

Catalogue of American Amphibians and Reptiles.

Walley, H.D., R.B. King, J.M. Ray, and T.L. Wusterbarth. 2012. *Nerodia sipedon*.

***Nerodia sipedon* (Linnaeus)
Northern Watersnake**

Coluber sipedon Linnaeus 1758:219. Type-locality, "North America". Holotype apparently lost as it is no longer available in the Uppsala University Zoological Museum (Wallin 1991). Type-locality restricted to the vicinity of New York City by Schmidt (1953).

Coluber paecilogaster Wied 1839:106. Type-locality "Dutotsburg, near Delaware Water Gap, Pennsylvania" (McCoy 1982). Holotype unknown.

Tropidonotus sipedon: Holbrook 1842:29.

Tropidonotus niger: Holbrook 1842:pl. IX. *Lapsus*.

Tropidonotus niger Holbrook 1842:37. Type-locality, "Cambridge, [Massachusetts]." Holotype, Academy of Natural Sciences of Philadelphia (ANSP) 4988, age and sex undetermined, collected by Dr. Storer, date of collection unknown (not examined by authors).

Nerodia sipedon: Baird and Girard 1853:38.

Nerodia agassizii Baird and Girard 1853:41. Type-locality, "Lake Huron [Michigan]." Holotype, National Museum of Natural History (USNM) 1350, age and sex undetermined, collected by Prof. Agassiz, date of collection unknown (not examined by authors).

Tropidonotus sepedon: Duméril, Bibron, and Duméril 1854:568.

Tropidonotus obliquus Hallowell 1857:248. Type-locality not given, listed as "Kansas" by Malnate (1971). Holotype, Academy of Natural Sciences of Philadelphia (ANSP) 5016, age and sex undetermined, collector and date of collection not stated (given as "Dr. Hammond" by Malnate [1971]) (not examined by authors).

Nerodia fasciatus var. *sipedon*: Jan 1863:71.

Tropidonotus sipedon sipedon: Yarow 1882:134.

Natrix fasciata sipedon: Cope 1892:671.

Natrix sipedon: Kirsch 1895:333.

Natrix sipedon: Fowler 1915:39. *Lapsus*.

Nerodia sipeodon: Errington, Hamerstrom, and Hamerstrom 1940:832. *Lapsus*.

Natrix hispidon: Quick 1951:288. *Ex errore*.

Natrix sipedons: Barrow and Stockton 1960:378. *Ex errore*.

• **CONTENT.** Four subspecies are recognized: *Nerodia sipedon sipedon*, *N. s. insularum*, *N. s. pleuralis*, and *N. s. williamengelsi*.

• **DEFINITION.** *Nerodia sipedon* is a moderately large watersnake, with a highly variable dorsal and ventral color pattern. The dorsal pattern ranges from a tan or brown to gray background, typically overlain by a variable pattern of black, dark brown, or reddish brown crossbands and blotches. Complete crossbands ("saddles") usually predominate on the anterior



FIGURE 1. *Nerodia sipedon sipedon*, DeKalb County, Illinois. Photograph by Mike Redmer.



FIGURE 2. *Nerodia sipedon insularum*, Middle Bass Island, Ottawa County, Ohio. Photograph by Kristin Stanford.

or third of the body, breaking up into smaller, alternating dorsal and lateral side blotches toward the tail. Older adults can appear solid brown or black, particularly when the skin is dry. The venter characteristically has a white, yellow, or orange ground color, usually marked with a pattern of reddish brown, half-moon-shaped blotches. The species reaches a maximum TL of 1450 mm, with adult males being much smaller than females, averaging 445 mm SVL and 575 mm total length. Females average 700 mm SVL with a maximum of 1450 mm. Head scales include 1 loreal, 2 internasals, 2 prefrontals, 1–2 preoculars, 2–3 postoculars (usually 2), 7–10 supralabials (usually 8), 9–12 infralabials (usually 10). Dorsal body scales are strongly keeled, and scale rows at midbody range from 21–25 in males and 23–25 in females. The cloacal scute is divided. Ventrals range from 127–149 (mean 138) in males and 128–149 (mean 138.5) in females, subcaudals range from 66–85 (mean 75.5) in males, 42–77 (mean 59.5) in females.

• **DESCRIPTIONS.** General descriptions are in Barbour (1943), Clay (1938), Conant (1938), Conant and Clay (1937), Conant and Lazell (1973), Cope (1892, [1898] 1900), Ernst and Barbour (1989), Ernst and Ernst (2003), Gibbons and Dorcas (2004), Krulikowski (2004), Schmidt and Davis (1941), Smith and Brodie (1982), Trauth et al. (2004), Wright and Wright

(1957), along with numerous other state and regional accounts cited elsewhere herein. Other descriptions include the karyotype (Kilpatrick and Zimmerman 1973), cranial musculature (Varkey 1973, 1979), dentition and osteology (Nakamura and Smith 1960), and hemipenis (Cope 1896, [1898] 1900).

• **ILLUSTRATIONS.** Color photographs or illustrations of adults were provided by Ballinger et al. (2010), Barbour (1971), Bartlett (2000, 2001), Bartlett and Tennant (2000), Behler and King (1979, 1995), Boundy (1997), Breen (1974), Brown and Erdle (2009), Busby et al. (2005), Christoffel et al. (2003), Coborn (1991, 1994), Cochran and Goin (1970), Collins (1974, 1981, 1993), Collins and Collins (2009), Conant (1958), Conant and Collins (1991, 1998), Cushing and Allan (2001), Denny (2002), Desroches and Rodrique (2004), Dickinson (1949), Dickson and Victoria (n.d.), Dorcas (2004), Dundee and Rossman (1989), Ernst and Barbour (1989), Fitch (1999), Gibbons and Dorcas (2004), Gibbons and West (2000), Green and Pawley (1987), Harding (1997, 2000), Hammerson (1999), Holbrook (1842), Holman et al. (1989), Hulse et al. (2001), Hunter et al. (1999), Irwin (2004), Jackson (1983), Johnson (1980, 1987a,b,

2000), Kelly et al. (1936), Klemens (1991, 1993), Krukowski (2004), Leviton (1972), MacGowan and Kingsbury (2001), Mara (1995), Martof et al. (1980), Mehrtens (1987), Meshaka and Collins (2009), Mitchell (1994a), Obst et al. (1988), Oldfield and Moriarty (1994), Palmer and Braswell (1995), Perry and Dexter (1989), Petersen and Fritsch (1986), Phillips et al. (1999), Preston (1982), Ransom (1981), Rossi (1992), Rossi and Rossi (1995, 2003), Schwartz and Golden (2002), Sievert and Sievert (1988), Smith and Brodie (1982), Snyder (1972), Tekiela (2004), Tennant and Bartlett (2000), Thompson and Backlund (1999), Tilley and Huheey (2001), Trauth et al. (2004), Tynning (1990), Vogt (1981), White and White (2002), and Zim and Smith (1953). Hammerson (1999) illustrated embryos of a recently killed specimen. Stanford et al. (2010a) provided a color photograph of a dissected female *N. s. insularum* that had died from retaining fully formed embryos through hibernation. Johnson (1987, 2000) illustrated the ventral and juvenile patterns. Tennant and Bartlett (2000) and Werler and Dixon (2000) provided color plates of *N. s. pleuralis*, and Palmer and Braswell (1995) and Tennant and Bartlett (2000) provided color plates for *N. s. williamsengelsi* and *N. s. insularum*. Cooper and Hunt (1982) provided a figure of copulating *N. s. sipedon*. Mead (1976) provided a color photograph of the vascular pattern in the spectacle.

Black-and-white photographs or illustrations of adults are provided by Anderson (1965), Anonymous (1962), Ballard (1998), Barker (1964), Bishop (1927), Blaney and Blaney (1979), Bleakney (1958a), Breckenridge (1944), Cochran and Goin (1970), Collins (1993), Conant (n.d., 1937a, 1952, 1957), DeGraaf and Rudis (1983), DeKay (1842), Ditmars (1907, 1941, 1943, 1949), Dixon (1987, 2000), Erickson (1991), Ernst and Barbour (1989), Fromm (1967, 1972), Funkhouser (1925), Garman (1883), Guthrie (1926), Harding (1981), Harrison (1950, 1971), Hudson (1942), Huheey and Stupka (1967), Lamson (1935), McCauley (1945), Minton (1966), Mitchell (1974), Morris (1987), Mount (1975, 1996), Murphy (1987), Nickerson and Krager (1975), Palmer and Braswell (1995), Pope (1944, 1946, 1956, 1964), Pope and Dickinson (1928), Roddy (1928), Ruthven et al. (1928), Schmidt and Davis (1941), H.M. Smith (1950, 1956a,b, 1961), P.W. Smith (1953), Surface (1906), Trapido (1937), Truitt (1966), and Wright and Wright (1957). Baarslag (1961) showed an albino specimen from Erie County, New York. Neill (1968) illustrated 2 captive *Nerodia sipedon* trying to swallow the same prey item. Casper (1993) showed a pair of *N. s. sipedon* copulating. Schmidt and Inger (1957a, b) illustrated a female with young. Pough (1976a, 1994) provided an illustration of crypsis resulting from a banded pattern. Gray (2002b) illustrated shed skins. Galois and Ouellet (2007) provided a photograph of a stillborn young. Wyman 1865 [1863] provided a drawing of a bicephalic specimen with a bifurcated tail.

Line drawings of dorsal, lateral, and ventral aspects of body scalation appear in Eckel and Paulmier (1902), and Hunter et al. (1992). Chiasson and Lowe



FIGURE 3. *Nerodia sipedon pleuralis*, Logan Hollow Fish Hatchery, Gorham, Jackson County, Illinois. Photograph by Mike Redmer.



