

REPTILIA: SQUAMATA: COLUBRIDAE

Catalogue of American Amphibians and Reptiles.

Ernst, C.H. 2012. *Storeria*.

***Storeria* Baird and Girard
American Brownsnakes**

Coluber: Linnaeus 1758:216. See **Remarks**.

Storeria Baird and Girard 1853:135. Type-species, *Tropidonotus dekayi* Holbrook 1842:135 (officially so designated by the International Commission of Zoological Nomenclature [ICZN] 1962:145; see **Remarks**).

Ischnognathus Duméril 1853:468. Type-species, *Tropidonotus dekayi* Holbrook 1842:53)

Tropidoclonion: Cope 1865:190.

Hemigenius Dugès 1888:182. Type-species, *Hemigenius variabilis* Dugès 1888:182 (= *Tropidoclonion storerioides* Cope 1865:190).

Natrix: Cope 1889:391.

Tropidonotus: Duméril, Bocourt, and Mocquard 1893: 750.

Thamnophis: Amaral 1929:21.

Tropidoclonion: Dunn 1931:163.

Storeia: Gray 2004:94. *Ex errore*.

• **CONTENT.** Four species are recognized: *Storeria dekayi*, *Storeria hidalgoensis*, *Storeria occipitomaculata*, and *Storeria storerioides*. See **Remarks**.

• **DEFINITION.** Snakes of the genus *Storeria* are slender, cylindrical, relatively short (max. TL 40.6 cm), live-bearing, terrestrial worm and slug predators.

Trunk vertebrae are small and elongate, with vaulted neural arches containing well developed low spines that extend posteriorly beyond the arch. The somewhat pointed hypapophyses is also directed posteriorly. Condyles and cotyles are usually round, with lateral foramina present on the cotyles. The prezygapophyseal accessory processes are well developed. A distinct haemal keel and subcentral ridges are present; and paired lateral processes occur on some caudal vertebrae. In the skull, the dentary bone is essentially not motile on the articular.

Dorsally the body is dark gray, olive gray, light brown or dark brown; juveniles are darker than most adults. The dorsum may be patterned with narrow cross bars or dark flecks. The venter ranges from gray to pink or orangish-red. The head may be darker than the body or of the same color.

The obtusely shaped head is small (length of anterior portion of skull 38.7–46.6% of the total) and distinct from the neck. The eyes are relatively large and dark. Body scales are keeled (the first row may be smooth or only weakly keeled) and pitless. They lie in 15–17 rows throughout the body, but usually only 15 rows near the tail (see individual species accounts for differences in scale row counts). Beneath are 107–148 ventrals, 34–69 subcaudals in two rows, and a divided cloacal scute (= anal plate).

Dorsal head scales include a broader than long rostral, 2 internasals, 2(1) prefrontals, 1 large medial



FIGURE 1. *Storeria dekayi texana*. Photograph by Suzanne L. Collins.



FIGURE 2. *Storeria hidalgoensis*. Photograph by Michael S. Price.



FIGURE 3. *Storeria occipitomaculata occipitomaculata*. Photograph by Suzanne L. Collins.



FIGURE 4. *Storeria storerioides*. Photograph by Erik Enderson.

frontal, 1(2) supraoculars, and 2 parietal scales. Lateral head scales are 2 (occasionally 1) nasals with the lateral naris positioned posteriorly in the first, 0–1 loreal, 2(1) preoculars, 2–3 (1–3) postoculars, 1 (2–3) + 2–3 (1–3) temporals, 6–7 (5–8) supralabials, and 7 (5–9) infralabials. Ventral head scales include 1 small mental, 4 chin shields (2 long anterior in contact, 2 shorter posterior that may be separated by small scales).

The single, short hemipenis has only been described for *S. occipitomaculata* and *S. storerioides*. It has a shallow medial sulcus spermaticus, which extends laterally from the posterior base and then straight to the apex; a flattened distal end; and 5 lateral spines, which are larger near the base, but no very enlarged spines; and small distal spines may be present which lengthen proximally.

All teeth are solid (aglyphous); no diastema is present so the teeth extend the entire length of the maxilla and dentary. Dentition consists of 13–19 maxillary teeth, 10–19 dentary teeth, and 27–35 teeth in the palato-pterygoid complex. The most posterior maxillary teeth are enlarged in some species.

The karyotype of species reported consists of 36 chromosomes (34 macro- and 2 micro-chromosomes); females are ZW, males are ZZ (Baker et al. 1972; Gilboa 1975; Hardy 1971; Hubble 1971).

