

## Catalogue of American Amphibians and Reptiles.

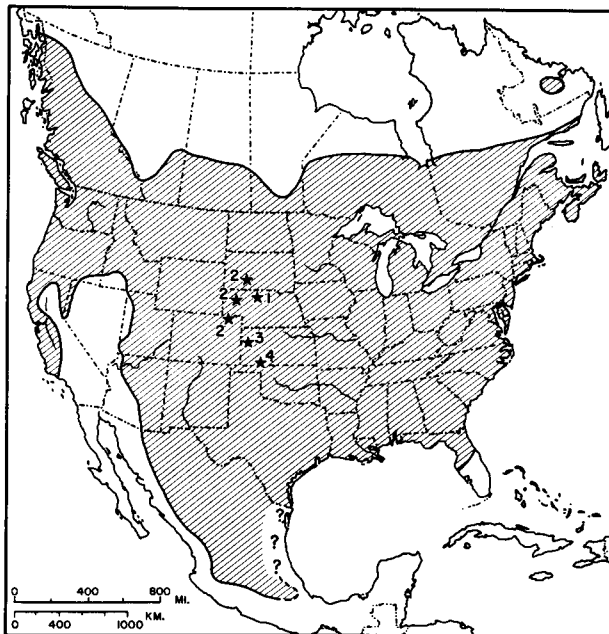
TIHEN, JOSEPH A. 1969. *Ambystoma*.*Ambystoma*