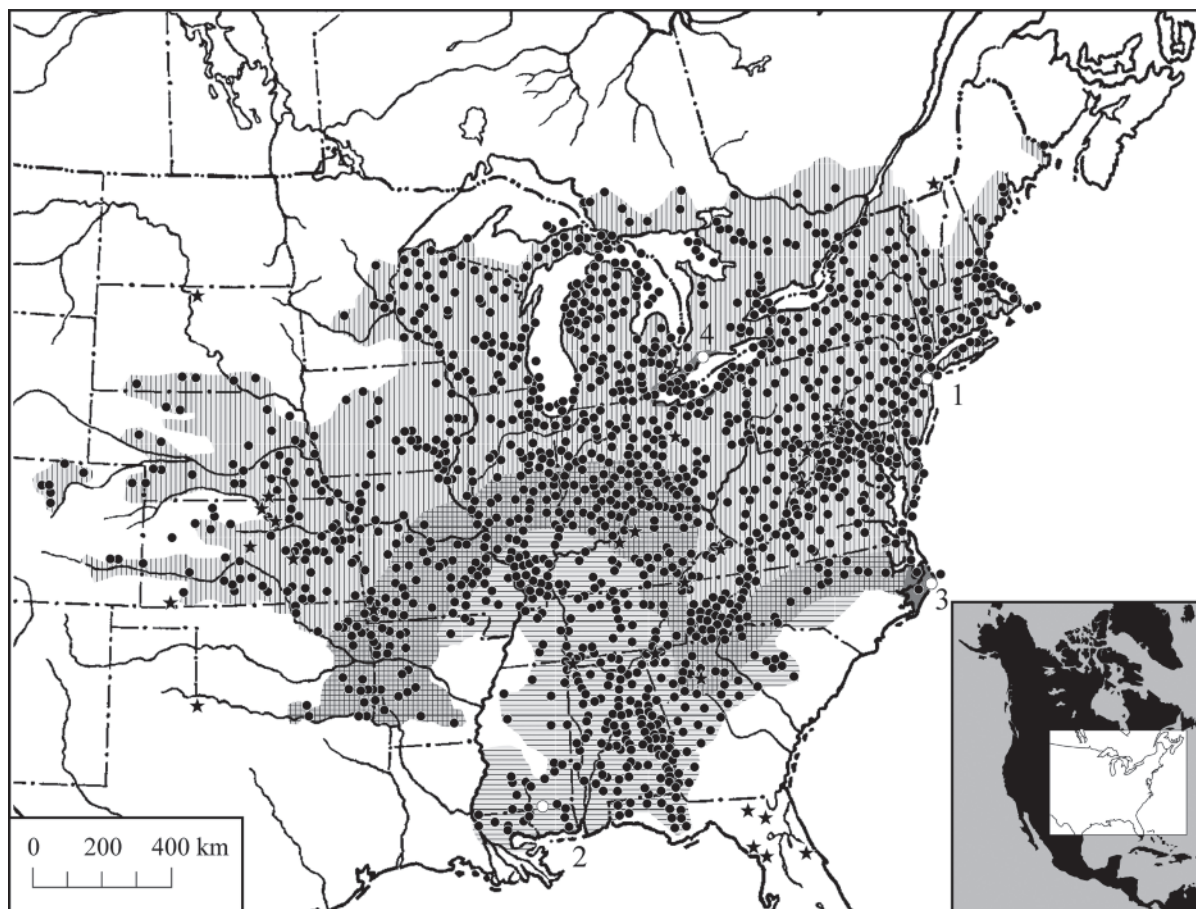
FIGURE 4. *Nerodia sipedon williamsengelsi*, Cedar Island, Carteret County, North Carolina. Photograph by Rufus W. Gaul, Jr.

(1989) showed the scale pore arrangement. Nakamura and Smith (1960) provided dorsal views of the skull, and Varkey (1973, 1979) provided illustrations of the posterior region of the skull and anterior region of the vertebral column showing the attached muscles. Bellairs and Kamal (1981) provided illustrations of skull development. Northcutt and Butler (1974) provided camera lucida drawings of the brain. Warner (1952) illustrated cross sections of the brain. The hyobranchial apparatus is illustrated by Langebartel (1968). Halpern (1980) illustrated the main olfactory bulb, and Zug and Dunson (1979) illustrated the oral sensory papillae. Chiodini et al. (1982) illustrated the oral cavity and visceral organs. Lateral views of the left quadrate and palatine are illustrated in Rossman and Eberle (1977), the premaxilla in Bogert (1947), and costal cartilage in Hardaway and Williams (1976). Holman (2000) provided illustrations of trunk vertebra showing anterior, posterior, lateral, and ventral views. A hemipenis is illustrated in Cope (1895, [1898] 1900) and Mittleman (1947). Bauman and Metter (1977) provided photomicrographs of histological sections of testes and ovarian follicles. Perry (1998) provided electron micrographs and cross sections of the lung. Oldak (1976) provided illustrations of thin layer chromatography showing fractionation of scent gland lipids. Dessauer (1967), Minton (1976),

and Minton and Salanitas (1972) showed immuno-electrophoretic patterns of serum proteins. The karyotype is illustrated by Kilpatrick and Zimmerman (1973).

• **DISTRIBUTION.** The species occurs from Maine, southern Quebec and southern Ontario westward to southeastern Minnesota, and thence southwestward through Nebraska to northeastern Colorado. The range extends to the southeast from Colorado throughout most of Kansas, eastern Oklahoma, and Arkansas, and eastward through Missouri to the Mississippi River. East of the Mississippi River it occurs from Canada to the Gulf Coast in Louisiana, from there eastward to the Florida Panhandle, and throughout the remainder of the eastern states except below the Fall Line in Georgia and the Carolinas. *Nerodia sipedon* can be found in virtually any body of water including man-made impoundments as well as natural lakes, rivers, and streams. *Nerodia sipedon* and *Nerodia fasciata* are sympatric at numerous points and hybridize in some areas (Gibbons and Semlitsch 1991; Gibbons and Dorcas 2004).

Nerodia sipedon appears in the following state and regional guides: **northeastern United States** (Conant 1957), **southeastern United States** (Jackson 1983), **New England** (DeGraff and Rudis 1983; Kruli-



MAP. Distribution of *Nerodia sipedon*. Circles indicate type-localities, dots mark other records, and stars represent fossil localities. Cross-hatching denotes areas of intergradation. Map adapted from Morris (1987), with additions from Gibbons and Dorcas (2004).

kowski 2004), **Alabama** (Boyles 1952; Haltom 1931; Linzey 1979; Löding 1922; Mount 1975, 1996), **Arkansas** (Albritton 1981; Dellinger and Black 1938; Dowling 1957, 1958; Hurter and Strecker 1909; Schwardt 1938; Taylor 1935; Trauth et al. 2004), **Colorado** (Albritton 1981; Ball 1980; Hammerson 1986, 1999; Hammerson and Langlois 1981; Maslin 1959; Smith et al. 1965), **Connecticut** (Dickson and Victoria n.d.; Klemens 1991; Lamson 1935), **District of Columbia** (McCauley 1945), **Florida** (Truitt 1966), **Georgia** (Jensen et al. 2008; Seyle 1980; Williamson and Moulis 1979, 1994a,b; Wright and Bishop 1915), **Illinois** (Ballard 1998; Blanchard and Princen 1976; Davis and Rice 1883; Garman 1892; Holman 1966; Kennicott 1855; Parmalee 1955; Phillips et al. 1999; Pope 1964; Rossman 1960; Smith 1961), **Indiana** (Brodie et al. 2002; Hay 1892; MacGowan and Kingsbury 2001; Minton 1966, 1972, 2001), **Iowa** (Christiansen and Bailey 1986; Christiansen and Mabry 1985; LeClere 1998), **Kansas** (Boles 1980; Busby et al. 1994, 1996, 2005; Clarke 1980; Collins 1974, 1982, 1993; Collins and Collins 1993; Smith 1950, 1956a; Taylor 1929), **Kentucky** (Barbour 1971; Collins 1964; Funkhouser 1925; Snyder 1972), **Louisiana** (Boundy 1997; Dundee and Rossman 1989; Keiser and Wilson 1969), **Maine** (Hunter et al. 1992, 1999; Ritter 1992), **Maryland** (Cooper 1960; Harris 1975; Kelly et al. 1936; McCauley 1945), **Massachusetts** (Lazell 1976; Storer 1839), **Michigan** (Carpenter 1957; Hatt et al. 1948; Holman et al. 1989; Langlois 1924; Ruthven 1911; Ruthven et al. 1911 [1912], 1928), **Minnesota** (Blasus 1997; Breckenridge 1944; Karns 1986; Oldfield and Moriarty 1994; Perry and Dexter 1989), **Mississippi** (Cook 1954, 1962; Lohoefer and Altig 1983), **Missouri** (Anderson 1965; Hurter 1911; Johnson 1980, 1987, 2000), **Nebraska** (Ballinger et al. 2010; Hudson 1942; Lynch 1985), **New Hampshire** (Oliver and Bailey 1939; Taylor 1993), **New Jersey** (Fowler 1906; Grant 1966; Schwartz and Golden 2002; Trapido 1937), **New York** (Baird 1854; DeKay 1842; Ditmars 1896; Eckel and Paulmier 1902), **North Carolina** (Dorcas 2004; Huheey and Stupka 1967; Martof et al. 1980; Palmer and Braswell 1995), **Ohio** (Conant 1934, 1938, 1951; Denny 2002; King 1987b, 1988; King et al. 1997; Morse 1904; Smith 1882), **Oklahoma** (Black 1974; Ortenburger 1927, 1929a,b; Sievert and Sievert 1988; Webb 1970), **Pennsylvania** (Harrison 1950; Hulse et al. 2001; McCoy 1982; Roddy 1928; Shaffer 1991; Surface 1906), **South Carolina** (Hall 1994; Martof et al. 1980; Penney 1952), **South Dakota** (Ballinger et al. 2000; Coues and Yarrow 1878; Fishbeck and Underhill 1960; Thompson and Backlund 1999), **Tennessee** (Barr 1961; Huheey and Stupka 1967; Johnson 1958; Rhoads 1895; Snyder 1972), **Texas** (Dixon 1987, 2000; Gloyd 1944; Werler and Dixon 2000), **Vermont** (Andrews 2001), **Virginia** (Martof et al. 1980; Mitchell 1974, 1994a; Mitchell and Buhlmann 1999; Mitchell and Reay 1999; Tobey 1985), **West Virginia** (Green and Pauley 1987; Richmond and Boggess 1941), **Wisconsin** (Casper 1996; Christoffel et al. 2003; Dickinson 1949; Higley 1889; Pope and Dickinson 1928; Tekiela 2004; Watermolen

and Murrell 2001), **Canada** (Bleakney 1958b; Cook 1984; Froom 1972; Logier and Toner 1955, 1961; Mills 1948), **Manitoba** (Preston 1982), **Ontario** (Anonymous 1962; Denman and Lapper 1964; Froom 1967; King 1987b, 1988; King et al. 1997; Logier 1925, 1939; Snyder et al. 1941; Weller and Oldham 1988), **Québec** (Bider and Matte 1996; Desroches and Rodrique 2004), **Saskatchewan** (Cook 1978). State and Canadian provincial publications are cited in Moriarty and Bauer (2000).

