

Catalogue of American Amphibians and Reptiles.

SALTHE, STANLEY N. 1973. *Amphiuma tridactylum*.*Amphiuma tridactylum* Cuvier
Three-toed congo eel*Amphiuma tridactylum* Cuvier, 1827:7-8. Type locality New Orleans, Louisiana. Holotype, Mus. Nat. Hist. Natur. Paris, 7821 (mounted), collected by Teinturier in 1826 (Guibé, 1950:6). Not examined by the author.*Siren quadrupeda* Barton, 1808; Gray, 1850:55. Not seen.
Muraenopsis tridactyla: Fitzinger, 1843:34. New combination.
Muraenopsis tridactylus: Cope, 1875:25. Emendation.
Amphiuma tridactyla: Boulenger, 1882:82. Emendation.
Amphiuma means tridactylum: Goin, 1938:128. See Remarks.

- CONTENT. No subspecies have been proposed.

- DEFINITION. A bicolored species of *Amphiuma*, dark dorsally and light ventrally, with a sharp line of demarcation between the two shades. The dark patch on the throat is distinct against the light background. Three toes are present on most limbs. The ratio of forelimb length to body length is, according to Baker (1947), 37, while according to Hill (1954), this ratio is 35-37. The ratio of hindlimb length to body length is given as 25 by Baker (1947) and as ranging from 22 to 23 by Hill (1954). The tail base is slightly compressed, having an oval outline in section.

- DESCRIPTIONS. See the generic account of *Amphiuma* for references on general anatomy, much of which is identical or similar between the living species. Good general descriptions are given by Cuvier (1827), Bishop (1943), and Baker (1945). The limb and girdle skeletons are described by Rabl (1901), Hilton (1947), and Stoudemayer (1949). Limb regeneration was shown to be poor by Morgan (1903), with the digits coming back very irregularly or not at all. The male cloaca is described by Baker (1937), Weigart and Churchill (1938), and Wilson (1941a), while the female cloaca is described by Baker (1937), Wilson (1941b), and Kreeger (1942). Cagle (1948) gives a general description of the spermatophore, and also describes the ripe ovum as being 5-7 mm in diameter with little or no pigment (see also Kammeraad, 1941). The eggs are described by Hay (1888), Kammeraad (1941), and Salthe (1963), who also describes the egg capsules. Kammeraad (1941) notes that the eggs undergo meroblastic cleavage, but nothing else is known of the developmental stages up to near hatching. Hatchlings are described by Hay (1888: 45 mm), Ryder (1889:38-54 mm), Baker (1945:55-62 mm), and Cagle (1948:43-51 mm). Transformation (loss of external gills) occurs just after hatching (Baker, 1945). Hay (1890), Kingsley (1892), and Winslow (1898) describe the gills and chondrocranium of the hatchling.

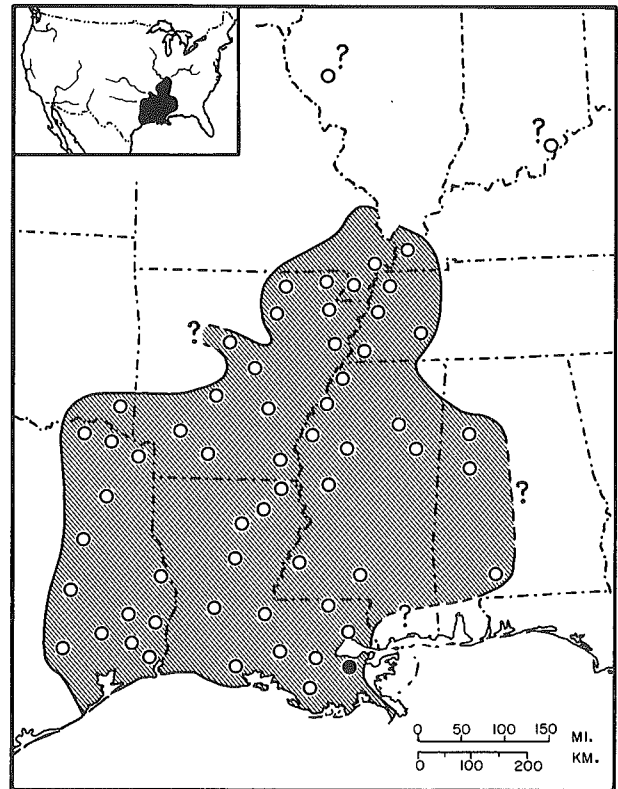
- ILLUSTRATIONS. An excellent painting of the adult is given by Holbrook (1842: plate 31); photographs of adults can be found in Baker (1937:208—both dorsal and ventral views), Bishop (1943:55), and Baker (1947:9—ventral view). Noble (1931:470) provides an ink drawing of the adult. Stoudemayer (1949:7) gives line drawings of the appendicular skeleton, while Rabl (1901: plate 23) gives drawings of the skeletons of both manus and pes. A photograph of a female on the nest site is shown by Baker (1945:62). The cloacas of breeding adults are shown by Baker (1937:209—drawing) and Cagle (1948:486—photograph). There is a drawing of the male cloaca dissected in Baker (1937:209) and of the female cloaca dissected in Kreeger (1942:241). The eggs are figured, in early stages by Cagle (1948:488—photograph) (see Comment), in later stages by Hay (1888:318; 1890: plate 1). The egg capsules are figured by Salthe (1963:163). Developmental stages have not been illustrated, but Hay (1890: plate 1) shows a larva just prior to hatching (see Comment). The chondrocranium and gill arches of the hatchling are figured by Hay (1890: plate 1) and also by Winslow (1898: figs. 17, 18, 19).