Adult females are generally longer (maximum TL 40.6 cm) and stouter than adult males (maximum TL 36.0 cm), but most individuals are 23–30 cm long. Adult females have 111–148 ventrals, 34–56 subcaudals, and shorter tails 17–30% of TL. The shorter males have 107–148 ventrals, 41–69 subcaudals, and longer tails 20–27% of body length.

- **DESCRIPTIONS.** General descriptions are in Anderson (1961), Boulenger (1893, 1896), Casas Andreu and McCoy (1979), Christman (1980, 1982), Cochran and Goin (1970), Duméril (1853), Duméril and Bibron (1854), Ernst (2002b), Ernst and Barbour (1989), Ernst and Ernst (2003), Günther (1858), Powell et al. (1998, 2012), Stuart (1948), Smith and Taylor (1950a, 1966), Trapido (1944), Wilson and Meyer (1982), and Wright and Wright (1957). Marx and Rabb (1972) described several morphological characters. Other descriptions by topic are: **vertebrae** (Auffenberg 1963; Holman 1962, 1995, 2000), **hemipenis** (Cope [1898] 1900; Trapido 1944), **karyotype** (Baker et al. 1972; Gilboa 1975; Hardy 1971; Hubble 1971), and **habitat** (Lazcano et al. 2006; Mendoza Quijano 1990; Stuart 1950, 1954, 1963).

- **ILLUSTRATIONS.** Color or black-and-white illustrations of *Storeria dekayi* and/or *S. occipitomaculata* are presented in Ballinger et al. (2010), Conant and Collins (1998), Ernst (2002b), Ernst and Barbour (1989), Ernst and Ernst (2003), and Tilley and Huheey (2001). Ernst (2008a) and Uribe-Peña et al. (1999) presented color photographs of *S. hidalgoensis* and *S. storerioides*, respectively, and Trapido (1944) has black-and-white photographs of the heads and bodies of *S. hidalgoensis* and *S. storerioides*.

