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CONCERNING THE REPRODUCTIVE HABITS OF TROPICAL PLETHODONTID SALAMANDERS

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ABSTRACT: Eggs of *Pseudoeurycea nigromaculata* (Taylor) from Cerro Chicahuaxtla, Veracruz, and eggs and embryos of *P. juarezi* Regal from Cerro Pelón, Oaxaca, México, are described for the first time. They exhibit many similarities to the eggs of *P. exspectata*, *Hydromantes*, and *Batrachoseps* in number of envelopes and in bead-like type of connection. The eggs of *P. bellii*, *Parvimolge townsendi*, and several species of *Bolitoglossa* are adherent rather than stranded. It is postulated that in some species of tropical plethodontid salamanders egg deposition is timed so that hatching occurs during the wet season, a more favorable time for the young.

ALTHOUGH some information concerning the reproductive biology of temperate representatives of the family Plethodontidae is available, little is known about the reproductive habits of tropical forms. Some authors (Peters, 1863; Posada Arango, 1909; Ruthven, 1922) have reported viviparity and ovoviviparity as the reproductive modes for the Colombian species *Bolitoglossa adspersa* and *B. savagei*, but Brame and Wake (1963) concluded that evidence was insufficient to support these statements. Subsequently Valdivieso and Tamsitt (1965) confirmed Nicéforo María's report (1958) of oviparity in *Bolitoglossa adspersa*. Oviparity probably is characteristic of all tropical species. However, the eggs of only 7 of about 130 tropical plethodontids have been described.

In January, 1969, we discovered egg clutches of two Mexican species of *Pseudoeurycea*. Because of the paucity of information concerning the reproductive habits of tropical plethodontids, descriptions of these eggs and comparisons with eggs of other forms are presented.

DESCRIPTIONS OF EGGS

Pseudoeurycea nigromaculata (Taylor).—Two egg clutches of this salamander were discovered on the top of Cerro Chicahuaxtla (elevation about 1600 m) near Cuautlapan, Veracruz, on 15 January 1969. All measurements were taken after the eggs were preserved in 10% neutral formalin (buffered with magnesium carbonate).

The first clutch, 25 eggs, was found on the northwest slope of the Cerro near the summit. This area is densely forested and quite wet. The eggs were buried about 6 cm below the surface in leaf litter. A female, measuring 52 mm in snout to posterior edge of vent (98 mm total), was with the eggs. The site was disturbed before the eggs

were noticed, and some eggs may have been overlooked. The eggs apparently were non-adherent, but joined in bead-like fashion by gelatinous connecting strands. We could not determine if all eggs were initially connected to each other. In life the vitellus (ovum) is white to cream without pigment. The eggs are in early stages of development (2, 4, and 8 cell stages). Two eggs are uncleaved. All eggs connected in strands are at the same developmental stage, except for one uncleaved egg, which may have been infertile.

The elliptical vitelli are surrounded by two gelatinous layers or envelopes (Fig. 1A). The long diameters of the vitelli lie between the gelatinous connecting strands and range from 3.3 to 3.6 mm ($\bar{x} = 3.41$, $N = 25$). The short diameters measure 3.0 to 3.3 mm ($\bar{x} = 3.19$). A vitelline membrane is evident in all except the two eggs that are uncleaved. The perivitelline space is extremely narrow. The perivitelline space ranges from 3.4 to 3.7 mm ($\bar{x} = 3.53$) in the long diameter and from 3.1 to 3.3 mm ($\bar{x} = 3.21$) in the short diameter. A thick gelatinous inner envelope surrounds the vitelline membrane. The long diameter of this envelope is 4.6 to 5.1 mm ($\bar{x} = 4.85$), and the short diameter is 4.0 to 4.25 mm ($\bar{x} = 4.10$). From the vitelline membrane to the outer envelope, the width of the inner envelope averages 0.66 mm on the long axis and 0.44 mm on the short axis. The inner envelope is divisible into two parts: an inner semi-opaque zone adjacent to the vitelline membrane and an outer, more transparent zone (Fig. 1B). The semi-opaque zone is about half the width of the transparent zone and may represent the capsular cavity containing gelatinous material, which would have become more fluid, or containing a capsular fluid which gelled when the eggs were preserved. The transparent zone appears to be composed entirely of fibers. External to the inner envelope is a thinner, transparent outer envelope. The outer envelope appears to be bounded externally by a thin membrane. The average width of the outer envelope is 0.08 mm. The maximum short diameters of the eggs measure from 4.1 to 4.4 mm ($\bar{x} = 4.27$). Because of the position of the connecting strands, the maximum long diameters were not measured.

