer 1956; Saint Girons 1968; Schwenk 1988; Stokely 1947a,b; Townsend et al. 2004; Underwood 1957, 1971; Vidal and Hedges 2004, 2005; von Nopsca 1928; Wermuth 1969; Wiens et al. 2006; Williams 1959), **dentition** (Edmund 1960, 1969; Mahler and Kearney 2006; Rieppel 1978b), **description and geographic distribution** (Bellairs 1969; Bocourt 1885a; Cogger and Zweifel 1998; Duméril et al. 1870; Flores-Villela 1993; Goin et al. 1978; Gray 1852;

Grismer 2002; Hunt 1983, 1984; Hutchins et al. 2003; Miller 1944; Obst et al. 1988; Pianka and Vitt 2003; Porter 1972; Pough et al. 2004; Richardson 1852; Schmidt and Inger 1972; Shaw 1940; Smith 1946; Stebbins 1954, 2003; Terent'ev 1961; Van Denburgh 1922; Zug et al. 2001), **ear** (Baird 1970; Glatt 1975; Miller 1966; Rieppel 1985; Toerien 1963; Wever 1973a,b, 1978), **eye** (Saint-Girons 1982; Ulinski et al. 1992; Underwood 1951, 1970; Walls 1942), **karyology and genetics** (Adest 1977; Ast 2001; Bertolotto et al. 2004; Bezy et al. 1977; Chakraborty et al. 1978; Good 1987; Gorman 1973; Gorman and Renzi 1979; Gorman et al. 1977; Macey et al. 1999; Matthey 1931a,b, 1948; Mezhzherin 2002; Pearse and Pogson 2000; Schulte et al. 2003; Sites and Murphy 1991), **nasal structure and function** (Bellairs and Boyd 1950; Halpern 1992; Malan 1946; Saint Girons 1975; Stebbins 1948), **parasites** (Arnold 1986), **parietal organ** (Gundy et al. 1975; Gundy and Wurst 1976a,b; Quay 1979; Schmidt 1909), **physiology** (Andrews and Pough 1985; Beck and Lowe 1994; Bennett and Dawson 1976; Dessauer 1970, 1974; Dial et al. 1987; Dunson 1976; Gatten 1985; Haas 1960; Hazard 2004; Kamel and Gatten 1983; Laszlo 1977; Minnich 1979; Pough 1969), **reproduction** (Blackburn 1985; Smith et al. 1972), **scale structure** (Friederich 1978).

• **KEY TO SPECIES.** Numbers in parentheses following the species name refer to the Catalogue account number.

1. Head slightly depressed with rostrum rounded in profile; typically 5 supralabials, the second supralabial usually largest; tail length 26%–42% of total length; 80–130 scales along dorsal midline of tail; maximum SVL 170 mm; black or brown vertebral stripe typically present, may be faint or distinct; 4–8 scale rows between vertebral stripe and first lateral stripe; 1–3 lateral stripes present along sides of body between scale rows; ventral surface of tail typically without stripes; preanal scales tipped with brown or black against lighter ventral color; dorsal color from jet black, dark chocolate brown, copper, tan, to metallic silver; ventral surface typically faint to bright yellow.....*pulchra* (850)

2. Head strongly depressed with rostrum cuneiform in profile; typically 5 supralabial scales, the fourth usually largest; tail length 26%–31% of total length; 72–86 scales along dorsal midline of tail; maximum SVL 142 mm; black or brown vertebral stripe present, usually distinct; 2–3 scale rows between vertebral stripe and first lateral stripe; 4 or more black or brown lateral stripes between scale rows along sides of body grading into longitudinal stripes on ventral surface of body; distinct stripes on ventral surface of tail; preanal scales cream-colored against darker ventral color; dorsal color typically copper to silver-gray.....*geronimensis* (849)

• **ETYMOLOGY.** John Edward Gray did not explain the derivation of the name *Anniella*, but often created

obscure or fanciful scientific names. It could be a given name, as the archaic Polish, Italian, and Spanish feminine cognates, 'Aniella' and 'Anniella', as well as the Christian feminine name, 'Agnes', are derived from the Latin noun "agnellus", meaning little lamb. Beltz (2006) speculated the name could be a combination of the Latin noun "anulus", meaning ring, and the feminine Latin diminutive "–ella", meaning little, possibly referring to the cylindrical shape and small size of the body, or even a combination of the pet name Annie and the suffix "–ella".