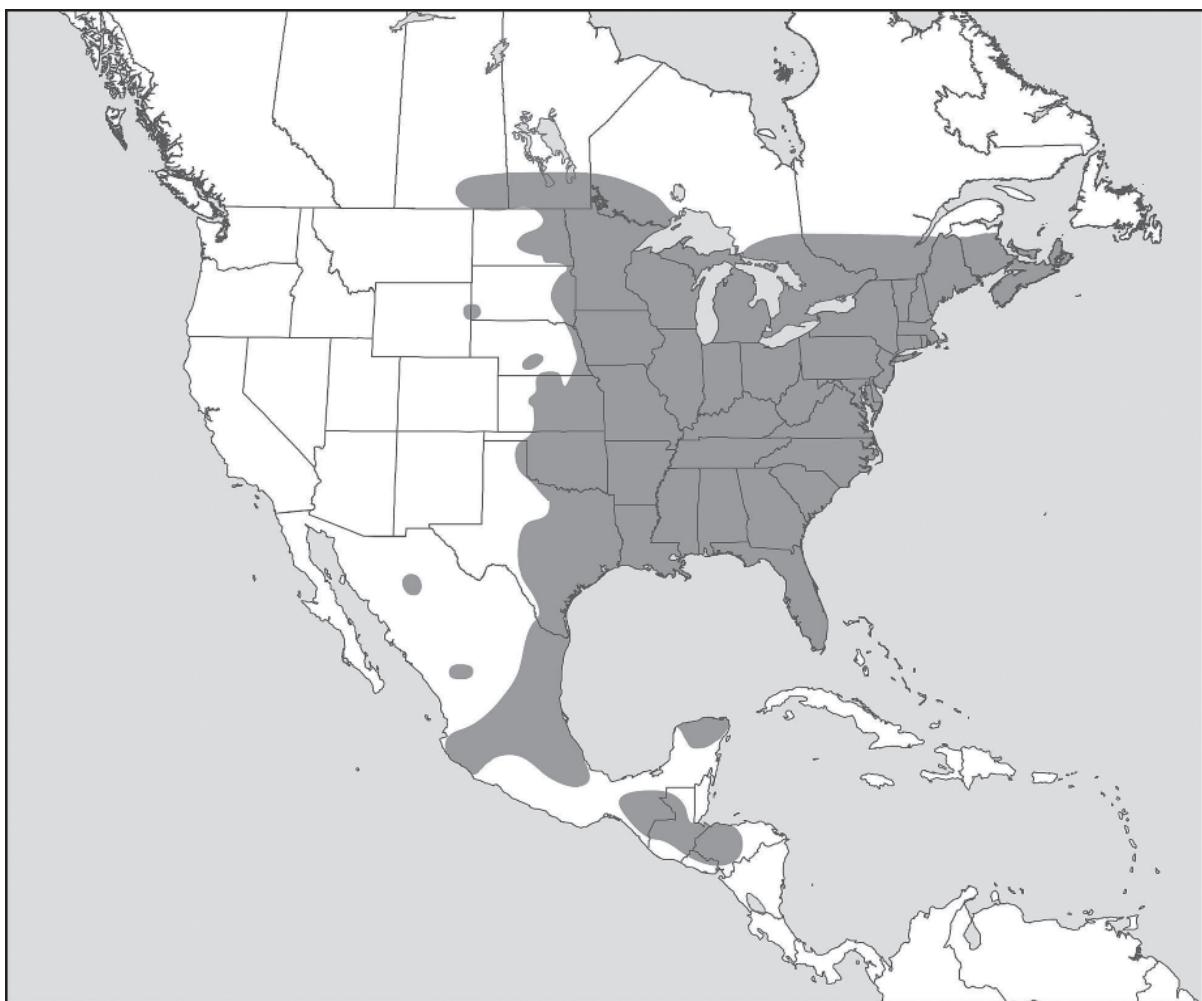


FIGURE 5. *Storeria occipitomaculata occipitomaculata* from the same small rockslide, Warren County, Pennsylvania. Photograph by Tom Sinclair.

Ernst (2008a) also presented a color photograph of habitat. Taylor and Smith (1939) illustrated the head, and illustrations of individual body size allometries versus prey size are presented in King (2002). Other illustrations are as follows: **vertebrae** (Holman 2000), **head scales** (Dugès 1888, 1890; Trapido 1944; Lee 1996, 2000), **body or tail scales** (Dugès 1888, 1890; Casas Andreu and McCoy 1979), **shed skins** (Gray 2005), and **hemipenis** (Cope 1895, [1898] 1900).

- **DISTRIBUTION.** The genus *Storeria* is found from Nova Scotia west to southeastern Saskatchewan and North Dakota, southward through Florida and to the Gulf Coast and southeastern Texas, through Mexico to Yucatan in the east and Guerrero in the west, and south to Guatemala and north central Honduras.

Papers discussing distribution include: Anderson (1960), Ashton and Ashton (1981), Barbour (1971), Bartlett and Bartlett (2003), Christman (1982), Collins (1993), Collins et al. (2010), Conant (1951), Conant and Collins (1998), Cook (1984), Davis and Smith (1953), DeGraaf and Rudis (1981, 1983), Duellman (1961), Dundee and Rossman (1989), Dunn (1936), Ernst (2002b), Ernst and Barbour (1989), Ernst and Ernst (2003), Gibbons and Dorcas (2005), Green and Pauley (1987), Hardy and McDiarmid (1969), Hulse et al. (2001), Jackson (1983), Lee (1996, 2000, 2005), Lindquist and Lindquist (2006); Linzey and Clifford (1981), Martin and Harrell (1957), McCoy (1982), Mendoza Quijano (1990), Minnesota Herpetological Society (1985), Minton (1972), Mitchell (1994), Moler (1992), Mount (1975), Palmer and Braswell (1995), Peters and Orejas-Miranda (1970), Ponce-Campos et al. (2003), Schmidt and Shannon (1947), Smith and Taylor (1950a, 1966), Stuart (1948, 1950, 1954, 1963), Tanner and Robison (1960), Taylor (1952), Taylor and Smith (1939), Tennent (1984, 1985, 1997, 1998), Tennant and Bartlett (2000), Tobey (1985), Trapido (1944), Trauth et al. (2004), Uribe-Peña et al. (1999), Vermersch and Kuntz (1986), Vogt (1981), Webb (1982), Werler and Dixon (2000), Wheeler and Wheeler (1966), Wilson and Meyer (1982), and Wright and Wright (1957).



MAP. Distribution of the genus *Storeria*.

- **FOSSIL RECORD.** Although no fossils assignable to *Storeria* have been reported from south of the United States, abundant middle Pliocene (Blancan) and Pleistocene (Irvingtonian, Mississippian, Rancholabrean fossils have been found in this country (Holman 1981, 1995, 2000).

