DIPSOSAURUS, D. DORSALIS

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Dipsosaurus Hallowell Desert Iguana

Dipso-saurus Hallowell, 1854:92. Type-species, Crotaphytus dorsalis Baird and Girard, 1852, by monotypy. Dipsosaurus: Hallowell, 1859:7. Emendation.

• Content. One species, D. dorsalis, is recognized.

• **Definition.** *Dipsosaurus* is a large lizard (maximum SVL 135 mm) with a short, blunt head. The tail is twice as long as the body. Forelegs are short, half the length of the hindlegs. Dorsal scales are

small and keeled, with a medial row of slightly enlarged, raised scales forming a weak to moderate keel extending from the nuchal region to the base of the tail. Ventral scales are smooth and imbricate, twice as large as the dorsals. Caudal scales are larger than the body scales, keeled, equal in size, and arranged in rings. The supratemporals are at the posterior surface of the supratemporal process of the parietals and the parietal foramen is in the frontal bones. The outline of the osseous labyrinth is moderately distinct. The coronoid has a large lateral blade. The splenial is reduced and the borders of Meckel's groove are fused to its anterior border. Meckel's groove is closed for more than half the distance between the splenial and the mandibular symphysis. Palatine teeth are lost, as may be the pterygoid teeth. The crowns of the posterior teeth are expanded and have secondary cusps. Ribs have been lost from the third and fourth cervical vertebrae. A scapular fenestra is present, but a posterior coracoid fenestra is lacking.



Map. The large open circles indicate type-localities or restricted type-localities, solid circles other records. The fossil locality is indicated by the star. An uncertain fossil locality from "near Agate, Nebraska" is not mapped (see text for details).

Dorsal background coloration is grayish to grayish brown with a pattern of pale spots surrounded by dark rings. Laterally this pattern dissolves into a series of dark broken lines. The ventral surface is immaculate cream to beige.

• **Diagnosis.** Dipsosaurus can be distinguished from other iguanines by the following combination of characters (de Queiroz, 1987): one subocular scale much longer than the others; superciliary scales greatly elongate and strongly overlapping; pterygoid teeth usually absent or, when present, lying along the medial edge of the pterygoid; crowns of posterior marginal teeth with four cusps; large, paired openings present at or near frontonasal suture; parietal foramen located entirely within frontal bone; lateral process of palatine behind infraorbital foramen small or absent; lateral pointed processes present on the cristae interfenestralis; posterior ends of lateral and medial crests of retroarticular process divergent ontogenetically to form quadrangular outline.

• Descriptions, Illustrtions, Distribution, Fossil Record, and Pertinent Literature. See species account.

• Etymology. The name *Dipsosaurus* is derived from the Greek words *dipsa* (- dry or thirsty) and *sauros*(- lizard), apparently in reference to the arid habitats in which members of the genus occur.

Dipsosaurus dorsalis (Baird and Girard) Desert Iguana

Crotapbytus dorsalis Baird and Girard, 1852:126. Type-locality, "Desert of Colorado, California," restricted to Winterhaven (-Fort Yuma), Imperial County, California by Smith and Taylor (1950). Holotype, National Museum of Natural History (USNM) 2699, an adult of indeterminate sex (see Comment), collected by John L. Leconte, date of collection unknown (examined by author).

Dipso-saurus dorsalis: Hallowell, 1854:92. Dipsosaurus dorsalis: Hallowell, 1859:7.

Diplosaurus dorsalis: Wong, Vorhaben, and Campbell, 1975:395. Labsus.

• Content. Five subspecies are recognized: dorsalis, carmenensis, catalinensis, lucasensis, and sonoriensis.

· Definition and Diagnosis. See generic account.

• Description. The original descriptions (Baird and Girard, 1852; Hallowell, 1854) were brief. Detailed descriptions of external characteristics are in Cope (1900), Van Denburgh (1922), Woodbury (1931), and Smith (1946). An extensive description of selected external and osteological characters within a phylogenetic framework was provided by de Queiroz (1987). Stebbins (1954, 1985), Cochran and Goin (1970), Leviton (1972), and Behler and King (1979) gave general descriptions. Cope (1892) and Camp (1923) commented on osteology. Etheridge (1967) described caudal vertebrae. Miller (1966) described cochlear ducts and Iverson (1980) discussed colic modifications. Peterson (1984) discussed scale microstructure.