The gelatinous strands are flexible and elastic. The strands connecting 13 eggs are 3.0 to 11.0 mm long ($\bar{x} = 7.28$), 0.2 to 0.4 mm in diameter and are composed of two layers. A fibrillar transparent central core is continuous with the transparent zone of the inner egg envelope, and the outer layer of the connecting strand is continuous with the outer egg envelope (Fig. 1A).

The second clutch of eggs was found on the southwest part of the summit in a moist, dense forest. The eggs lay exposed at the base of a leaf. No salamanders were found nearby. The 19 eggs in this clutch are similar to the eggs in the first clutch, but average slightly larger

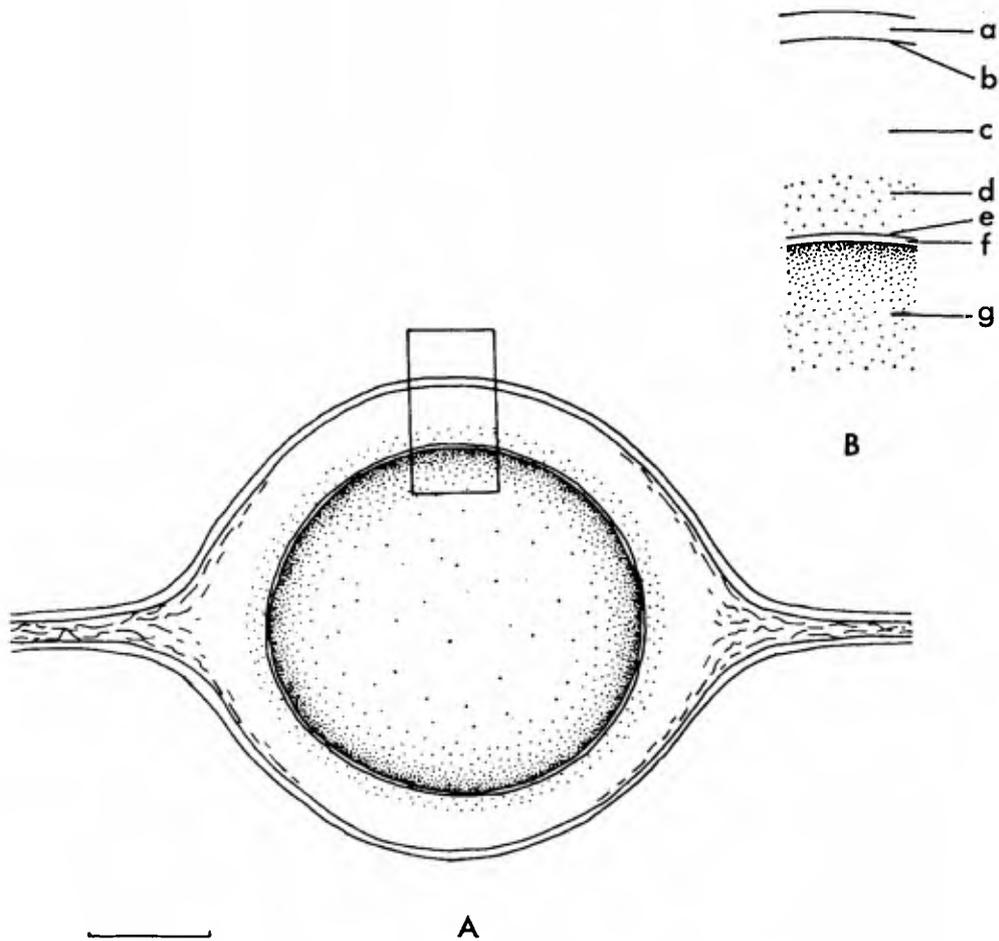


FIG. 1.—A. Egg of *Pseudoeurycea nigromaculata* showing gelatinous envelopes and connecting strands. Line equals 1 mm. B. Section of the egg showing: (a) outer envelope; (b) membrane separating inner and outer envelopes; (c) fibrillar, transparent zone of inner envelope; (d) semi-opaque zone of inner envelope; (e) vitelline membrane; (f) perivitelline space; (g) vitellus.

in most dimensions. The vitelli appear dented and puffy on the cleavage surface, and they were not measured. Cleavage patterns are difficult to discern and probably were abnormal, perhaps due to the exposure of the eggs. The 19 eggs measure as follows: long diameter of perivitelline chamber, 3.45 to 4.1 mm ($\bar{x} = 3.75$); short diameter of perivitelline chamber, 3.2 to 3.7 mm ($\bar{x} = 3.41$); long diameter of the inner gelatinous envelope, 4.9 to 5.8 mm ($\bar{x} = 5.31$); short diameter of the inner gelatinous envelope, 4.3 to 4.7 mm ($\bar{x} = 4.53$); maximum short diameter of the egg, 4.55 to 5.1 mm ($\bar{x} = 4.77$). Twelve intact gelatinous connecting strands measure 6.5 to 11.0 mm ($\bar{x} = 9.08$) in length.