Fossils assignable only to the genus *Storeria* are numerous and include: **Blancan** – Nebraska (Holman 2000); **Irvingtonian** – Kansas (Brattstrom 1967), Maryland (Holman 1995, 2000), Nebraska (Ford 1992), **Texas** (Holman and Winkler 1987), and West Virginia (Holman and Grady 1987, 1989); **Mississippian** – Indiana (Richards and Munson 1988); **Rancholabrean** – Alabama (Holman et al. 1990), Georgia (Fay 1988), Kansas (Brattstrom 1967; Preston 1979), Missouri (Saunders 1977), Pennsylvania (Guilday et al. 1964; Richmond 1964), Tennessee (Klipfel and Parmalee 1982), Texas (Preston 1979), and Virginia (Guilday 1962; Holman and McDonald 1986).

Rancholabrean remains of *Storeria dekayi* have been identified from deposits in Florida (Auffenberg 1963; Gut and Ray 1963; Holman 1995), Georgia (Fay 1988; Holman 1967), Kansas (Holman 1987; Preston 1979), Pennsylvania (Holman 1995), Texas

(Holman 1962; Preston 1979), and Virginia (Fay 1988; Guilday 1962). Rancholabrean fossils of *Storeria occipitomaculata* have been reported from Pennsylvania (Holman 1995, 2000) and Virginia (Fay 1984, 1988; Guilday 1962). For localities of fossil *S. dekayi* and *S. occipitomaculata*, see the maps in Christman (1982) and Ernst (2002b). Russell et al. (2009) placed this record in the context of a warm Late Pleistocene climate in the southeastern United States.

- **PERTINENT LITERATURE.** Species accounts published in the Catalogue of American American Amphibians and Reptiles include *Storeria dekayi* (Christman 1982), *Storeria hidalgoensis* (Ernst 2008a), *Storeria occipitomaculata* (Ernst 2002b), and *Storeria storerioides* (Ernst 2008b). General accounts are in Trapido (1944) and Lee (1996). Other selected papers by topic are as follows: **albinism** (Camper and Dixon 1988; Cebula 1983; Dyrkacz 1981; Hensley 1959), **allometry** (King 2002), **blood chemistry** (Dessauer 1970), **checklists and similar compendia** (Crother et al. 2000; Liner 1994, 2007; Luhring 2007), **conservation** (Bowers et al. 2000; Kilpatrick et al. 2010; Mitchell 1995; Smith and Riss-

ler 2010), **cranial myology** (Varkey 1979), **digestive tract** (Skoczyłas 1978), **disease** (Hartup 1996), **ear** (Baird 1970), **ecology and distribution** (Ball 1980; Bonati 1980; Bumpus 1885; Cobb and Summerhill 1996; Cromer et al. 2002; Crosswhite et al. 2004; Davis et al. 2010; Fitch 2006; Gibbons and Semlitsch 1981; Gray and Lethaby 2008; Holman 1961; Johnson 1964; Kilpatrick et al. 2010; Kjoss and Litvaitis 2001a,b; Meyers and Pike 2006; Paton 2005; Shipman et al. 2004; Taggart 2000; Viets 1993), **embryology** (Parsons 1959), **endocrinology** (Clausen 1940; Yaron 1985), **feeding behavior and adaptations** (Catling and Freedman 1980b; Cunningham and Burghardt 1999; Ernst and Zug 1996; Gans 1978; King 2002; Rossman and Myer 1990), **fossil history and zoogeography** (Holman 1981, 1995, 2000; Martin and Harrell 1957), **functional anatomy** (Blackburn et al. 2009), **general morphology** (Marx and Rabb 1972), **hibernation** (Gregory 1982; Zug and Ernst 2004), **karyotype** (Baker et al. 1972; Gilboa 1975; Hardy 1971; Hubble 1971), **letisimulation** (Liner 1977), **longevity** (Snider and Bowler 1992), **lungs** (Wallach 1998), **metabolism** (Bennett and Dawson 1976; Clausen 1936), **nasal anatomy and function** (Halpern 1992; Parsons 1959), **parasites** (Baker 1987; Chambers and Hulse 2006; Ernst and Ernst 2006; Harwood 1930; Keegan 1943; McKinstry 1973; Rankin 1945; Rau and Gordon 1980), **predation** (Barbour 1956; Burns 1911; Cahn and Kemp 1930; Errington and Breckenridge 1938; Fisher 1893; Fogarty and Hetrick 1973; Gehlbach 1994; Penak 1982; Sandidge 1953; Taylor 1970; Telfair 1983; Tyler 1991); **renal function** (Dantzler 1976; Fox 1977), **reproduction** (Alvarado-Diaz 2005; Clausen 1940; Ernst and Zug 1996; Fitch 1970, 1985; Noble 1937; Rahn 1938, 1939, 1940; Saint Girons 1985; Seigel and Fitch 1984; Shine 1992; Stuart 1948; Trapido 1940; Turner 1977; Wusterbarth et al. 2010; Yaron 1985; Zug and Ernst 2004), **sexual dimorphism** (Fitch 1981; King et al. 1999), **stereotyped behavior** (Carpenter 1977; Ferguson 1977), **systematics, taxonomy or evolution** (Anderson 1961; Boulenger 1893, 1896; Christman 1980; Crother et al. 2000; Dunham and Miles 1985; Dunn 1931; Ernst and Zug 1996; Fischer 1882; Garman 1883, 1884; Marx and Rabb 1972; Peters and Orejas-Miranda 1970; Schmidt 1953; Stuart 1963; Taylor 1942; Trapido 1944; Werner 1929; Williams and Wallach 1989; Yarrow 1882; Zug and Ernst 2004), **teeth** (Kearney and Rieppel 2006), **type-localities** (Smith and Taylor 1950b), and **type-specimens** (Cochran 1961; IZN 1962; Smith and Huheey 1961; Smith et al. 1964; Taylor 1933).