• **FOSSIL RECORD.** Parmley (1990) distinguished *Nerodia erythrogaster* and *N. fasciata* from *N. sipedon* on the basis of a higher neural spine in the latter. Eshelman (1975) and Parmley (1989) followed Holman (1962, 1968, 1971) in suggesting that *N. sipedon* and *N. hibbardi* (an extinct species) have neural spines that are longer than high, whereas those of *N. erythrogaster* are as long as high, with the caveat that “neural spine height may not always be a diagnostic character.” Fay (1988) determined that the length-width ratio in *Nerodia* is less than or equal to 1.5. Holman (1969) used the basisphenoid-parasphenoid element as a diagnostic feature for separation on the species level. Holman (1965) separated *Thamnophis* and *Nerodia sipedon* on the basis of the quadrate; in *Thamnophis* the mandibular end is narrower and more expanded than in *Nerodia*.

Pleistocene (except where noted) fossils have been reported from the following states: **Alabama** (Holman 1995, 2000), **Florida** (Auffenberg 1963), **Georgia** (Fay 1988; Holman 1967, 1985a,b, 1990, 1995, 2000), **Kansas** (Brattstrom 1967; Eshelman and Hager 1984; Hibbard and Taylor 1960; Hibbard et al. 1978; Holman 1971, 1972b, 1980, 1981, 1984, 1986, 1987a,b, 1995, 2000; Preston 1979; Rogers 1982), **Maryland** (Holman 1977a, 1980, 1981, 1995, 2000), **Michigan** (Holman 1990 [mid-Holocene], 2001a), **Missouri** (Holman 1974, 1980, 1981, 1995, 2000; Hood and Hawksley 1975), **Nebraska** (Ford 1992; Holman 1972a, 1995, 2000; Holman and Schloeder 1991 [Pliocene]; Parmley and Holman 1995; Rogers 1984), **Ohio** (Holman 1995, 1997, 2000), **Pennsylvania** (Church 1994; Fay 1984, 1988; Gilmore 1938; Guilday et al. 1964, 1978; Holman 1981, 1995, 2000; Richmond 1964), **South Dakota** (Holman 1977b, 2000), **Tennessee** (Corgan and Breitburg 1996; Fay 1988; Holman 1981, 1995, 2000; Lundelius et al. 1983), **Virginia** (Fay 1984, 1988; Gehlbach 1965; Holman 1981, 1987c, 1995, 2000; Holman and McDonald 1986), **West Virginia** (Holman 1982, 1995, 2000; Holman and Grady 1987, 1989, 1994), and **Canada** (Fay 1984).

Lundelius et al. (1983) and Holman (1995, 2000) gave an excellent overview of Pleistocene fossil history and review of pertinent literature, and Holman (2001) provided data on unique herpetological habitat in the fossil dunes and soils near Saginaw Bay, Michigan.

Fossils of *Nerodia sipedon* are associated with a number of Native American sites, either as intrusives or subsistence items (Adovasio et al. 1980; Bense 1969; Duncan 2002; Gardner 1992; Holman 1978;

Lovis et al. 2001; Madrigal 1999; Parmalee 1967; Percy 1974; Redmond and Tankersley 2005; Russell et al. 2009; Stafford et al. 2000; Waselkov 1984; Whyte 2002).

• **PERTINENT LITERATURE.** General works on historical and natural history on *Nerodia sipedon* include Ballinger et al. (2010), Gibbons and Dorcas (2004), Krulikowski (2004), and Wright and Wright (1957). Additional literature follows by topic: **activity and movement** (Aldridge and Bufalino 2003; Blanchard and Finster 1933; Blasus 1997; Breckenridge 1944; Brimley 1925; Brown 1940; Brown and Parker 1976; Camp 1980; Carbone 1993; Clarke 1958; Collins and Collins 1993; Conant 1949; Diener 1957; Fitch 1958; Fitch and Shirer 1971; Fraker 1970; Greshock 1998; Hammerson 1999; Hendry et al. 2001; Huey 1982; King 1985, 1986a; Kitchell 1969; Klimstra 1958; Klemens 1993; Landreth 1973; Lillywhite 1987; Meyer 1992; Palmer and Braswell 1995; Pattishall and Cundall 2008a; Roe 2002; Roe et al. 2003; Semlitsch and Bodie 2003; Stickel and Cope 1947; Swanson 1952; Tiebout and Carey 1987; U.S. Fish and Wildlife Service 2003; Werler and Dixon 2000; Zug 1993), **aggregations** (Barry et al. 1992; Brown and Weatherhead 2004; Foster and Hampton 2003; Greenberg et al. 2006; Gregory 1982, 2004; Krulikowski 2004; Parker and Brown 1973; Pough et al. 1998, 2001; Prosser et al. 2002), **anatomy and morphology** (Baird 1970; Baker et al. 2007; Bellairs and Boyd 1947; Bellairs and Kamal 1981; Brongersma 1957; Bursey 1986; Butner 1963; Chiasson and Lowe 1989; Chiodini et al. 1982; Cruce and Newman 1984; Cundall 1983; Cundall and Shardo 1995; Cunningham and Dunn 1928; Dessauer 1967; Drummond 1985; Dowling and Savage 1960; Erickson 1991; Fish 1893; Fitch 1999; Gage 1945; Garrigues 1962; Gratz 1983, 1984; Halpern et al. 1976; Hartman 1971; Holliday et al. 2010; Holman 1962, 1965, 1969a; Kearney and Rieppel 2006; Keiser 1970; King 2002; King et al. 1999; Krohmer 2004; Langebartel 1968; Mahler and Kearney 2006; Mason 1992; McDonald 1960, 1976; Mead 1976; Miller 1968, 1978, 1980; Nakamura and Smith 1960; Pallot 1974; Palmer and Braswell 1995; Papez 1936; Pough 1994; Quay and Wilhoft 1964; Queral-Regil and King 1998; Ramsay 1979; Rieppel 1980; Rossman et al. 1982; Schroeder 1986; Schwab 1979; Smith et al. 1953; Taub 1967; Tavares-Bastos et al. 2008; Ten Eyck 1989; Thompson 1911; Toland and Dehne 1960; Ulinski 1975, 1976a,b, 1977, 1981; Ulinski and Rainey 1980; Varkey 1973; Velhagen 1995; Voris and Jayne 1976; Walls 1931; Wang et al. 1998; Warner 1946a,b, 1947, 1955; Warner and Hindle 1952; Weil 1984; Wever 1978; Whiting 1969; Young et al. 1999), **anthropology** (Hayden 1863; Moore 1949; Putnam 1868; Speck 1923; Speck and Dodge 1945), **behavior (courtship and mating)** (Aldridge et al. 2003, 2005; Anderson 1965; Barry 1992; Barry et al. 1992; Bauman and Metter 1977; Blasus 1997; Brodie and Garland 1993; Brown 1940; Brown and Weatherhead 1999b, 2004; Cagle 1942; Davis 1936; Ernst and Barbour 1989; Gloyd 1928; King 1939; King 1986a,b;