Pseudoeurycea juarezi Regal.—A clutch of 20 eggs together with an attending female *P. juarezi* was found beneath a rock in a stream bank 0.7 mile by road NE of Cerro Pelón, Sierra de Juárez, Oaxaca,



FIG. 2.—Photograph of an egg clutch and attending female of *Pseudoeurycea juarezi* found beneath a small rock on Cerro Pelón, Oaxaca.

México, on 20 January 1969. The female was coiled about the eggs in a depression under the rock (Fig. 2). She measured 47 mm in snout to posterior vent length and 90 mm in total length. The eggs were in a cluster but not suspended in the cavity. The following description is based on the preserved clutch.

The eggs, all of which contain advanced embryos, are non-adherent, attached in a bead-like fashion by gelatinous connecting strands, and aggregated into a grape-like cluster. The precise way in which the string of eggs is twisted and wound into the cluster could not be determined. Both strands of each egg pass into a "knot" at the center of the clutch before passing to other eggs.

The individual eggs are elliptical with the long diameter in the direction of the gelatinous connecting strands. The embryos are surrounded by a vitelline membrane, the long diameter of which ranges from 5.2 to 5.6 mm ($\bar{x} = 5.37$) and the short diameter from 4.35 to 4.6 mm ($\bar{x} = 4.48$). No capsular cavity is evident. A thick gelatinous inner envelope surrounds the vitelline membrane. It has a long diameter of 5.7 to 6.4 mm ($\bar{x} = 5.89$) and a short diameter of 4.6 to 4.9 mm ($\bar{x} = 4.78$). The inner envelope averages about 0.5 mm wide in the long diameter and 0.3 mm wide in the short diameter. The maximum short diameter of the egg is 4.75 to 5.05 mm ($\bar{x} = 4.91$). A thin outer envelope (ca. 0.06 mm) is continuous with the gelatinous connecting strands; this envelope is much thicker at the ends of the egg where it expands to form the gelatinous connect-