## Mole salamanders

- Axolotus* Jarocki, 1822:179. Type-species *Siren pisciformis* Shaw, 1802 (= *Gyrinus mexicanus* Shaw, 1789), by subsequent designation (Smith and Tihen, 1961b). See Nomenclatural History.
- Phyllhydrus* Brookes, 1828:16. Type-species *Siren pisciformis* Shaw, 1802 (= *Gyrinus mexicanus* Shaw, 1789), by monotypy. See Nomenclatural History.
- Siredon* Wagler, 1830:209, 210. Type-species *Siredon axolotl* Wagler, 1830 (= *Gyrinus mexicanus* Shaw, 1789), by monotypy. See Nomenclatural History.
- Phyllhydrus* Gray, 1831:108. Type-species *Siren pisciformis* Shaw, 1802 (= *Gyrinus mexicanus* Shaw, 1789), by monotypy (although Gray suggested other species as possibly referable to this genus). See Nomenclatural History.
- Axolot* Bonaparte, 1831:77. Type-species *Siren pisciformis* Shaw, 1802 (= *Gyrinus mexicanus* Shaw, 1789), by implication and by explicit subsequent designation of Smith and Tihen (1961a). See Nomenclatural History.
- Sirenodon* Wiegmann, 1832:204. Type-species *Siredon axolotl* Wagler, 1830 (= *Gyrinus mexicanus* Shaw, 1789), by monotypy. See Nomenclatural History.
- Stegoporus* Wiegmann, 1832:204. A substitute name for *Siredon* Wagler, 1830, hence with the same type species, *Siredon axolotl* Wagler, 1830. The species actually listed under this name is *Siren pisciformis* Shaw, 1802; in any event, both names are junior synonyms of *Gyrinus mexicanus* Shaw, 1789. See Nomenclatural History.
- Ambystoma* Tschudi, 1838:92. Type-species *Lacerta subviolacea* Barton, 1804 (= *Lacerta maculata* Shaw, 1802), by original designation. See Nomenclatural History.
- Xiphonura* Tschudi, 1838:95. Type-species *Salamandra jeffersoniana* Green, 1827, by monotypy. This name became a junior synonym of *Ambystoma* by the action of Baird (1850:283), the first reviser within the meaning of Article 24 of the International Code.
- Phyllhydrus*: Swainson, 1839:94. Contrary to the statement of Smith and Tihen (1961a), this is an incorrect subsequent spelling of *Phyllhydrus* Brookes, 1828, not an emendation of *Phyllhydrus* Gray, 1831. It thus has no status in nomenclature.
- Salamandroidis* Fitzinger, 1843:33. Type-species *Lacerta subviolacea* Barton, 1804 (= *Lacerta maculata* Shaw, 1802), by original designation and monotypy.
- Axolotes* Owen, 1844:23. Type-species *Axolotes guttata* Owen, 1844 (= *Gyrinus mexicanus* Shaw, 1789), by implication and by stated (but erroneous) belief that the name had been used generically by Cuvier and others to refer to *Gyrinus mexicanus* Shaw.
- Ambystoma* Agassiz, 1844:2. An unjustified emendation *pro* *Ambystoma* Tschudi, 1838, hence with the same type species. See Nomenclatural History.
- Phyllidrus* Agassiz, 1845:6. An unjustified emendation *pro* *Phyllhydrus* Gray, 1831, hence with the same type species.
- Axolotus* Gray, 1850:49. Type-species *Axolotus mexicanus* (= *Gyrinus mexicanus* Shaw, 1789), by monotypy. Gray erroneously attributes this name and combination to Cuvier in Bibron, but Gray's use is actually the first. This is a junior homonym of *Axolotus* Jarocki, 1822, a usage of which Gray was apparently unaware.
- Heterotriton* Gray, 1850:33. Type-species *Salamandra ingens* Green, 1831 (= *Salamandra tigrina* Green, 1825), by monotypy.
- Plagiodon* Duméril, Bibron and Duméril, 1854:101. Substitute name for *Ambystoma* Tschudi, 1838, hence with the same type species.
- Desmiostoma* Sager, 1858:428. Type-species *Desmiostoma maculatus* Sager, 1858, by monotypy. The name is not precisely allocable (see Dunn, 1940), but is almost certainly based on some race of *Ambystoma tigrinum*.
- Camarataxis* Cope, 1859:122. Type-species *Ambystoma maculatum* Hallowell, 1857 (? = *Ambystoma nebulosum* Hallowell, 1853; see Gehlbach, 1966), by original designation and monotypy.
- Acholotes*: Cope, 1867:184. An incorrect subsequent spelling of *Axolotes* Owen, 1844; without nomenclatural status.
- Pectoglossa* Mivart, 1867:698. Type-species *Plethodon persimilis* Gray, 1859 (= *Salamandra jeffersoniana* Green, 1827), by monotypy.
- Salamandroides*: Boulenger, 1882:38. An incorrect subsequent spelling of *Salamandroidis* Fitzinger, 1843; without nomenclatural status.
- Linguaelapsus* Cope, 1887:88. Type-species *Amblystoma annulatum* Cope, 1886, by subsequent designation (Dunn and Dunn, 1940).
- Plioambystoma* Adams and Martin, 1929:17. Type-species *Plioambystoma kansense* Adams and Martin, 1929, by monotypy.
- Bathysiredon* Dunn, 1939:1. Type-species *Siredon dumerilii* Dugès, 1870, by original designation.
- Lanebatrachus* Taylor, 1941:180. Type-species *Lanebatrachus martini* Taylor, 1941 (= *Plioambystoma kansense* Adams and Martin, 1929), by original designation.
- Ogallalabatrachus* Taylor, 1941:181. Type-species *Ogallalabatrachus horarium* Taylor, 1941 (= *Plioambystoma kansense* Adams and Martin, 1929), by original designation.

• CONTENT. Twenty-nine species are currently recognized, of which three are known only as fossils. Of the 26 extant species, 14 occur in the United States; six of these 14 also are found in Canada, and one in Mexico. An additional 12 species are limited to Mexico; the proper status of many of the Mexican forms is not fully established. Tihen (1958) recognized three subgenera: *Bathysiredon*, with one species *dumerilii*; *Linguaelapsus*, comprised of the species *annulatum*, *cingulatum*, *mabeei*, *schmidti* and *texanum*; and *Ambystoma*, to which all remaining species were referred. Freytag (1959) believed that *Linguaelapsus* should be accorded full generic status. Tihen (*op. cit.*) suggested the subdivision of the subgenus *Ambystoma* into four indistinctly delimited species groups, but neither the validity nor the appropriate content of these groups is clearly established.