• Illustrations. Cochran and Goin (1970), Behler and King (1979), Smith and Brodie (1982), Burghardt and Rand (1982), Switak (1984), and Obst et al. (1988) provided color photographs and/or illustrations. Black and white photographs and/or illustrations are in Van Denburgh (1922), Woodbury (1931), Ditmars (1936), Smith (1946), Pickwell (1947), Norris (1953), Stebbins (1954, 1985), Leviton (1972), Howland (1988), and Obst et al. (1988). Black and white photographs of typical habitat are provided by Gloyd (1937) and Banta (1962). Hallowell (1859), Cope (1900), and Smith (1946) presented line drawings of scutellation. Osteology was illustrated by Etheridge (1967) and Avery and Tanner (1971); musculature by the latter, Pough (1969a), and Russell (1988). Norris (1953) and Carpenter (1961) presented behavioral postures. Schwenk and Throckmorton (1989) provided an extensive series of black and white photographs and line drawings illustrating feeding kinematics. Iverson (1980) included a photograph of colonic valves. Irish et al. (1988) provided a series of scanning electronmicrographs illustrating the skin shedding cycle. Other electronmicrographs of scales are in Stewart and Daniel (1975) and Peterson (1984), and of egg shells in Packard et al. (1982). Savage (1958) and Parsons (1970) illustrated nasal structures. Mayhew (1971) illustrated spermiogenesis and Schmidt (1964) the

inner ear. Norell (1989) provided black and white photographs of Pliocene fossil and comparative Recent material.

• Distribution. Dipsosaurus dorsalis ranges from southern Nevada, extreme southwestern Utah along the Virgin River in the vicinity of Beaver Dam Wash, and California east of the Sierra Nevada and Coast ranges, southward through central California to the eastern coast of Baja California del Norte and from there to the tip of Baja California del Sur in the vicinity of Cabo San Lucas. The species is restricted to the eastern side of the central mountains (Sierra San Pedro Mártir, Sierra Columbia, and Sierra de la Giganta) throughout most of its range in Baja California. It is present on many of the land bridges and deep water islands in the Sea of Cortez, but conspicuous by its absence from Isla Tiburón (Murphy and Ottley, 1984). The only Pacific islands on which the species has been found are Magdalena and Sta. Margarita. These lizards are known from western and central Arizona southward through Sonora, west of the Sierra Madre Occidental, to extreme northern Sinaloa, México in the vicinity of Tupolobampo. The northern limit of the species' range appears to coincide with that of Larrea divaricata (Norris, 1953). Muth (1980) presented evidence that D. dorsalis may be limited by edaphic conditions and associated hatching success.

• Fossil Record. Norell (1989) reported Pliocene fossils from San Diego County, California. An early Miocene fossil from "near Agate, Nebraska," originally described as *Tetralophosaurus minutus* (Olson, 1937) may be referable to this species (de Queiroz, 1987; Norell, 1989). Norell and de Queiroz (1991) described a fossil from the early Miocene of New Mexico which appears to represent the sister group of *Dipsosaurus* within the Iguaninae.

• Pertinent Literature. Physiology of this species has been studied extensively as follows: thermoregulation by Mosauer (1936), Cowles and Bogert (1944), Dawson and Bartholomew (1958), Licht (1964, 1965, 1972), Brattstrom (1965), McGinnis and Dickson (1967), Porter (1967), DeWitt (1967, 1971), Kemp (1969, 1972), Weathers (1970, 1971), McGinnis and Falkenstein (1971), Kluger et al. (1973), Berk and Heath (1975a,b), Callard et al. (1975), Barber and Crawford (1979), and Dupre and Crawford (1985); water balance and osmoregulation by Templeton (1960, 1966), Minnich (1970a,b), Murrish and Schmidt-Nielsen (1970), Templeton et al. (1972a), Shoemaker et al. (1972), Munsey (1972), Ellis and Goertemiller (1974), and Maderson et al. (1978); metabolism by Bennett and Dawson (1972), Bennett and Licht (1972), John-Alder (1984), Gleeson (1985), and Gleeson and Dalessio (1989); endocrinology by Lisk (1967), McWhinnie and Cortelyou (1968), Chan et al. (1970), Bradshaw (1972), Callard and Chan (1972), Gerstle and Callard (1972), Templeton et al. (1968, 1972b), Walker (1973), Yousef et al. (1973), and John-Alder (1984); blood vascular properties by Dawson and Poulson (1962), Pough (1969b, 1979), Dessauer (1970), Withers (1978), and Bickler (1986); immune response and fever by Evans and Cowles (1959), Evans (1963), Wright and Schapiro (1973), Vaughn et al. (1974), and Bernheim and Kluger (1976); muscle physiology by Adams (1987, 1989), Gleeson and Johnston (1987), Gleeson and Harrison (1988), and Marsh (1988); and sleep by Huntley (1987). Anatomical studies have included: osteology by Etheridge (1967), Hoffstetter and Gasc (1969), and Avery and Tanner (1971); musculature by Pough (1969a) and Avery and Tanner (1971); digestive system by Iverson (1980); dentition by Taylor (1940), Hotton (1955), and Edmund (1969); epidermis by Maderson et al. (1970), Stewart and Daniel (1975), and Peterson (1984); nasal structure by Stebbins (1948), Savage (1958), Parsons (1970), and Ulinksi and Peterson (1981); cardio-vascular system by Zug (1971); urogenital system by Bolton and Beuchat (1991); ear by Schmidt (1964) and Wever (1978); and coloration by Norris (1967).