Literature regarding *Storeria dekayi* and *S. occipitomaculata* published after or not included in Christman (1982) and Ernst (2002b) are as follows: ***S. dekayi*** (Applegate et al. 1995; Ashton and Ashton 1981; Baker 1987; Ballinger et al. 2010; Barbour 1971; Bartlett 1988; Bartlett and Bartlett 2003; Bloch 1993; Boundy 1997; Breckenridge 1944; Burghardt 1983; Byrd and Jenkins 1996; Camper and Dixon 1988; Casper 1987, 1999; Catling and Freedman 1980a,b; Cebula 1983; Cebula and Redmer 1988; Clawson

and Basket 1982; Cochran 1992; Cochran and Goin 1970; Cochran et al. 2001; Collins 1993, 2004; Collins et al. 2010; Conant 1951; Cook 1954, 1984; Cordes 1988; Cunningham and Burghardt 1999; Degraaf and Rudis 1981, 1983; Dellinger and Black 1938; Ditmars 1935, 1936, 1939; Ducey et al. 1999; Dundee and Rossman 1989; Ernst 2003; Ernst and Barbour 1989; Ernst and Ernst 2003, 2006; Ernst et al. 1997; Farley 1999; Ferner and Wilson 2005; Fitch 1982, 1999, 2003; Ford 1990; Freedman and Catling 1979; Gibbons and Dorcas 2005; Gray 2002a, 2005, 2006; Green and Pauley 1987; Greenbaum and Davis 2006; Greene 1984; Gregory 1984, 2004; Groves 1984; Haast and Anderson 1981; Hammerson 1986; Hall 1980; Harding 1997; Hayes 1987; Held 2003; Herrington 1999; Holman et al. 1993; Holycross 1990, 1992; Hulse et al. 2001; Hunley 2003; Hunter et al. 1992, 1999; IZN 1962; Jackson 1983; John-son 1987; Kargas 1978; Keiser and Wilson 1979; Kelly 1936; King 1993, 1997, 2002; King and Lawson 2001; King et al. 1999; Krysko and Reppas 1998; Lee 2005; Linzey 1979; Linzey and Clifford 1981; Logier 1958; Logier and Toner 1961; Long et al. 1987; Mala-ret and Fitch 1984; Marion and Chandler 1983; Mar-tof 1956; Martof et al. 1980; McAllister and Twilley 2002; McCauley 1945; McCoy 1982; Mecham 1982; Mehrtens 1987; Meshaka 1988, 1994; Michels 1979; Mineau and Markel 1981; Minton 1972; Mitchell 1994; Mitchell and Anderson 1994; Moler 1992; Mount 1975; Murren and Murren 1980; Olson 1987; Palmer and Braswell 1995; Pauly and Brown 2005; Petzing 1994; Petzing and Phillips 1998; Petzing et al. 1998; Pewtress 1981; Powell et al. 1998, 2012; Ramsey and McAllister 2004, 2005; Rau and Gordon 1980; Reichenbach and Dalrymple 1981; Robison and Rader 2005; Roddy 1928; Rossi 1992; Rossman and Myer 1990; Scharf and Jorae 1980; Schmidt 2004; Schmidt and Davis 1941; Schluter 1995; Schuett and Kraus 1981; Simpson 1987; Smith 1943; Smith and Brodie 1982; Smith et al. 1996; Snyder 1972; Stevenson and Crowe 1992; Surface 1906; Tennent 1984, 1985, 1997, 1998; Tennant and Bartlett 2000; Toal 1992; Tobey 1985; Trauth et al. 2004; Trutnau 1986; Tucker and Theiling 1994; Tucker et al. 1994, 1995; Vance and Edwards 1980; Vermersch and Kuntz 1986; Vogt 1981; Volkmann 2003; Watermolen 2000; Weekly and Haynes 1992; Werler and Dixon 2000; Willson and Dorcas 2004; Wilson 1999; Wilson and Porras 1983), ***S. occipitomaculata*** (Anderson 1960; Andre and Walley 2002; Baker 1987; Ballinger et al. 2010; Bartlett 1988; Bartlett and Bartlett 2003; Bittner and Bittner 2001; Boundy 1997; Cabe 2002; Camp-bell and Christman 1982; Casper 2001; Cochran and Goin 1970; Collins 2003; DeGraaf and Rudis 1981, 1983; Ernst and Ernst 2003, 2006; Fitch 2003; Gibbons and Dorcas 2005; Gray 2002a,b, 2004, 2005, 2006; Gregory 1984, 2004; Haast and Anderson 1981; Hall 1980; Hulse et al. 2001; IZN 1962; Irwin and Blihovde 2001; Keiser and Wilson 1979; Krusling et al. 2004; Lindquist and Lindquist 2006; Martof 1956; Muenz and Smith 2005; Pope 1964; Renkin and Fantz 2002; Ross 1989; Shaw and Campbell