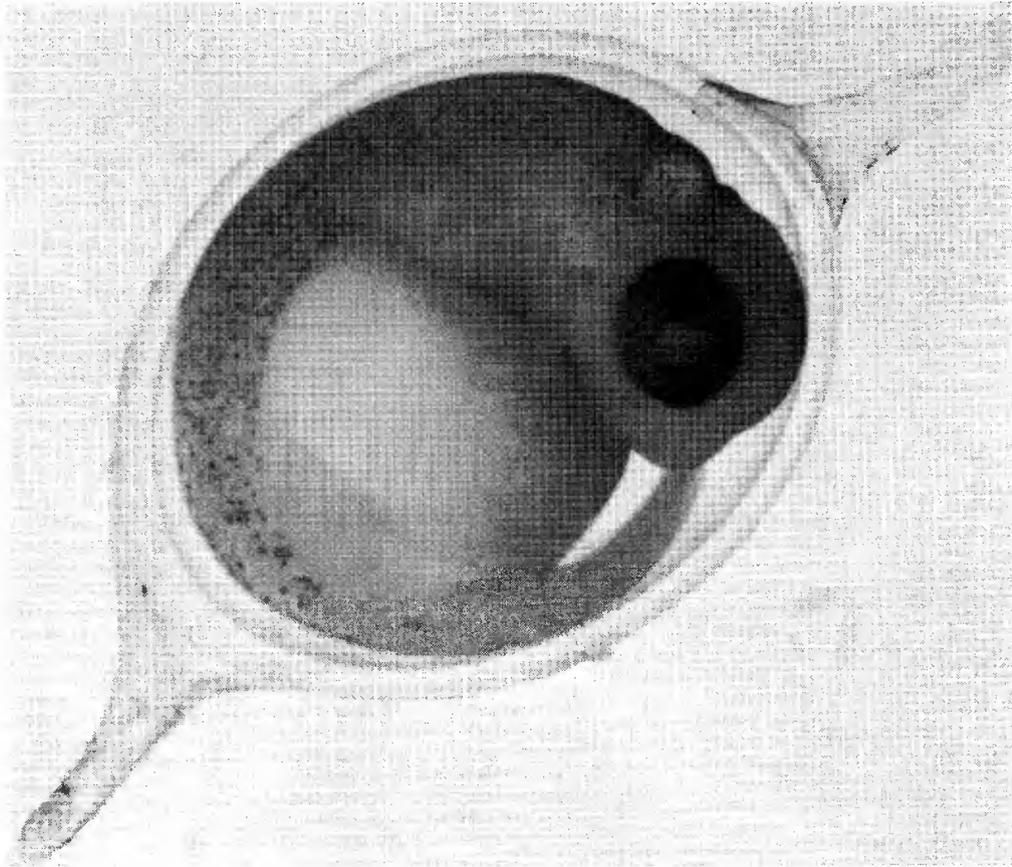


FIG. 3.—Egg of *Pseudoeurycea juarezi* showing the coiled position of the embryo around the yolk.

ing strands. The connecting strands average 0.4 mm in diameter and lack the distinct central core found in the *P. nigromaculata* eggs. The connecting strands were tightly tied into the central knot and could not be measured.

All embryos are in a similar stage of development. The yolk is still large, accounting for about one-third of the volume of the vitelline chamber. Each embryo is tightly coiled around the yolk (Fig. 3). The total length of each embryo is about 12.0 mm; the tail about 4.0 mm. The eyes consist of prominently pigmented optic cups which have a diameter of 1.2 mm horizontally and 1.0 mm vertically. A distinct choroid fissure is evident on the ventral side of the cup, and a lens is visible through the pupil. Posterior to the eyes, crystalline material is visible through the skin as a pair of white patches in the endolymphatic sacs (Fig. 3). Limb buds are present but show no differentiation. The anterior limb buds are about 1.2 mm long and the posterior buds about 1.05 mm. Externally the mouth is distinct, the nostrils are faintly discernible, and no nasolabial groove is evident. Scattered melanophores occur over the sides and dorsum of the head, trunk, and base of the tail. An area