• DEFINITION. Ambystomatidae in which the costal grooves are conspicuous; the eyes are small (horizontal dimension less than distance from anterior corner of the eye to tip of snout); an ypsiloid cartilage and lungs are present and well developed;



MAP. The numerals indicate Tertiary fossil localities. 1—*A. minshalli*, Miocene-Pliocene transition. 2—*A. cf. minshalli*, Middle and Upper Miocene. 3—*A. kansense*, (? Lower to) Middle Pliocene. 4—*A. hibbardi*, Upper Pliocene. For Pleistocene records, see species accounts for *A. maculatum*, *A. texanum*, and *A. tigrinum*.

there is no independent lacrimal bone. In addition, the vomerine teeth of adults are arranged essentially transversely, not parallel to the maxillary tooth row; in mature metamorphosed individuals the dorsal premaxillary fontanelle is nearly or completely obliterated and the maxillae are not reduced. The hyobranchium usually remains mostly cartilaginous throughout life; the second basibranchial is ossified in advanced larvae or adults, but the first basibranchial and parts of the epi-branchials and first ceratobranchial only occasionally ossify. Larvae are of the pond type, with well developed gill slits (4), gill rakers and gills (3); the dorsal fin extends anteriorly at least to midbody, usually to the level of the gill insertions. The three subgenera may be distinguished as follows:

*Ambystoma*: Size and proportions vary, but many species have stout bodies with strong limbs, and a relatively large, broad skull. The plicae of the tongue are longitudinal, nearly parallel, or radiating from a poorly defined area in the posterior part of the tongue; there is no prominent median furrow. The teeth are in a single row on each dentigerous element in adults; the ascending processes of the premaxillae are not exceptionally long and narrow, and do not bear vertical laminae or thickenings on their ventral surfaces. Some species are customarily neotenic, others occasionally so, and in yet others neoteny is unknown. Larval characteristics vary, but the gill filaments are largely restricted to the inner surfaces of the gill rami, and the head is not depressed.

*Linguaelapsus*: The body is slender and relatively elongate with short limbs and a relatively small, narrow skull. The tongue bears a median furrow, from which the plicae branch. The teeth are in multiple rows on some or all dentigerous elements (additional rows incomplete or lacking in *mabeei*). The ascending processes of the premaxillae are very long and narrow, with a ventral thickening or vertical lamina. Neoteny is unknown. The larvae are generally similar to those of the subgenus *Ambystoma*.

*Bathysiredon*: A consistently neotenic form; the larvae are distinctive in having the head somewhat depressed, particularly anteriorly, and in having long gill rami bearing rather long slender filaments, profusely distributed over both the inner and outer surfaces, giving the gills a "bushy" appearance. Other characters mentioned by Dunn (1939), and Tihen (1958), will serve in combination to distinguish this form from larvae of other subgenera, but considerable overlap occurs in each individual feature.

• DESCRIPTIONS AND ILLUSTRATIONS. The genus includes the largest known terrestrial salamanders; Smith and Reese (1968) mention an individual *A. tigrinum* of 346 mm total length. The largest individuals probably result from the metamorphosis of neotenic larvae; individuals metamorphosing prior to sexual maturity rarely exceed 250 mm total length. Most species are stout-bodied, with a large, broad head and blunt snout. Coloration varies; orange occasionally occurs, but no red markings are found in the genus. The conspicuous costal grooves rarely exceed 15 in number, and are usually fewer. *A. opacum* lays its eggs on land in situations that later become flooded or submerged. All other species breed in lakes, ponds, or the deeper, quiet pools of streams. Larvae are of the "pond" type; balancers are usually, but not universally, present in young larvae.