1974; Smith and Huheey 1961; Townsend et al. 2001; Trauth et al. 2004; Trutnau 1986; Walley 2001; Watkins-Colwell 2002; Werler and Dixon 2000; Wheeler and Wheeler 1966; Willson and Dorcas 2004).

• **KEY TO SPECIES.** The catalogue account numbers are given in parentheses after the name.

1. a. Body scales in 15 rows.....2
- b. Body scales in 17 rows.....*S. dekayi* (306)
2. a. Loreal scale present.....*S. storerioides* (860)
- b. Loreal absent.....3
3. a. Venter gray, whitish, or pink; head dark with dark posterior fork.....*S. hidalgoensis* (859)
- b. Venter reddish.....*S. occipitomaculata* (759)

• **REMARKS.** The name *Coluber leberis* Linnaeus, 1758:216 is a senior synonym of *Coluber occipitomaculatus* Storer, 1839:230, a species accepted as a taxon in the genus *Storeria* since 1853 (Baird and Girard 1853:137). It is also a senior synonym of *Regina septemvittatus* Say, 1825:240 (see Ernst 2002a). Consequently, the generic name *Regina* Baird and Girard, 1853 has priority over the name *Storeria* Baird and Girard, 1853. Smith and Huheey (1961:347) petitioned the ICZN to use its plenary powers to preserve the generic names *Regina* Baird and Girard, 1853 and *Storeria* Baird and Girard, 1853, particularly since *Storeria* had been used for over 100 years as the name for the genus of the North American Brown-snakes. Responding to the petition, the ICZN (1962: 145) placed the two genera on the Official List of Generic Names in Zoology. See Smith and Huheey (1961) for complete details, which also included the designation of a type-species for each of the two genera.

Christman (1980) reviewed the morphology of the taxon *Storeria dekayi victa* Hay, 1892, and considered it sufficiently different from the other subspecies of *S. dekayi* to warrant its elevation to full species rank. Crother et al. (2000) followed his suggestion, although few others have. However, Christman (1982), in his later review of *S. dekayi*, retained *victa* as a subspecies. Because of Christman's uncertainty, and until such time as further molecular and morphological studies of its relationships to the other subspecies of *S. dekayi* are published, the taxon should remain the subspecies *S. d. victa*.

• **ETYMOLOGY.** The name *Storeria* is a patronym honoring David Humphreys Storer, Massachusetts physician and naturalist and author of classic works on the fishes and reptiles of Massachusetts, resulting from his appointment in 1837 as a commissioner of the natural history survey of that state (Scudder 1891–1982).

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