Kissner et al. 2005; Kraus and Schuett 1982; Miller 1979; Mushinsky 1979; Neill 1949; Noble 1937; Perry 1920; Pope 1964; Pough et al. 1998, 2001; Prosser 1999; Saint Girons 1985; Shine 2003; Shockley 1952; Tinkle and Liner 1955; Trauth et al. 2004; Warner 1955; Weatherhead et al. 1995, 2002), **behavior (orientation)** (Aldridge et al. 2005; Balent and Andreadis 1998; Breckenridge 1944; Brown and Parker 1976; Czaplicki and Porter 1974; Dummond 1979, 1985; Dunbar 1979; Ford 1986; Ernst and Barbour 1989; Fraker 1970; Godard et al. 1998; Gove 1971, 1979; Gove and Burghardt 1975; Gregory et al. 1987; Halpern 1980, 1992; Himes 2003b; Kellogg and Pomerooy 1936; Landreth 1973; Mason 1992; Newcomer et al. 1974; Robison 1976; Schaeffel and de Queiroz 1990; Scudder et al. 1980; Ulinski and Rainey 1980), **behavior (other)** (Burghardt 1977; Cundall 2000; Ferguson 1977; Ford and Burghardt 1993; Osten Sacken 1884; Reese 1927), **biochemical genetics** (Cundall 1970; Dessauer and Fox 1958; Dohm et al. 2007; Eberle 1972; Feldman et al. 2009; Ferguson 1932; George and Dessauer 1970; Gibbs et al. 1998; Glaberman et al. 2008; Grossberger and Parham 1992b; Hegeman 1961; Highton et al. 2002; Hille et al. 2002; King and Lawson 1995, 1996; Lawson et al. 1991; MacCulloch et al. 1996; Miller et al. 2006; Prosser et al. 1999; Rodriguez-Robles and Thomas 1992; Tiersch et al. 1989; Tsudzuki et al. 1998; Velhagen 1997), **biochemistry** (Ahouse et al. 1993; Barry et al. 1992; Boyd and Goodyear 1971; Bragdon et al. 1954; Burger et al. 2005, 2007; Campbell et al. 2005; Carraway et al. 1982; Cohen 1954, 1955; Culbertson and Talbot 1935; Dessauer 1967, 1970; Dessauer and Fox 1956, 1958; Dessauer et al. 1962, 1987; Deutsch and McShan 1949; Duguy 1970; Ernst and Barbour 1989; Frye 1991; Hegeman 1961; Hurlbert 1970; Hutton 1958; Mao and Dessauer 1971; Minton 1976; Minton and Salanitro 1972; Murdaugh and Jackson 1962; Rodriguez-Robles and Thomas 1992; Sullivan 1967; Temple and Barthalmus 1994; Weil and Aldridge 1981; Wintrobe 1933), **biogeography** (Bleakney 1958b; Boback 2003; Brown 1904; Burbrink et al. 1998; Hecnar et al. 2002; Holman 1960, 2004; Johnson 1958; King 1988; King et al. 1997; Lardie 1982; Long 1993; Lundelius et al. 1983; Mao and Dessauer 1971; Mitchell and Pague 1984; Owens 1989; Owens and Dixon 1989; Placyk and Gillingham 2002; Robinson 2005a; Ward et al. 1990), **birth** (Aldridge and Bufalino 2003; Barron 1995; Barron and Andraso 2001; Batson 1949; Bleakney 1958a; Brown 1940; Dunn 1915a; Hulse et al. 2001; Martin 1998; Saint Girons 1985; Shockley 1952; Slevin 1951; White et al. 1982), **body size and growth** (Balent and Andreadis 1998; Barron 1995; Blanchard and Finster 1933; Boundy 1995; Brock and Myers 1979; Brown 1940; Brown 1992; Brown and Weatherhead 1997, 1999a,c, 2004; Burghardt 1968; Collins and Collins 1993; Conant 1975; Feaver 1977; Finkler and Claussen 1999; Fitch 1999; Graham 1982; Hammerson 1999; King 1985, 1986a, 1989a, 1993c; King et al. 1999; Langlois 1924; Magee 1961; Martin 1998; Palmer and Braswell 1995; Pope 1964; Powell et al. 1982;

- Prosser et al. 2002; Queral-Regil 1997; Queral-Regil and King 1998; Raney and Roecker 1947; Scribner and Weatherhead 1995; Seigel and Ford 1987; Shockley 1952; U.S. Fish and Wildlife Service 2003; Velhagen and Savitzky 1998; Weatherhead and Brown 1996; Zerwekh 2003), **captive husbandry** (Bennett 1991; Boever and Caputo 1982; Clark et al. 1985; Frye 1991; Hartup 1996; Hohn 2003; Klingelhöffer 1959; Littleford and Keller 1946; Rossi 1992; Rossi and Rossi 1995, 2003; Strathemann 1995; Vacik 1992), **checklists, keys and similar compendia** (Ballinger and Lynch 1983; Barbour and Loveridge 1946; Benke and Cushing 2005; Bider 1976; Blanchard 1925b; Breukelman and Downs 1936; Brimley 1926, 1944; Brown 1901; Brown and Erdle 2009; Cagle 1941, 1964, 1968; Chermock 1952; Cochran 1961; Collins 1990, 1997; Collins and Taggart 2009; Collins et al. 1978, 1982; Conant et al. 1956; Cope 1893; Crother et al. 2000; Delis et al. 2010; Dunn 1915b–d, 1920; Ellis 1917; Ellis and Henderson 1913; Fishbeck and Underhill 1960; Fitch 1965; Fogg and Verrill 1862; Force 1925; Fowler 1917; Frank and Ramus 1995; Gaines 1894; Hardy and Mansueti 1962; Hay 1902; Henshaw 1904; Herdendorf 1992; Higgins 1873; Hoy 1883; Keim 1914; Keiser and Wil-son 1969; Kluge 1984; Levell 1997; Linsdale 1927; Malnate 1971; Mombert 1869; Myers [1925] 1926, [1926] 1927; Ortenburger 1927, 1930; Perkins 1940, 1949; Peters 1952; Potts and Collins 2005; Powell et al. 1998; Purdue and Webb 1986; Revillod 1913; Richmond and Boggess 1942; Ruffer et al. 1968; Simon et al. 1992, 2002; Sokolov 1988; Somes 1911; Springer [1927] 1928; Street 1914; Stejneger and Barbour 1917, 1923, 1933, 1939, 1943; Tilley and Huheey 2001; Verrill 1862; Wallin 1991, 1992; Whitaker 1968; Wright 1950; Wright and Wright 1952; Yarrow 1876, 1882), **color and pattern variation** (Beatson 1976; Bowen 2003; Brodie and Garland 1993; Bulmer 1985; Clay 1935; Cooper 1957; Dyrkacz 1981; Ernst et al. 1997; Fitch 1959; French 1981; Fromm 1972; Haub 1962; Hendry et al. 2001; Hensley 1959; Hulse et al. 2001; King 1985, 1987a, 1992, 1993a,b, 1994, 2004; King and Lawson 1995, 1996, 1997; McAlpine 1983; Mitchell 1994b; Neill 1946; Nickerson and Krager 1975; Ortenburger 1922; Pfingsten and Walker 1978; Phillips et al. 1965; Ray 2004; Ray and King 2006; Rhoads 1895; Robertson 1985; Sattler and Guttman 1976; Smith 1956; Smithberger 1995; Svihla 1936; Viosca 1924; Wood 1959), **conservation** (Anonymous 1993; Ashton et al. 1976; Attum et al. 2007; Barrett and Guyer 2008; Burton and Uzarski 2009; Busby and Parmelee 1996; Cagle 2008; Cook 2008; Cooper et al. 1977; Dodd 1984; Eldridge and Winsor 1993; Fazio and Szymanski 1999; Greenberg and Waldrop 2008; Hammerson 2007; Herman 2005; Hohn 2003; Homyack and Giuliano 2002; Jones 2010; King 2009; King et al. 2006; Kingsbury and Attum 2009; Kjoss and Litvaitis 2001a; Loehle et al. 2005; Loughman 2005; McCoy 1989; McKeating and Bowman 1977; McLeod and Gates 1998; Mifsud and Mifsud 2008; Millsap et al. 1990; Mitchell 1995; Muenz 2004; Nogle 2010; Renken et al. 2004; Rightmire 2001; Riley 1960; Roe et al. 2003, 2004, 2006, 2010; Sarakinos et al. 2001; Severson 2007; Shepard et al. 2008; Tennant and Bartlett 2000; U.S. Fish and Wildlife Service 2003; Wilgers et al. 2006; Williams 2003; Witczak and Dorcas 2009), **disease** (Andrews et al. 1965; Brown and Sleeman 2002; Burns et al. 1996; Bursey 1986; Chiodini 1982; Chiodini et al. 1980, 1983; Clark and Shepard 1963; Galois and Ouellet 2007; Hayes et al. 1964; Hoff and Trainer 1973; Karstad 1961; McKinstry 1982; Paterson 1957; Ratcliffe 1943; Ratcliffe and Geiman 1934; Smith and Desser 1998; Smith and Hong 1994; Smith et al. 1994, 1996, 1999), **ecdysis** (Brown 1940, 1956; Littleford and Keller 1946; Schaefer 1933; Stabler 1939), **ecology and distribution** (Adams and Clark 1958; Adler 1961; Adler and Dennis 1960, 1961; Albritton 1981; Aldrich 1943; Allen 1938; Anderson 1941; Anderson et al. 1952; Andrews 2001; Anonymous 1972; Anton 1999; Applegate and Zim-bleman 1978; Applegate et al. 1995; Arndt 1977; Ash 1945; Ashley and Robinson 1996; Ashton 1976; At-kinson 1901; Attum et al. 2008; Backlund 1999; Bahret 1996; Ball 1980; Ballard 1998; Ballinger et al. 2000; Barbour 1950, 1956; Barker 1964; Bartlett 2001; Bartlett and Tennant 2000; Bauer and Witwer 1995; Bauman and Metter 1975; Beane 1998; Beat-son 1976; Behler and King 1989; Bekker 2007; Bider and Matte 1996; Bishop 1915, 1923, 1926; 1927; Black 1974; Blanchard 1922, 1925a,b,c; Blanchard and Princen 1976; Blatchley 1900; Blem 1972; Blem and Blem 1995; Boles 1980; Bonati 1980; Bond 1931; Boundy and Burbrink 1998; Bowen and Gill-ingham 2004; Boyer and Heinze 1934; Boyles 1952, 1953; Brady 1925; Branson 1904; Branson and Ba-ker 1974; Brennan 1937; Breukelman and Clarke 1951; Brimley 1927, 1928; Brimley and Sherman 1908; Brodie et al. 2002; Brodman 2001, 2003; Bro-phy and Brophy 1998; Brothers 1965; Brown 1940; Brown 1992; Brown and Erdle 2009; Bruce 1965; Brumwell 1951; Bumpus 1885; Burch 1940; Burger 2004; Bush 1959b; Burbrink et al. 1998; Burger et al. 2004; Burke et al. 1999; Burt 1927, 1931, 1933a–c, 1935, 1946; Burt and Burt 1929a,b; Burt and Hoyle 1935; Busby et al. 1994, 1996, 2005; Cagle 1942; Cahn 1929; Carbone 1993; Carpenter 1952, 1955, 1957; Casper 1997; Cecala et al. 2010; Chamber-laine 1993; Christiansen and Mabry 1985; Cink 1994; Clark 1903, 1904; Clark 1961; Clarke 1949, 1956, 1958; Clarke et al. 1958; Clausen 1943; Cliburn 1957; Cobb and Summerhill 1996; Cochran 1982, 1983, 1987, 1998, 2001; Collins 1959, 1964, 1981; Conant 1934, 1937a,b, 1938, 1951, 1952, 1955, 1963, 1979, 1982; Conant and Bailey 1936; Conant et al. 1990; Connior et al. 2008; Cook 1954; Cooper 1956, 1960; Cope 1896; Coulson 1986; Creaser 1944; Creque 2001; Crosswhite et al. 2004; Daniel 1984; Davenport 2005; DeGraaf and Rudis 1983; De-Kay 1842; Dellinger and Black 1938; DeLotelle 1976; Delzell 1979; Denman and Lapper 1964; Dennis 1958a,b, 1959; DePoe et al. 1961; Dickinson 1950; Ditmars 1941; Dopirak 2002; Dorcas et al. 2006, 2010; Dowling 1957, 1958; Dozeman 2004; Drought 1987; Drowne