There has been no comprehensive description of the genus since that of Cope (1889) who recognized three genera within the assemblage of species currently included in *Ambystoma*. Brief descriptive comments may be found in various handbooks or manuals, e.g., Stebbins (1951) or Conant (1958). Others (e.g., Bishop, 1943) contain descriptions of many individual species, but do not collate them into a generic description. Tihen (1958) and Freytag (1959) discussed certain osteological features, with brief comments on other characteristics. Valentine and Dennis (1964) briefly described certain larval characteristics. Salthe (1963) described the eggs and the same author (1967) summarized information on courtship patterns. For references to descriptions, illustrations and life histories of individual species see species accounts in this catalogue.

• DISTRIBUTION. From Labrador, James Bay, and extreme southeastern Alaska, southward throughout southern Canada, most of the United States, and the Sierra Madre Occidental and central plateau of Mexico. Apparently lacking in most of the Florida peninsula; also absent from Nevada, southern California, southwestern Arizona, Baja California, and the tropical lowlands of Mexico.

• FOSSIL RECORD. Three species are known only as fossils. The earliest record of the genus is that of *A. minshalli* (Tihen and Chantell, 1963) from beds of Upper Miocene or lowermost Pliocene age in north central Nebraska (1 on map). However, individual skeletal elements recovered from scattered deposits (2 on map) of Middle Miocene age in western Nebraska, northeastern Colorado and southern South Dakota are probably *A. minshalli*. *Ambystoma kansense* (Adams and Martin, 1929) occurs in the Middle Pliocene of northwestern Kansas (3 on map), and *A. hibbardi* (Tihen, 1955) in the Upper Pliocene of southwestern Kansas (4 on map). Elements recovered from a number of Upper Pliocene localities in the Central Plains are inadequate for specific identification, but may be referable to *A. hibbardi*. Of the extant species, *A. maculatum*, *texanum*, and *tigrinum* have been recorded from the Pleistocene, the last quite extensively. For details, refer to the species accounts.

• PERTINENT LITERATURE. An extensive literature exists on all aspects of the biology of members of this genus, but little is pertinent at the generic level other than that cited elsewhere in this account. The reader should refer to the individual species accounts.

• NOMENCLATURE HISTORY. At least seven generic names were based on species now referred to *Ambystoma* prior to the proposal of the name *Ambystoma* itself. These are: 1) *Axolotus* Jarocki, 1822; 2) *Philhydrus* Brookes, 1828; 3) *Siredon* Wagler, 1830; 4) *Phyllhydrus* Gray, 1831 (This name may have been an emendation, or an incorrect subsequent spelling, of *Philhydrus* Brookes, 1828; but since no mention is made of Brookes' genus, it should not be so considered.) 5) *Axolot* Bonaparte, 1831; 6) *Sirenodon* Wiegmann, 1832; and 7) *Stegoporus* Wiegmann, 1832. In Opinion 649, the International Commission on Zoological Nomenclature (1963) ruled that these seven names be suppressed and placed on the Official Index of Rejected and Invalid Generic Names in Zoology. Their numbers in the Index are 1591-1597, in the sequence listed above. The name "*Amblystoma* Agassiz, 1846" (but see below) was also placed on this Index as Name No. 1598. And, in the same Opinion, *Ambystoma* Tschudi, 1838, was placed on the Official List of Generic Names in Zoology, with the Name No. 1509.

The emendation *Amblystoma* Agassiz, widely used for a time, has customarily been cited as appearing in 1846 (see above). Agassiz's *Nomenclator zoologicus* . . . was completed in 1846, and this date appears on most copies. There is, however, ample evidence that the individual fascicles were published prior to the completion of the entire work, and that Fasciculus VI, in which this name appears, was actually published in 1844.

• ETYMOLOGY. There is a widespread belief that the name *Ambystoma* was a *lapsus calami* for *Amblystoma* (Greek *amblys*, blunt, and *stoma*, mouth). This was the basis for Agassiz's 1844 emendation, accepted by many later workers. However, Stejneger (1907:24), in an almost universally overlooked passage, disagreed with this interpretation. He stated: "This emendation is utterly unwarranted for not only does Tschudi use the word *Ambystoma* four times, but it is plainly a legitimate contraction for *Anabystoma*, with allusion to the phrase [*ana stoma bucin*], to cram into the mouth."