Cowles and Bogert (1936), Cowles (1941), Norris (1953), Carpenter (1961) Krekorian et al. (1968), Minnich and Shoemaker (1970), Moehn (1974), Gelderloos (1976), and Alberts (1989, 1992) studied behavior. Carothers (1984) employed data on *Dipsosaurus* in a study of sexual selection in herbivorous lizards. Ecological studies have included: general ecology by Norris (1953), Pianka (1971, 1986), Parker (1972), Luckenbach and Bury (1983), and Krekorian (1984); home range and homing by Krekorian (1976, 1977); chemoreception and femoral gland secretions by Krekorian (1989), Alberts (1991), and Dussault and Krekorian (1991); reproduction by Shaw (1952), Mayhew (1964, 1971), Fitch (1970), Minnich (1971), Licht (1973), and Muth (1977, 1980, 1981); feeding and diet by Norris (1953), Minnich and Shoemaker (1970), Pianka (1971), Karasov et al. (1986), Mautz and Nagy (1987), and Cooper and Alberts (1990); physiological ecology by Minnich (1970a), Muth (1980, 1981), Bradshaw (1986), and Mautz and Nagy (1987); and density by Krekorian (1983). Baker (1987) provided a synopsis of nematodes parasitizing the species. Lefcort and Blaustein (1991) employed data on this species in a study of the relationship between parasite load and sexual selection. Janzen and Paukstis (1991) included this species in a study of environmental sex determination in reptiles. Phylogenetic relationships have recently been discussed by de Queiroz (1987), Etheridge and de Queiroz (1988), Frost and Etheridge (1989), and Lang (1989). Hulse (1988) provided a bibliography and Malkin (1956) discussed ethnozoology.

• Etymology. The name *dorsalis* is derived from *dorsum* (L., "the back") and refers to the enlarged row of vertebral scales. The names *lucasensis, catalinensis, carmenensis,* and *sonoriensis* are all geographical names referring respectively to the region around Cabo San Lucas, Baja California del Sur; Isla Catalina; Isla Carmen; and to the Mexican state of Sonora.

• **Comment.** Additional studies are needed to validate the taxonomic status of the Baja California del Sur forms (*D. d. lucasensis*, *D. d. catalinensis*, and *D. d. carmenensis*).

The holotype of *D. d. dorsalis* is poorly preserved and as a consequence its' sex can't be determined.

1. Dipsosaurus dorsalis dorsalis (Baird and Girard)

- Crotaphytus dorsalis Baird and Girard, 1852:126. See species synonymy.
- Dipsosaurus dorsalis dorsalis: Van Denburgh, 1920:33. First use of trinomial.

• **Diagnosis.** This subspecies differs from *D. d. sonoriensis* in usually having the rostrals and nasals separated by two rows of small scales, in having 2-3 rows of scales ($x = 2.8 \pm 0.3$, N = 31) between the suboculars and supralabials, and in having a greater number of supralabials ($x = 10.1 \pm 0.79$, N = 31) and infralabials ($x = 10.3 \pm 0.83$, N = 31); and differs from all other subspecies in having a much higher number of scale rows at midbody ($x = 107 \pm 4.6$, N = 31).

2. Dipsosaurus dorsalis carmenensis Van Denburgh

- Dipsosaurus carmenensis Van Denburgh, 1922:81. Type-locality, "Near Puerto Bellandro, Carmen Island, Gulf of California, Mexico." Holotype, California Academy of Sciences (CAS) 50504, an adult male collected by Joseph R. Slevin on 21 May 1921 (not examined by author).
- Dipsosaurus dorsalis carmenensis: Savage and Cliff, 1954:74. First use of trinomial.