- 1905; Duellman 1947, 1951; Dunn 1940; Dunn and Allen 1935; Dury 1932a,b; Dury and Gessing 1940; Eckel and Paulmier 1902; Eckerlin 1991; Edgren 1944; Edgren and Stille 1948; Edmond 1993; Edwards 2007; Ehrhart 1960; Endsley 1954; Engelhardt et al. 1915; Ernst 2003, Ernst et al. 1997; Evans 1947; Evans and Rocker 1951; Evermann and Clark [1914] 1915; Ferguson 1961; Fichter 1947; Finneran 1948; Fiorentino 2002; Fitch 1939, 1951, 1952, 1956, 1958, 1978, 1982, 1993, 1999, 2000, 2003a, 2006; Fitch and Shirer 1971; Fogarty 2005; Force 1930; Foster and Hampton 2003; Foster and Mullin 2007; Foster et al. 2004; Fowler 1925, 1942; Fraker 1970; Frese 2001; Froom 1967, Gaige 1914; Garman 1883, Gehlbach and Collette 1959; Gentry 1941, [1955] 1956; Giazzone 2002; Gibbons and Dorcas 2004; Gibson 2002, 2004a,b; Gier 1967; Gloyd 1928; Goin and Goin 1953; Goodman 1948; Gordon 1952; Gorelick and Bertram 2008; Graham 1982; Grant 1935, 1936, 1937; Grant 1966; Gray 1941; Gray 2002a; Gray and Lethaby 2008; Graziano 2010; Green 1937; Gregory 2009; Greshock 1998; Grogan and Bystrak 1973; Hahn 1958; Hall 1969, 1994; Hall and Smith 1947; Hambrick 1976; Hamilton 2003a,b; Hammerson 1999; Hanebrink and Byrd 1986; Hankinson 1917; Harding 1997; Hardy 1972; Harlan 1827; Harris 1967; Hassell 1961; Hassinger et al. 1970; Hatt et al. 1948; Haub 1962; Heatwole and Getz 196; Hedrick and Holmes 1956; Heilman 1951; Henderson 1974; Henning 1938; Hibbard 1936; Higley 1889; Himes 2004; Hoffman 1945; Hoffman 1986; Holbrook 1843; Holland et al. 1994; Holman 1960, 1966, 2001b; Hooper and Elmeer 1996; Hopey and Petranka 1994; Hoyle 1936; Hudson 1942, 1954; Hulse et al. 2001; Hunter et al. 1999; Hurter and Strecker 1909; Hutchison 1956; Jackson 1961; Jensen and Moulis 1997; Johnson 1925; Johnson 1958, 1964; Johnson and Van Deusen 1980; L. Jones 1912; Jones 1928; Jopson 1984; Kelly et al. 2005; Kennicott 1855; Kiviat 1978; King 1939; King 1985, 1986a,b, 1989a, 1993a,b; King and Lawson 1995; King et al. 2006; Kirsch 1895; Kissner and Weatherhead 2005; Klein 1989; Klemens 1983, 1993, 1995; Klimstra 1950; Klimstra and Hutchinson 1965; Kong 2006; Kraatz 1921; Kraus and Schuett 1982; Lacy 1995; Laderman 1989; Langebartel 1947; Langlois 1924, 1964; Lannoo et al. 2009; Lardie 1982; Laurent and Kingsbury 2003; Lazell and Musick 1973; Lee 2009; Lohofener and Altig 1983; Logier 1939; Long 1993; Long and Long 1976; Long et al. 1978, 1987; Loomis 1948; Lord 1956; Lovich and Jaworski 1988; Ludwig et al. 1992; Luhring 2007; Lutz 2009; Lynch 1985; Lynn 1936; Manville 1951, 1952; Mansueti 1941, 1958; Markezich and Beckett 2001; Martin 1981; Martof 1963; Mauger and Anton 2003; Maxwell et al. 2000; McAllister and Tabor 1985; McCauley and East 1940; McDermott 1947; McKinstry and Cunningham 1980; McKinstry et al. 1987; Mebert 1996, 2003, 2008; Meshaka 2010a,b; Metts et al. 2001; Meyers and Klimstra 1963; Mierzwa 1985, 1990; Mierzwa et al. 1999/2000; Mills 1948; Miller et al. 2005; Minton 1944, 1968; Mitchell 1974, 1994a; Mitchell and Georgel 1996; Mitchell and Pague 1984; Mitchell and Reay 1999; Morse 1902; Mullin and Eubank 1997; Murphy 1987; C.W. Myers 1957, 1959; G.S. Myers 1929; Myers and Klimstra 1963; Necker 1934, 1939; Neely et al. 2003; Neill 1951a,b, 1954, 1957; Netting 1936a,b; Newcombe 1929; Niemiller 2005; Norden 2005; Northrop 2009.; Norton and Harvey 1975; Oldham and Sutherland 1986; Oliver and Bailey 1939; Olson 1956; Olson and Walk 1999; Ortenburger 1921, 1922, 1929a,b; Osbourn 2005; Owen 1989; Owens 1941, 1949; Palmer and Braswell 1995; Palmer and Fowler 1975; Parker 1937, 1939, 1947, 1948; Parker and Plummer 1987; Pasachnik 2003; Paton 2005; Pattishall and Cundall 2008b, 2009; Pawling 1937; Penn 1940; Penney 1952; Pentecost and Vogt 1976; Peters 1942, 1946; Petzing et al. 1998, 2000; Phillips et al. 1965; Piatt 1931; Pickens 1927; Pinder 1997; Platt 2003; Placyk et al. 2002; Platt 1973; Platt et al. 1989; Prince et al. 1955; Poly 1999; Pope 1964, 1966; T.E.B. Pope 1930; Potter 1920; Prosser et al. 1999; Pryor 1996a,b; Ransom 1981; Ray 2004; Ray and King 2006; Reams et al. 2008; Reddick [1895] 1896; Redmer and Ballard 1995; Reed 1956; Rhoads 1895; Rice et al. 2001; Richards 1967; Richmond and Goin 1938; Riedle and Hackler 2006; Riedle and Hynek 2002; Robertson 1988; Robertson and Weatherhead 1992; Roble 1999; Roddy 1928; Roe 2002; Roe et al. 2003; Ross et al. 2000; Rossman 1960; Roth 2005; Roth and Greene 2006; Rosenzweig et al. 2007; Rubo et al. 2003; Rush and Fleharty 1981; Ruthven 1910, 1911; Sattler 1995; Schmidt and Necker 1935; Schueler 1975; Schuier et al. 1972; Schwaner 1969; Scott 1967; Scott and Snyder 1968; Scott and Twombly 1994; Seehorn 1982; Sexton et al. 2007; Seyle 1980; Shetter 1949; Shipman et al. 2004; Shockley 1952; Shoup et al. 1941; Smith 1947, 1955, 1961; Smith and Minton 1957; Smith and Powell 1993; Smith et al. 1965, 1993; Snyder 1972; Snyder et al. 1941; Spurgeon 2002; Stanford et al. 2010a,b; Stehr and Branson 1938; Stewart 1961; Stewart and Rossi 1981; Stickel and Cope 1947; Stille and Edgren 1948; Stone 1906; Storer 1839; Swanson 1952; Taggart 1992, 2000; Taylor 1929, 1935; Taylor et al. 1998; Thomas 1949; Thompson and Thompson 1912a,b; Thompson and Wilson 1999; Thurow and Silwinski 1991; Tiebout and Cary 1987; Tihen 1937; Tihen and Sprague 1939; Tinkle 1957; Tobey 1985; Toner 1935; Townsend and King 2001; Trapp 1959; Trowbridge 1937; Tuberville et al. 2005; Tucker 1994, 1995; Turner and Fowler 1981; Twombly and Scott 1988; U.S. Fish and Wildlife Service 2003; Van Devender 1983; Viets 1993; Vincent and Herrel 2007; Vincent et al. 1999; Viosca 1923; Vradenburg 2005; Walley 2002; Ward et al. 1990; Watermolen 1992; Watkins-Colwell et al. 2006; Webb 1970; Weber 1928; Weller 1930; Weller and Oldham 1988; Welter and Carr 1939; Werler and McCallion 1951; Werner 1959; Wheeler et al. 1935; Wiggs and Angelo 2003; Wilson and Fridle 1950; Wood 1949, 1959; Wood and Duellman 1947; Woodman 1959; Woolcott 1981; Wright and Weed 1923; Young 1993; Zirkle 1993; Zug 1993), **embryology and gestation** (Aldridge 1979; Barron 1995, 1997a; Barron and Andraso 2001; Bauman and