• KEY TO SPECIES (Mature Metamorphosed Individuals). Our knowledge of larval characteristics and variation is insufficient to allow their inclusion in a key. Therefore no key to the larval stages is attempted, and the species *A. dumerilii*, never known to metamorphose, is perforce omitted from this key. Several other Mexican forms metamorphose only infrequently. The key will not always serve for the identification of newly metamorphosed individuals, nor can we be certain of the extent of variation in the various features used as key characters for several of the Mexican species. The alternatives presented in couplet No. 13 will rather consistently distinguish the two diploid members of the *A. jeffersonianum* complex, but variation of the triploid members with respect to these features may overlap appreciably (see Uzzell, 1964, and species accounts).

A parenthetic numeral following the name of a species is the number of the account for that species in this Catalogue. Species that rarely metamorphose in nature are indicated by an asterisk.

1. Tongue with a median furrow, from which the plicae diverge ..... (subgenus *Linguaelapsus*) 2
- No median furrow on tongue; plicae longitudinal,

- nearly parallel or radiating slightly from posterior portion of tongue ..... (subgenus *Ambystoma*) 6
2. Multiple rows of maxillary teeth ..... 3  
—Single row of maxillary teeth or at most indistinct and incomplete suggestions of an additional row - *mabeei*
3. Dark brown to black with conspicuous, narrow, yellow, buff or whitish cross bands (some of which may be incomplete or interrupted) ..... *annulatum* (19) 4  
—No conspicuous cross bands in pattern
4. Ground color chocolate to black; grayish light markings forming a "frosted" or reticulated pattern, or series of light rings, over most of back and sides ..... *cingulatum* (57) 5  
—Light markings lacking, or in the form of small spots, flecks, or lichen-like blotches
5. Small, total length about 90 mm; small, scattered, cream-colored spots on sides of head, body and tail; venter yellowish ..... *schmidti* 5  
—Variable in size and color, but usually over 90 mm total length; light markings in form of flecks or lichen-like gray blotches, but not spotted; venter usually not yellowish ..... *texanum* (37)
6. Dorsum boldly marked with contrasting black and light gray or white; light markings basically cross bands, but may coalesce to enclose dark spots ..... *opacum* (46) 7  
—Dorsum not so marked
7. Integumentary glands in region back of eye very numerous and concentrated to form a parotoid gland; a prominent glandular ridge along top of tail, at least in proximal one-half or one-third ..... 8  
—No parotoid gland or prominent glandular ridge along top of tail
8. Palmar tubercles lacking; parotoid gland prominent; glandular ridge along most of length of tail ..... *gracile* (6) 9  
—Two palmar tubercles; parotoid gland less prominent; glandular ridge tends to be limited to proximal portion of tail ..... *rosaceum*
9. A broad, conspicuous, yellowish to tan or orange middorsal stripe on body, extending onto tail ..... *macroductylum* (4) 10  
—No conspicuous broad middorsal stripe
10. One or no palmar tubercles; adpressed limbs often overlap by less than two costal folds ..... 11  
—Two palmar tubercles; adpressed limbs usually overlap by at least two costal folds ..... 16
11. Pattern of moderately large yellowish to orange spots, arranged in an irregular dorsolateral row on each side ..... *maculatum* (51) 12  
—Pattern without yellow or orange spots; often with grayish or bluish to white flecks or lichen-like blotches along sides
12. Costal grooves 10 or 11; relatively short (usually under 100 mm, maximum 125 mm, total length) and very stout-bodied; head broad (width more than 22% of snout-vent length) ..... *talpoideum* (8) 13  
—Costal grooves usually more than 11; body and head relatively slender (head width 14-18% of snout-vent length); usually over 100 mm total length