• **COMMENT.** Morphological specializations associated with its fossorial lifestyle have obscured the systematic position of *Anniella* and made it the subject of considerable taxonomic debate. When Gray named this lizard in 1852, he placed it in the Scincidae. Richardson (1852) followed this arrangement. Cope (1864) established the then monotypic family Aniellidae [sic] and placed it along with the scincid families Anelytropsidae and Feyliniidae in the tribe Typhlophthali within the Lacertilia, a classification he continued to promote in later publications (Cope [1870] 1871, 1875). Duméril et al. (1870) considered *Anniella* to be a scincomorph, but noted significant differences in the osteoderms and integument of *Anniella* compared to limbless skinks. Boulenger (1884, 1885b) was the first to ally the Aniellidae with anguids and helodermatids. Gill (1886) supported this classification, but considered *Anniella* to be sufficiently distinct to warrant placing the family in a separate superfamily, the Annielloidea. Cope (1887, 1889) adopted this arrangement, but later (1892a,b) concluded that *Anniella* formed a distinct family within the Amphisbaenia. Baur (1894) thought that *Anniella* formed a monotypic family and supported Gill's classification, noting close similarities with the anguid genus *Anguis*. Since then, numerous morphological and genetic studies have supported the hypothesis that *Anniella* is an anguimorph (Bezy et al. 1977; Camp 1923; Coe and Kunkel 1906; Dowling and Duellman 1978; Estes 1983; Gao and Norell 1998; Gauthier 1982; Good 1987; Hallermann 1998; Hoffstetter 1962; Kearney 2002a, 2003; Macey et al. 1999; McDowell and Bogert 1954; Rest et al. 2003; Rieppel 1980a,b; Romer 1956; Schwenk 1988; Townsend et al. 2004; Underwood 1971; von Nopsca 1928; Wiens and Slingluff 2001; Wermuth 1969). During this time, some studies continued to underscore particular anatomical and chromosomal similarities between *Anniella* and scincomorphs (Bellairs 1950; Bezy and Wright 1971; Malan 1946 [however, see Bellairs 1969]). Most authorities now consider the similarities displayed by *Anniella*, amphisbaenids, and scincomorph lizards to be homoplasies and not an indication of close common ancestry.

The taxonomic position of *Anniella* within the Anguimorpha has not been resolved. Allozyme (Good 1987) and some mitochondrial DNA studies (Macey et al. 1999) concur that the Aniellidae, Gerrhonotinae, and Anguinae comprise monophyletic groups, and both studies recommended familial recognition for *Anniella*. However, phylogenetic analyses based

on morphological characteristics disagree as to whether *Anniella* should be afforded familial rank or be included in the Anguinae as either a distinct subfamily or a member of the Anguinae (e.g. Underwood 1957 - Anniellinae within Anguinae; Underwood 1971 - Anniellidae; Rieppel 1980a,b - Anniellidae; Gauthier 1982 - Anguinae; Estes 1983 - Anniellinae within Anguinae; Carroll 1988 - fossil *Anniella* in Anguinae, recent *Anniella* in Anniellidae; Schwenk 1988 - Anniellidae; Gao and Norell 1998 - Anguinae within Anguinae; Lee 1998 - Anguinae; Caldwell 1999 - Anguinae; Wiens and Slingluff 2001 - Anniellinae within Anguinae; Vidal and Hedges 2004, 2005 - Anguinae). Most recent phylogenetic studies place *Anniella* as either an annielline or anguine within the Anguinae (Pough et al. 2004).

Cope (1892b) and Coe and Kunkel (1906) stated that pectoral girdle elements were absent in *Anniella*, but Camp (1923) and Stokely (1947a) described rudimentary shoulder girdle elements that they considered to be paired remnants of the clavicles. McDowell and Bogert (1954) and Gao and Norell (1998) described an interclavicle that is either vestigial or lost entirely in adults. Kearney (2002a) found no evidence of any pectoral elements in the specimens she examined and concluded that this feature could be variable within the genus.

Although two species are currently recognized in this genus, it is clear from studies of chromosomal variation (Bezy and Wright 1971; Bezy et al. 1977), morphological variation (Hunt 1984), and mitochondrial DNA sequence variation (Pearse and Pogson 2001; J. Parham and T. Papenfuss, pers. comm.) that more than one clade occurs within the taxon currently recognized as *A. pulchra* (see species account).

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