- Metter 1977; Bragdon 1951; Brown and Weatherhead 2000; Conway and Fleming 1960; Cunningham and Dunn 1928; Nelsen 1953; Saint Girons 1985; Shockley 1952; Smith et al. 1953; Trauth et al. 1994; Velhagen and Savitzky 1998), **endocrinology** (Bragdon 1953b; Clark 1970; Fingerman 1967; Gabe 1970; Hebbard and Charipper 1955; Justy and Mallory 1985; King et al. 1999, 2000; Krohmer 1986; Krohmer et al. 2004; Lynn 1970; Neudeck 1969; Quay 1965, 1979; Quay and Wilhoft 1964; Riley and Callard 1988; Schaefer 1933; Seigel and Ford 1987; Shockley 1952; Smith and White 1955; Spaur and Smith 1971; Sykes 2008; Thompson 1911; Underwood 1992; Weil 1980, 1982; Weil and Aldridge 1981), **environmental contaminantion** (Bishop and Gendron 1998; Bishop and Rouse 2000, 2006; Brisbin et al. 1974; Burger 2007a,b; Burger et al. 2005, 2007; Campbell et al. 2005; Cosgrove 1965; Fernie et al. 2008; Fleet et al. 1972; Fleet and Plapp 1978; Fontenot et al. 2000; Giles 1970; Goodrum et al. 1949; Heinz et al. 1980; Herald 1949; Hoffman and Curnow 1979; Hoffmann and Surber 1948; Kim 2007; Lacki et al. 1992; Meeks 1968; Moriarty 1972; Neuman-Lee 2010; Niethammer et al. 1985; Parker et al. 1973; Peterle 1966; Punzo et al. 1979; Smith and Glasgow 1965; Wong et al. 2001; Wood et al. 2010), **field techniques** (Blanchard 1937; Blanchard and Finster 1933; Browder et al. 1995; Clark 1966; Ernst and Barbour 1989; Feaver 1976, 1977; Fitch 1951; Fitch and Shirer 1971; Gibbs and Weatherhead 2001; Harris 1965; Jenkins et al. 2003; King 2004; King et al. 2006; Kjos and Litvaitis 2001b; Langen et al. 2007; Nickerson 1970; Olson and Warner 2003; Osgood 1970; Roe 2002; Roth and Greene 2006; Stickel and Cope 1947), **food habits and predation** (Abbott 1870; Alexander 1977; Alexander and Shetter 1969; Anderson 1965; Atkinson 1901; Babbitt 1937; Barbour 1950; Bartlett and Tennant 2000; Bauman and Metter 1975; Bishop 1927; Blackburn et al. 2003; Bowen 2004b; Brimley 1905; Brown 1958; Brown 1979a,b; Bush 1959a; Cagle 1942; Camp 1980; Camp and Tilley 2005; Camp et al. 1980; Carbone 1993; Carpenter 1958; Cochran 1911; Collins 1980; Collins and Collins 1993; Corse et al. 1974; Cuthbert 1954; DeKay 1842; Dence 1933; DeVault and Krochmal 2002; Ditmars 1912; Drummond 1980; Eckel 1901; Evans 1942; Fitch 1963, 1999; Fontenot and Platt 1993; Forester and Thompson 1998; Fraker 1970; Freeman and Grossman 1992; Gerhardt et al. 1996; Gross and MacMillan 1981; Hamilton 1951b; Hamilton and Pollack 1956; Hammerson 1999; Hankinson 1915, 1917; Harding 1981; Harrison 1971; Heinen 1994; Himes 2002a,b, 2003a,b, 2004; Hobson 2002; Holomuzki 1989, 1997; Huey 1982; Huheey and Stupka 1967; Hunter et al. 1999; Iverson 1975; Jones et al. 2009; Kats 1986, 1988; King 1939; King 1985, 1986a, 1989a, 1993c, 2002, 2004; King et al. 1999, 2006; Klemens 1993; Lacy 1995; Laforce 2004; Lagler and Lagler [1943] 1944; Lagler and Salyer 1945, [1945] 1947; Laughlin 1959; Laurent and Kingsbury 2003; Lotrich 1973; Martof 1956, 1962; McCallum 1995; McCauley 1945; McFadden 1961; McGrew 1963; Meyer 1992; Minckley 1963; Mitchell 1986, 1994a; Morris 1974; Mount 1975, 1996; Mushinsky 1987; Neill 1951a, 1968; Ortmann 1906; Palmer and Braswell 1995; Palmer and Fowler 1975; Parkhurst et al. 1992; Pauley 2005; Perrill and Magier 1988; Petit and Petit 1996; Pope 1944, 1964; Porter and Czaplicki 1977; Raney and Roecker 1947; Ray 2004; Ray and King 2006; Richmond 1944; Robinson 2005b; Roe 2002; Rummel 2010; Rundquist and Collins 1977; Schmidt and Davis 1941; Schwartz et al. 2000; Sheppe 1965; Shockley 1952; Smith and Powell 1993; Snyder 1972; Stahl 1996; Stoner 1941; Suedkamp Wells et al. 2007; Surface 1906; Swanson 1952; Tack 1941; Timm and Meretsky 2004; Tilley 1973; Trauth et al. 2004; U.S. Fish and Wildlife Service 2003; Uhler et al. 1939; Warren et al. 2004; Weatherhead and Brown 1996; Welter and Carr 1939; Wetzel and Shelar 1964; Wigley 1959; Wood 1938; Zelnick 1966), **foraging behavior** (Abbott 1887; Albanese 2001; Aldridge et al. 2003; Andreadis and Burghardt 2005; Balent and Andreadis 1998; Barron 1995; Barron and Andraso 2001; Bilke et al. 2006; Bowen 2001; Brown 1940, 1958; Carbone 1993; Conant 1937b; Cundall and Pattishall 2011; Cunningham and Burghardt 1999; Czaplicki and Porter 1974; DeVault and Krochmal 2002; Diener 1957; Dix 1968; Drummond 1980, 1985; Eisner et al. 1990; Ernst and Zug 1996; Eubanks and Pecor 2003; Gans and Pough 1982; Gillingham and Rush 1974; Gove 1979; Hamilton 2003a,b; Hansknecht 2003; Harding 1981; Himes 2002, 2003a; Holt and Johnston 2009; King 1985, 1986a; Lagler and Salyer 1945, [1945] 1947; Lutterschmidt and Reinert 1990; McFall 1981; Meyer 1992; Mushinsky 1987; Plummer 1985; Pope 1964; Porter and Czaplicki 1977; Pough and Groves 1983; Raney and Roecker 1947; Sievert 1989; Swanson 1952; Welsh and Lind 2000; Zielinski and Barthalmus 1989), **genetics and karyotypes** (Eberle 1972; Ernst and Barbour 1989; Kilpatrick and Zimmerman 1973), **hibernation** (Abbott 1884; Blasus 1997; Cagle 1942; Carpenter 1953; Johnson 1925; Grant 1935; Gregory 1982; Keller and Heske 2000; Kingsbury and Coppola 2000; Kiviat 1978; Ludwig et al. 1992; Mattison 1995; Neill 1948; Parker and Brown 1973; Shirer and Fitch 1970; Wasser 1985), **immunology** (Grossberger and Parham 1992a; Maha 1982), **longevity** (Bowler 1977; Flower 1937; Snider and Bowler 1992; Wright and Wright 1957), **mimicry** (Fitch 1959; Goode 1873; Pough 1994; Roe 2002), **parasites** (Anderson 1935; Ash 1962; Ash and Beaver 1963; Baker 1987; Baneth and Shkap 2003; Baneth et al. 2007; Barrow and Stockton 1960; Bast et al. 1973; Blackburn et al. 1973; Booker and Yongue 1979, 1982; Boyko 1996; Brackett 1938; Britt 1947; Brown 1940; Bursey 1986; Bush et al. 1990; Byrd 1935; Byrd and Denton 1938; Byrd and Maples 1969; Byrd et al. 1940; Cable and Sanborn 1970; Cairns 1953; Camin 1948; Canavan 1937; Chambers and Hulse 2006; Chioldini et al. 1980; Chu 1936a,b; Collins 1969, 1973; Corkum 1966; Cort and Brooks 1928; Dettlerline et al. 1984; Dukes et al. 1971; Fantham and Porter 1954; Finneran 1948; Fowler 1941; Geiman and Ratcliffe 1936; Gerbod et al. 2004; Gibson