13. Snout-vent length usually less than 69 mm in mature males, 75 mm in mature females; internarial distance usually less than .062 of snout-vent length in males, less than .059 of snout-vent length in females; adpressed limbs of males overlap by 1½ costal folds or less; black to gray, often with light flecks, venter only slightly lighter than dorsum ..... 14  
—Snout-vent length usually 69 mm or more in mature males, 75 mm or more in mature females; internarial distance .062 or more of snout-vent length in males, .059 or more in females; adpressed limbs of males usually overlap by more than 1½ costal folds; brownish-gray, sometimes with light flecks, venter decidedly lighter than dorsum
14. Diploid; bisexual; erythrocyte area less than 850  $\mu^2$  ..... *laterale* (48) 15  
—Tripliod; males unknown; erythrocyte area greater than 850  $\mu^2$  ..... *tremblayi* (50)
15. Diploid; bisexual; erythrocyte area less than 890  $\mu^2$  ..... *jeffersonianum* (47) 16  
—Tripliod; males extremely rare; erythrocyte area more than 890  $\mu^2$  ..... *platineum* (49)
16. Color pattern consisting of a dark background with prominent (though not necessarily large) light (yellowish, olive, orange or cream-colored) spots or blotches on back or sides, or both (spots may coalesce to form a prominent ventrolateral light line on each side) ..... 17  
—Dorsum nearly uniform in color, or with scattered dark markings on lighter background ..... 21
17. Light markings confined to lower portion of sides, i.e., lateral or ventrolateral, or both ..... 18  
—Light markings not confined to sides; some or all are dorsal or dorsolateral in position ..... 19
18. Light spots moderately large, confined to a ventrolateral row on each side; individual spots may tend to coalesce to form a ventrolateral light line ..... *amblycephalum* 19  
—Light markings consist of flecks, dots, or small spots, irregularly distributed on sides ..... *mexicanum*\*
19. Body and limbs slate black, with numerous small bright yellow spots scattered over dorsal surface of head, body, tail and limbs; venter with broad black stripe enclosing two longitudinal, broken yellow lines ..... *flavipiperatum* 20  
—Color pattern variable, but not as above
20. Pattern of irregular blotches, or of fairly numerous yellowish to olive spots irregularly distributed on body and tail ..... *tigrinum* (part) (52) 21  
—Four or five pairs of large buff or cream-colored spots on body, tending to be arranged into a dorsolateral row; a similar number of spots on tail ..... *subsalsum*\*
21. Uniformly dark above, or dark with scattered light flecks that tend to disappear in preservative ..... 22  
—Not uniformly dark above; often with blackish markings on a lighter background ..... 25
22. Fewer than 50 premaxillary-maxillary teeth on each side; black or grayish black above; venter nearly uniform dull creamy gray ..... *ordinarium* 23  
—More than 50 premaxillary-maxillary teeth on each side; color variable ..... 23
23. Grayish-brown to lavender brown above; skin appears exceptionally smooth and shining; a diastema between palatine and vomerine teeth ..... *bombypellum* 24  
—Dark gray to blackish above; skin not exceptionally smooth and shining; usually no diastema between palatine and vomerine teeth
24. Venter mottled or blotched; usually at least 24 teeth on each side in vomeropalatine series ..... *tigrinum* (part) (52) 25  
—Venter dark and relatively uniform; fewer than 24 teeth on each side in vomeropalatine series ..... *lermaensis*\*
25. Dorsal caudal fin high; fewer than 24 teeth on each side in vomeropalatine series; yellowish olive to olive, with scattered dark spots that may become obsolete on body, but remain distinct on tail ..... *granulosum* 26  
—Caudal fin represented only by a low ridge; usually at least 24 teeth on each side in vomeropalatine series; color and pattern variable
26. Dull olive above, with a few scattered dark spots or flecks on head and back; lighter (yellow-cream) color of venter extends halfway up sides ..... *lacustris*\* 26  
—Pattern variable, but light color of venter not extending halfway up sides ..... *tigrinum* (part) (52)

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