- DISTRIBUTION. The range extends along the Gulf Coastal Plain from the Brazos River valley in Texas through the Mississippi alluvial valley to where this meets the eastern Gulf Coastal Plain, with records extending eastward into the western half of Alabama, and continues north up the Mis-

issippi valley as far as the western tip of Kentucky and the southeastern corner of Missouri, up the Arkansas River valley an unknown distance beyond Little Rock, Arkansas, and up the Red River valley as far as the southeastern corner of Oklahoma. Two unconfirmed and probably spurious records some 200 miles north of the northernmost genuine locality would extend the range up the Illinois River valley to Scott County, Illinois (Weed, 1923), and in the opposite direction up the Ohio River valley to Clark County, Indiana (Bishop, 1943). Like *A. means*, this is a lowland species, extending its range into hilly regions only along valleys and streams. Common habitats include wooded alluvial swamp lands, calcareous streams, marshes and lakes in floodlands, the seepy pools and swampy banks of bayous, and cypress sloughs. Baker (1947) suggests that this species is specifically adapted to dense clayey soils of alluvial or loess origin, most of which are high in lime content. Extensive and intricate networks of crayfish burrows are an important feature of most habitats, the animals being intolerant of sunlight (Darnell, 1948), and unable themselves to burrow into the dense soils.

- FOSSIL RECORD. None reported, but see this heading under *A. means*.

- PERTINENT LITERATURE. See generic account of *Amphiuma* for references on cytology, cell physiology, and physiology. Mating occurs in Louisiana from December to May, with a peak in late February and early March (Wilson, 1940, 1941a; Cagle, 1948; Rose, 1967), some years being shifted to the early part of this range, some to the later part. In Tennessee mating occurs from December to June (Sturdivant, 1949). Courtship has been sketchily described by Baker (1937), Baker et al (1947), and Cagle (1948), and it is evident that this behavior differs from that found in any other salamander (Salthe, 1967). Females evidently have a biennial reproductive cycle (Wilson, 1941c, 1942; Cagle, 1948), although Rose (1967) reports vitellogenesis as taking place over seven months beginning in October. Egg laying in Louisiana can take place any time from April through early September (Wilson, 1940; Cagle, 1948; Rose, 1967) depending upon the year. In Tennessee nests have been found from August through mid-winter (Parker, 1937). Eggs ready to hatch were found



MAP. Solid symbol indicates type-locality, open symbols mark other localities including questionable ones in Illinois and Indiana. Shaded area estimates total range.