- and Rabalais 1973; Goodman 1959; Hampl et al. 2007; Harwood 1932; Holl and Allison 1935a,b; Hughes 1929; Hughes et al. 1941a,b, 1942; Hull and Camin 1960; Jacobi 1961; James 1968; Jenkins 1948; Johnston and DeGiusti 1961; Keegan 1943a,b; La Rue 1911; Langmann 1899; Lee 1960; Leidy 1856, 1891 [1890]; Lincicome and Van Cleave 1949; Lindmark and Müller 1974; Little 1966; Loomis 1956; Mattern et al. 1972; McAllister et al. 1995, 2008; McCauley 1945; McCoy 1928; McKinstry 1973; McMullen 1938; Meerovitch 1961; Miller et al. 1965; Mirza and Roberts 1957; Moskowitz 1951; Mundt 1963; Muzzall et al. 2001; Nelson 1950; Norris 1951; Odlaug 1938; Overstreet et al. 1985; Pearson 1959; Powell 1979; Pratt 1902; Price 1936; Rabalais 1968; Rau and Gordon 1980; Rau et al. 1978; Richardson and Nickol 1995; Riley and Self 1980; Schad 1962; Smith and Desser 1997, 1998; Smith et al. 1994, 1996, 1999; Sprent 1979, 1988; Stang and Cable 1966; Talbot 1934; Taylor 1892; Thomas 1937, 1941; Tills et al. 1977; Van Cleave 1921; Vernberg 1952; Voss 1961; Wacha and Christiansen 1974, 1975; Walker 1939; Walton 1927; Ward 1940; Ward and Whipple 1918; Yongue 1964, 1965; Zwart et al. 1970), **phylogenetics and evolution** (Ashton and Feldman 2003; Brodie and Garland 1993; Caprette 2005; Charnov et al. 1993; Clay 1935; Conant 1946; Dunn 1942; Fisher 1968; Gartner et al. 2010; Hendry et al. 2001; Himes 2002; King 1989b, 1992, 1993b, 1994; Jetz et al. 2009; King and Lawson 1995; Lawson 1987; Lee and Scanlon 2002; Makowsky et al. 2010; Martin 1998; Neff and Gross 2001; Pyron et al. in press; Ray and King 2006; Sattler and Guttman 1976), **physiology** (Aldridge and Brown 1995; Baker et al. 2007; Barthalmus 1989; Barthalmus and Meadows 1990; Barthalmus and Zielinski 1988; Barthalmus et al. 1993; Belkin 1964; Bennett 1982; Bennett and Licht 1975; Blem and Blem 1990; Blouin-Demers et al. 2000b; Bragdon and McManus 1952; Brongersma 1957; Brown 1958; Clark and Dantzler 1972; Dantzler 1967a,b, 1968a,b, 1970, 1976a,b; Dean and Gratz 1983; Dessauer 1970; Dunson 1978, 1980; Elliott 1978; Ferguson and Thornton 1984; Gans et al. 1968; Gratz 1984; Hartman and Lessler 1964; Heatwole 1977; Hegeman 1961; Howell and Rahn 1976; Hutton 1958; Kardong 1972; Keegan and Andrews 1942; Komadina and Solomon 1970; Krohmer 2004; Lillywhite and Maderon 1982; Martin 1998; Mautz 1982; McDonald 1959; Minnich 1982; Murdaugh and Jackson 1962; Nandi 1967; Oldak 1976; Perry 1983, 1998; Pettus 1958; Pough 1976b, 1978, 1980; Ramsay 1979; Roberts and Lillywhite 1980; Rodriguez-Robles and Thomas 1992; Scudder 1977; Skoczylas 1978; Stokes 1981; Stokes and Dunson 1982; Swanson 1946; Temple and Barthalmus 1994; Tracy 1982; Turner and Leftwich 1972; Wallach 1998; Wang et al. 1977; Zug and Dunson 1979), **population biology** (Brandley et al. 2010; Brodie and Garland 1993; Brown and Weatherhead 1999a; Clarke 1958; Gibbs and Weatherhead 2001; Hendry et al. 2001; King and Lawson 1995, 1996, 1997, 2001; Kissner and Weatherhead 2005; Marshall 2008; Pettus 1956; Prosser et al. 1999; Ray 2004; Ray and King 2006; U.S. Fish and Wildlife Service 2003; Weatherhead and Brown 1996), **predators, predation, and mortality** (Allen et al. 2008; Anderson 1978; Beatson 1976; Bednarz and Dinsmore 1985; Bider and Matte 1996; Black 1983; Blanchard 1921; Blatchley 1900; Bowen 2004a; Brodie 1968; Brown 1940; Brown and Weatherhead 1997, 1999a,c, 2004; Brown 1940; Burns 1911; Burr and Stoeckel 1999; Cooper et al. 2008; Cross 2002; Davis 1933; Drummond 1979; Dunson 1980; Ernst 1945; Ernst 1986a; Ernst et al. 1997; Errington et al. 1940; Fauth and Welter 1994; Feaver 1976, 1977; Fisher 1893; Fitch 1963, 1999; Fitch and Bare 1978; Forbush 1945; Fulk and Whitaker 1969; Gates and Thompson 1982; Gibbons 1970; Godard et al. 1998; Goldman 1971; Gray 1978; Greene 1994; Guthrie 1932; Hamilton 1951a; Hammerson 1999; Harding 2000; Hedeon 1986; Herrington 1985; Himes 2002, 2003a,b; Hoff 1975; Hoffman and Curnow 1979; Holomuzki 1997; Hudson 1942; Hulse et al. 2001; Jackson et al. 1976; Jacobi 1961; Janik and Mosher 1982; Kauffeld 1954; Kent 1951; Kern 2006; King 1985, 1986a, 1989a,b, 1993c; Kissner and Weatherhead 2005; Klemens 1993; Koczaja et al. 2005; Lacy 1995; Lagler and Salyer 1945, [1945] 1947; Lindsay 1966; Marchisin and Petranksa 1984; Marshall 1942; McCauley 1945; McDermott 1947; Miller 1909; Mori and Burghardt 2008; Morris 1974; Naylor 1978; Neill 1948; Niemiller et al. 2009; Outten 1958; Owen and Gordon 2005; Palmer and Williamson 1971; Petranksa 1998; Plummer 1985; Pough 1994; Pough et al. 1998, 2001; Pryor 1996; Ray 2004; Schueler 1975; Schwartz et al. 2000; Scribner and Weatherhead 1995; Scudder and Burghardt 1983; Shine and Charnov 1992; Shipley 1979; Shockley 1949; Smith 1977; Stafford 1952; Stanford et al. 2010a; Thompson et al. 2005; Toland 1990; Trautman 1940; U.S. Fish and Wildlife Service 2003; Weatherhead and Robertson 1991; Welch 1987; Werler and Dixon 2000; Whitaker 1971; Wilson and Friddle 1946), **reproduction** (Barron 1995; Barry et al. 1992; Bartlett and Tennant 2000; Bauman 1974; Bauman and Metter 1977; Bidmon and Stumpf 1992; Blackburn 1998; Brock and Myers 1979; Brodie and Garland 1993; Brown 1940; Brown and Weatherhead 2004; Casper 1993; Conway and Fleming 1960; Ernst et al. 1997; Feaver 1977; Ferguson 1932; Fitch 1970, 2003b; Gerald et al. 2007; Gibbs and Weatherhead 2001; Graham 1982; Hammerson 1999; Hay 1891; Iverson 1975; King 1986a, 1993d; Kissner 2002; Kissner et al. 2005; Klemens 1993; Martin 1998; Nickerson 1970; Oliver and Bailey 1939; Pike et al. 2008; Prosser et al. 2002; Rivas and Burghardt 2005; Saint Girons 1982, 1985; Shine and Charnov 1992; Shockley 1952; Skalka and Vozenilek 1986; Trauth 1991; U.S. Fish and Wildlife Service 2003; Uller and Olsson 2008; Velhagen and Savitzky 1998; Weatherhead et al. 1999, 2002; Yaron 1985), **reproduction (female)** (Aldridge 1982; Aldridge and Bufalino 2003; Bauman and Metter 1977; Barron 1995, 1997b; Barron and Andraso 2001; Barry et al. 1992; Bishop 1927; Bleakney 1958a; Boback 2003; Boback and Guyer 2003; Bragdon 1951, 1953a,b,c; Brown 1992; Cagle 1942;

Callard et al. 1991; Camp 1980; Clausen 1940; Cragin 1879; Ditmars 1896; Dunn 1915a; Ernst et al. 1997; Fitch 1970, 1985, 1999; Gerald et al. 2007; Gratz 1984; Himes and Beckett 2003; Jellen 2010; King 1986a, 1993d; Kitchell 1969; Langebartel 1947; Langlois 1924; Long et al. 1978; Loomis 1948; Martin 1998; Oliver and Bailey 1939; Palmer and Brawell 1995; Piatt 1931; Prosser 1999; Reed and Boback 2002; Schmidt and Davis 1941; Selvin 1951; Shockley 1952; Seigel and Ford 1987; Thomas 1949; Tiebout 1983; Touzeau and Sievert 1993; Trauth et al. 1994; Velhagen and Savitzky 1998; Weller 1930; Wilson and Friddle 1950), **reproduction (male)** (Aldridge 1977, 1982; Aldridge and Brown 1995; Bauman and Metter 1977; Ernst and Barbour 1989; Ferguson 1932; Jamieson and Koehler 1994; King et al. 2000; Krohmer and Aldridge 1985; Mitchell and Zug 1984; Saint Girons 1982; Schulte-Hostedde and Montgomerie 2006; Seigel and Ford 1987; Shockley 1952; Trauth et al. 2004; Van Wyk 1995; Weil and Aldridge 1981), **sex ratios** (Bleakney 1958a; Camp 1980; Fitch 1999; Weatherhead et al. 1995, 1998, 2006), **sexual dimorphism** (Barry 1991; Blanchard 1931; Bleakney 1958a; Brown 1940; Brown and Weatherhead 1999a,b, 2000, 2004; Clark [1966] 1967; Collins and Collins 1993; Elgee 2007; Fitch 1981, 1999; Grant 1935; Harding 2000; Hulse et al. 2001; Keiser 1970; King 1986a, 1989a,b; King et al. 1999; McCauley 1945; Palmer and Braswell 1995; Pope 1964; Prosser 1999; Qural-Regil and King 1998; Schaefer 1934; Shine 1991, 1993; Shockley 1952; Smith 1961; Weatherhead et al. 1995, 2002, 2006), **sexual selection** (Barry 1992; Brown and Weatherhead 1999b; Gibbs and Weatherhead 2001; King 2002; Prosser 1999; Prosser et al. 2002; Shine 1978; Weatherhead et al. 2002), **swimming and diving** (Drummond 1980; Pattishall and Cundall 2008a; Scribner and Weatherhead 1995; Weatherhead and Robertson 1991), **systematics and taxonomy** (Alfaro and Arnold 2001; Baird and Girard 1853; Barbour 1943; Blaney and Blaney 1979; Boback 2003; Boulenger 1893; Brothers 1965; Cagle 1942; Clark 1903, 1952; Clay 1932, 1938; Cliburn 1957, 1960, 1961; Cochran 1961; Conant 1942, 1963; Conant and Clay 1937a,b, 1963; Conant and Lazell 1973; Cope 1860, 1875, 1894; Dessauer 1967; Dessauer and Fox 1958; Dessauer et al. 1987; Dowling and Duellman 1978; Dowling et al. 1983, 1996; Dundee and Rossman 1989; Ernst and Barbour 1989; Ferguson 1961; Frost and Hillis 1990; Gaul 1996; Gibbons and Dorcas 2004; Günther 1858; Hamilton 1947; Hardaway and Williams 1976; Highton et al. 2002; Jamieson and Koehler 1994; Johnson 1955; Klauber 1948; Kraus and Schuett 1982; Lawson et al. 1991; Maha 1982; Malnate 1960; Mao and Dessauer 1971; McDowell 1961; Mebert 1996, 2008; Mertens 1964; Morris 1987, 1991; Mount 1975, 1996, 2003; Nakamura and Smith 1960; Pettus 1963; Pope 1964; Robertson and Tyson 1950; Rose and Selcer 1989; Rossman 1995; Rossman and Eberle 1977; Rubo et al. 2003; Schwaner 1969; Schwaner and Mount 1976; Schwaner et al. 1980; Seyle 1980; Smith 1956, 1961; Smith and Huheey