• **Diagnosis.** This subspecies differs from *D. d. dorsalis* and *D. d. sonoriensis* in having a lower number of scales around the body ($X = 92.9 \pm 4.9$, N = 12); and differs from *D. d. lucasensis* in having a higher number of femoral pores ($X = 43.1 \pm 2.1$, N = 12), and from the former in having the postmentals in contact rather than being separated by small scales.

• **Remark.** Distribution is restricted to Isla Carmen and Isla Coronados in the Sea of Cortez.

3. Dipsosaurus dorsalis catalinensis Van Denburgh

- Dipsosaurus catalinensis Van Denburgh, 1922:83. Type-locality, "Santa Catalina Island, Gulf of California, Mexico." Holotype, California Academy of Sciences (CAS) 50505, an adult male collected by Joseph R. Slevin on 12 June 1921 (not examined by author).
- Dipsosaurus dorsalis catalinensis: Soule and Sloan, 1966:141. First use of trinomial.

• **Diagnosis.** This subspecies differs from all others by having the medial region of the chin heavily suffused with dark brown or chocolate pigmentation which extends into the anterior gular region; and differs specifically from *D. d. dorsalis* and *D. d. sonoriensis* in

• Remark. Distribution is restricted to the type-locality.

4. Dipsosaurus dorsalis lucasensis Van Denburgh

Dipsosaurus dorsalis lucasenis Van Denburgh, 1920:33. Type-locality, "San Jose del Cabo, Lower California, Mexico." Holotype, California Academy of Sciences (CAS) 46090, an adult male collected by Joseph R. Slevin on 31 July 1919 (not examined by author).

• **Diagnosis.** This subspecies differs from *D. d. dorsalis* and *D. d. sonoriensis* in having a lower number of scales around the body ($X = 88.8 \pm 4.2$, N = 53), from *D. d. carmenensis* in having a lower number of femoral pores ($X = 37.5 \pm 2.3$, N = 53), and from *D. d. catalinensis* in having a single row of scales separating the rostral from the nasal ring and in usually having the postmentals in contact rather than separated by small scales.

• **Remarks.** Asplund (1967) discussed reproduction, food habits and behavior. Murray (1955) discussed coloration and Scudder et al. (1983) compared mainland populations with those from Isla Cerralvo.

The distribution of the subspecies is restricted to the southern two thirds of Baja California del Sur, several islands in the Sea of Cortez (Murphy and Ottley, 1984) and the Pacific Coast islands of Magdalena and Sta. Margarita.

5. Dipsosaurus dorsalis sonoriensis Allen

Dipso-saurus dorsalis sonoriensis Allen, 1933:4. Type-locality, "Hermosillo, Sonora, Mexico," restricted to 15 mi southeast of Hermosillo by Peters (1952). Holotype, University of Michigan Museum of Zoology (UMMZ) 72121, an adult male collected by J. Piatt, J. Scofield, and M.J. Allen on 1 July 1932 (examined by author).

Dipsosaurus dorsalis sonoraensis: Malkin, 1956:80. Lapsus.

• **Diagnosis.** This subspecies differs from *D. d. dorsalis* by the following combination of characters: usually one row of scales separating the rostral from the nasals, 1-2 rows of scales ($X = 1.5 \pm 0.5$, N = 34) separating the suboculars from the supralabials, a lower number of supralabials ($X = 8.4 \pm 0.6$, N = 34) and infralabials ($X = 8.3 \pm 0.8$, N = 34); and differs from all other subspecies by having a higher number of scales around the body ($X = 108 \pm 4.9$, N = 34).

• **Remarks.** Some confusion exists concerning the typelocality and date of collection of the type-specimen. Peters (1952) restricted the type-locality to 15 mi southeast of Hermosillo; however, the locality most recently recognized by the University of Michigan Museum of Zoology is 8.1 km SE of Hermosillo (Kluge, 1984). In addition, Morrow gave the date of collection as July 1, 1932, but the date in both the museum records and Peters (1952) is June 21-24, 1932.

This subspecies is restricted to the arid lowland regions of central and southern Sonora and extreme northern Sinaloa, México, west of the Sierra Madre Occidental. Bogert and Oliver (1945), Langebartel and Smith (1954), and Hardy and McDiarmid (1969) discussed the range of the subspecies; the latter provided a locality map for Sinaloa.

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Arthur C. Hulse, Department of Biology, Indiana University of Pennsylvania, Indiana, PA 15705.

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