in Arkansas in August (Hay, 1888) and in November in Louisiana (Baker, 1945), while young with vestiges of external gills have been taken in Louisiana in November by Cagle (1948). Liner (1954) found young in Alabama that must have hatched at about that same time (November). The data given by Cagle (1948) suggest about a 5 month incubation period. Cagle (1948) found the number of ripe follicles in gravid females to vary about a mean of 98, while Rose (1966), in a more detailed study, found the mean to be 200. Assuming the ovum diameter to be about 5 mm (estimated from Cagle, 1948), a mean clutch size of 200 better fits *A. tridactylum* into the body volume—clutch volume relationship discovered for salamanders by Salthe (1969) than does a mean of 98. The female remains coiled about the eggs during incubation (Hay, 1888; Baker, 1945). A nest site was found under a log in a nearly dried-up cypress swamp (Hay, 1888), another about 12 feet from the shore of a bayou under a log in dry soil, others under logs closer to the water's edge (Parker, 1937). It was suggested by Cagle (1948) that, in the absence of submerged debris under which to lay eggs, the female may deposit them in burrows above the water level. Despite the fact that all records of *Amphiuma* nests have been out of water, Baker (1945) maintained that the usual site of deposition was under water, and that the nests that have been found were exposed during droughts (see Comment). Young animals have been found schooling (Parker, 1939; Baker, 1945). Rose (1968) found that maxillary tooth number increased with size. The snake *Farancia abacura* is a major predator of this species (Viosca, 1923; Meade, 1934; Parker, 1947; Curd, 1950; Tinkle, 1959), and Curd (1950) suggested that the two species have coextensive ranges. *Agristrodon* has been found to prey on this species in Alabama (Liner, 1954). Intense snake predation probably explains the violent behavior toward a dead snake by one of these animals reported by Schufeldt (1883). Except for habitat data (see Distribution), little further is known about the ecology of this species, the major paper being that of Cagle (1948), who gives data on growth and age distribution. The diploid chromosome number is given as 28 by Donnelly and Sparrow (1963).

• REMARKS. Cuvier (1827) erected this species on the basis of digit number alone. Tschudi (1838), Ryder (1880), Cope (1886, 1889), and Van Pée (1903, 1904) all found specimens with too few or too many digits on some of the limbs or noted that the number of carpals or tarsals was extremely variable and, concluding that taxa could not be separated on the basis of such a variable trait, placed one or another taxon into synonymy. Brimley (1909) revived the two-species (*tridactylum* and *means*) concept by finding a difference in coloration (see diagnoses). In 1938, Goin recommended trinomial (placing *tridactylum* with the species *means*) on the grounds that 1) certain characters (number of costal grooves, ratio of total length to body length) showed clinal variation along the Gulf Coastal Plain where the two groups of populations meet, and 2) the presence of 6 out of 84 specimens that appeared to be intergrades (especially in digit number) in the Gulf coastal states. Baker (1947) demonstrated that many of these intergrades were spurious, noting that it would be more important to find individuals with 3 toes on some limbs in the range of *A. means* than 2-toed individuals in the range of *A. tridactylum*, which could more likely represent developmental abnormalities. He also found that ratios of total length to body length, total length to forelimb length, and total length to hindlimb length effectively separated the three-toed and two-toed groups, although there was overlap in the distributions in each case. He opted strongly for reviving the two-species arrangement. Hill (1954), noting that Baker did not take into account ontogenetic changes, conducted a statistically adequate inquiry and came to essentially the same conclusion as Baker on the limb length—body length ratios. She noted, however, that digit number and coloration remain the best indicators of specific status for any given individual, and regarded only 3 out of 131 individuals from the Gulf coastal region as intergrades. She too concluded that there are two species (*A. pholeter* had not yet been described), with occasional hybrids being produced in the area of sympatry. At present the weight of evidence favors this view.

• ETYMOLOGY. The specific epithet comes from the Greek *tri*, thrice, and *dactylos*, finger, referring to the number of digits characteristic on both sets of limbs in members of this species.

From the photograph on page 488 in Cagle (1948), it is clear that in the egg of *Amphiuma* a capsular chamber forms prior to the beginning of development. This is a primitive trait (Salthe, 1963) and is different from the derived condition in the plethodontids.

The external gills of the encapsulated larva (Hay, 1888, 1890) can be used as indicators of the normal site of development, made controversial by Baker (1945) (see Pertinent Literature). The three gill rami (not fused as in the plethodontids, and so primitive in regard to the condition in the latter) are long and have relatively few fimbriae, a condition (of relatively small surface area) found elsewhere only in larvae developing in terrestrial situations (Salthe and Mecham, in press). Therefore, the nests that have been located so far may be taken as probably typical for the genus.

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