1960; Townsend 2003; Underwood 1967; Viosca 1924; Woodman 1959), **teratology** (Bennett and Licht 1975; Blatchley 1906; Drowne 1905; McDonald 1960; Murphy et al. 1987; Rubin et al. 1967; Smith et al. 2000; Swanson et al. 1997), **thermoregulation** (Avery 1982; Barron 1995; Blouin-Demers et al. 2000a, 2003; Brown and Weatherhead 1999c, 2000; Brattstrom 1965; Bulte and Blouin-Demers 2006; Burger 2001, 2004; Burns et al. 1996; Camp 1980; Carpenter 1953; Clarke 1958; Collins and Collins 1993; Dean and Gratz 1983; Denny 2002; Finkler and Claussen 1999; Fitch 1956; Justy and Mallory 1985; Kitchell 1967, 1969; Lillywhite 1987; Lueth 1941; Lutterschmidt and Reinert 1990; Mautz 1982; Meyer 1992; Osgood 1970, 1978; Peterson et al. 1993; Pough 1978; Robertson 1988; Robertson and Weatherhead 1992; Saint Girons and Saint Girons 1956; Shine 1980; Sievert and Andreadis 1999; Sykes and Klukowski 2009; Weatherhead and Robertson 1991; Weil and Aldridge 1981).

• **ETYMOLOGY.** The most favored plausible suggestion comes from Brown (1956), "*Nerodia sipedon* (Linnaeus, 1758), from the Greek *SEPEDON* meaning "rotteness" or "decay"; a serpent whose bite causes mortification.

1. *Nerodia sipedon sipedon* (Linnaeus) Northern Water Snake

Coluber sipedon Linnaeus 1758:219. See species synonymy.

Coluber paecilogaster Wied 1839:106. See species synonymy.

Tropidonotus niger Holbrook 1842:37. See species synonymy.

Nerodia sipedon: Baird and Girard 1853:38.

Nerodia agassizii Baird and Girard 1853:41. See species synonymy.

Tropidonotus obliquus Hallowell 1857:249. See species synonymy.

Tropidontus sipedon sipedon: Yarrow 1882:134.

Natrix sipedon: Kirsch 1895:333.

Natrix sipedon sipedon: Stejneger and Barbour 1917:96.

• **DEFINITION.** Dorsal blotches on the body from neck to above the vent usually number 30 or more and are separated laterally by paler interspaces narrower than the bands (Gibbons and Dorcas 2004). Red or brown crescentric and other distinct ventral markings on belly extend past the 50th ventral scute. Considerable variation in coloration occurs over the range, with older specimens becoming melanistic. Ventrals range from 127–149 (mean 138) in males, 123–155 (mean 139) in females, with subcaudals ranging from 66–84 (mean 75) in males and 42–77 (mean 59.5) in females.

2. *Nerodia sipedon insularum* (Conant and Clay) Lake Erie Water Snake

Natrix sipedon insularum Conant and Clay 1937:1.

Type-locality, "Pelee Island, Lake Erie". Holotype, University of Michigan Museum Zoology (UMMZ) 80457, male, collected by Roger Conant, William M. Clay et al., 9 June 1935.

Nerodia sipedon insularum: Rossman and Eberle 1977:42.

• **DEFINITION.** This pale subspecies is confined to islands in the Ohio and Ontario, Canada, portions of Lake Erie. The dorsal pattern is reduced or completely lacking, and the dorsal ground color is usually green or brown with occasional pinkish or orange tinges. The dorsal pattern, when visible, is similar to that of the nominate subspecies. Ventrals range from 141–153 (mean 146.3) in males, and 137–152 (mean 145.9) in females, with subcaudals ranging from 70–81 (mean 75.6) in males and 58–68 (mean 63.3) in females.

3. *Nerodia sipedon pleuralis* (Cope) Midland Water Snake

Natrix fasciata pleuralis Cope 1892:672. Type-locality unknown (given as Summerville, Dorchester, South Carolina by Cochran [1961]). Neotype, National Museum of Natural History (USNM) 1080; designated by Clay (1938). See **Remarks**.

Natrix sipedon pleuralis: Clay 1938:178.

Nerodia sipedon pleuralis: Rossman and Eberle 1977:42.

• **DEFINITION.** The dorsal pattern is similar to that of *N. s. sipedon*, but the dark dorsal markings usually number 30 or fewer and are separated by paler interspaces that are wider than the bands (Gibbons and Dorcas 2004). The crescentic ventral spots often break up and disappear, and are not nearly as bright in hue as in *N. s. sipedon*.

• **REMARKS.** Cope (1892) described *Natrix s. pleuralis* (= *Nerodia sipedon pleuralis*) on the basis of three specimens in the National Museum of Natural History, USNM 1092 from "Mississippi" and USNM 8786 (2 specimens), from "Augusta, Georgia." Cope did not indicate which specimen he intended to be the holotype. Possibly because of that, Neill (1947) considered the type-locality of *Natrix sipedon pleuralis* to be unknown.

Clay (1938) noted that USNM 1092 is a specimen of *Nerodia fasciata* from Ft. Morgan, Baldwin County, Alabama, but also noted that in the same jar was a specimen (USNM 1080) of *Nerodia fasciata pleuralis* (= *Nerodia sipedon pleuralis*), which he designated as the neotype for *N. f. pleuralis*. The type-locality given in the USNM catalogue is "Summerville, South Carolina." Neill (1947) stated that *N. s. pleuralis* does not occur in the Summerville, South Carolina, area, and thought that it might be possible that the specimen had been collected in Summerville, North Carolina. Schmidt (1953) listed "Summerville, Harnett Co., North Carolina," as the type-locality. Morris (1991) re-examined these specimens and noted that the latter specimen bears two tags, one numbered

1080 and the other 1092. Ronald I. Crombie and Traci D. Hartsell (pers. comm.), collection managers at USNM, think that this specimen was wrongly tagged as 1092 initially and subsequently was retagged as 1080. Cope (1892) listed two specimens under USNM 8786, and stated that the larger specimen was *N. fasciata*. Later (Cope [1898] 1900), clearly stated that this specimen was *N. pleuralis*, although the specimen is no longer extant. The other specimen is *N. s. pleuralis*. Cope ([1898] 1900) repeated his original description of *Natrix fasciata pleuralis* with only minor changes, but he also listed 1092 and 8786 (as one specimen) under his account of *N. fasciata sipedon*. Morris (1991) follows Cope (1892) and recommended the type-locality be restricted to "Mississippi," a locality consistent with the known range of *N. s. pleuralis*. Morris' (1991) proposal would make USNM 1080 the neotype, and USNM 8786 a para-neotype.

4. *Nerodia sipedon williamengelsi* (Conant and Lazell) Carolina Water Snake

Coluber sipedon Linnaeus 1758:219. See species synonymy.

Nerodia sipedon: Baird and Girard 1853:38.

Natrix sipedon engelsi Barbour 1943:1. Type-locality, "Mullett Pond, Shackelford Banks, Carteret Co., North Carolina". Holotype, Museum of Comparative Zoology (MCZ) 46688, age and sex undetermined, collected by Dr. R.E. Coker, 29 July 1942 (not seen by authors).

Natrix sipedon williamengelsi Conant and Lazell:1973:3. Type-locality, "Island Creek on Ocracoke Island, Hyde Co., North Carolina". Holotype, Museum of Comparative Zoology (MCZ) 129298, young adult male, collected by Paul Elias, 14 June 1971.

• **DEFINITION.** This dark, coastal subspecies closely resembles *N. s. sipedon* in lepidosis but differs in having the dorsum of adults essentially black with the interspaces between the crossbands and blotches so dark that pattern details can be difficult to see. The venter posterior to midbody is predominantly black, and no red or brown-centered crescentic markings are present. Ventrals range from 129–143 (mean 137) in males, 133–143 (mean 138) in females, with caudals numbering 62–84 (mean 75) and 57–70 (mean 64), respectively.

• **ACKNOWLEDGMENTS.** We are indebted to Kraig Adler for supplying several references, and also to Whit Gibbons and Mike Dorcas for furnishing a pre-publication copy of their section on *Nerodia sipedon* for review from their book on North American water-snakes which has been used extensively in preparation of this manuscript. We are also indebted to Kent Bekker, Rufus Gaul, Jr., Mike Redmer, and Kristin Stanford for the privilege of using their photographs in this publication. We also wish to acknowledge Ned Gilmore, Academy of Natural Sciences of Philadel-

phia, and Tracy D. Hartsell, National Museum of Natural History, for providing data on type-specimens. Also we must mention Barbara Ball for printing off copies of the photographs and also designing the distributional map. Cherie Hauptman and the staff at Northern Illinois University Interlibrary Loan Service have been extremely helpful in locating obscure publications, which we truly appreciate.

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Primary co-editors for this account, Andrew H. Price and Josiah H. Townsend.

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