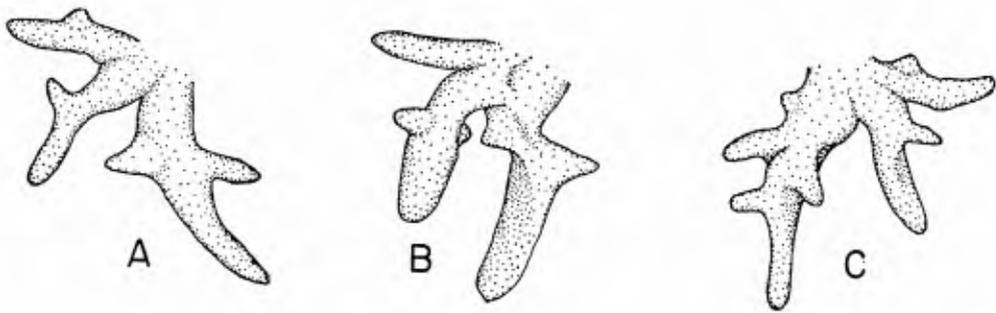


FIG. 4.—Drawings of gill structures showing patterns of variation. A. Right gill with typical branching; B. Right gill with slightly modified branching; C. Left gill showing extensive branching of anterior segment.

between the eyes usually lacks melanophores. Pigment gaps also are scattered irregularly over the dorsum of some individuals. The posterior half of the tail lacks pigment (Fig. 3), and in some individuals the entire tail is free of melanophores. Costal grooves are well developed.

One embryo was prepared for histological examination by paraffin infiltration, sectioned at $10\ \mu$ and stained with Van Gieson's Connective Tissue Stain. In this embryo the brain is roofed over and differentiated into the major embryonic areas. The epiphysis, hollow otic capsules and tongue rudiment are evident. Nasal capsules with cavities are well developed, but the nasal openings, both external and internal, are extremely small. Although the brain and associated structures are well differentiated, there is no indication of any skeletal rudiments in the head. The notochord, notochordal sheath and spinal nerves with associated ganglia are well developed, yet there is no evidence of vertebral formation. The gut tube is distinct anteriorly. A pair of pronephric units has well-developed tubules and open peritoneal funnels. Dorsal to the archinephric duct there are at least four pairs of apparently segmentally arranged mesonephric rudiments. The limb buds are undifferentiated internally.

The gills consist of three branches (Fig. 4). The anterior branch (ca. 1.6 mm) has two secondary branches, the middle branch (ca. 1.35 mm) has one or two secondary branches, and the posterior branch (ca. 0.9 mm) usually has a short secondary branch.

COMPARISON WITH OTHER SPECIES

In his monograph of the salamander family Plethodontidae, Wake (1966) placed all neotropical genera, together with *Hydromantes* and *Batrachoseps*, in the tribe Bolitoglossini of the subfamily Plethodontinae. It is reasonable, therefore, to compare the eggs of *Pseudoeurycea nigromaculata* and *juarezi* with other species in the genus and with species of other genera in the same tribe.

The eggs of only two of the 20 species of *Pseudoeurycea* are known. In the description of *Pseudoeurycea exspectata* Stuart (1954) mentioned two clutches of this species. Four egg clutches of *Pseudoeurycea bellii* from Michoacán were described and an egg illustrated by Duellman (1961). Salthe (1963) reported three capsules in *Pseudoeurycea exspectata*.

The eggs of *Pseudoeurycea nigromaculata* and *P. juarezi* are similar in shape, in the presence of two gelatinous envelopes, and in being connected by gelatinous strands. They differ in that the eggs of *P. nigromaculata* apparently are not aggregated into a cluster and have a central fibrillar core within the gelatinous strand which is absent from the eggs of *P. juarezi*. Possibly the fibrillar core is present only in early developmental stages and disappears later in embryogenesis.

Eggs of *Pseudoeurycea exspectata* show many similarities to those of *P. nigromaculata* and *P. juarezi*. They are connected in a bead-like fashion by gelatinous strands. Salthe (1963) indicated three gelatinous capsules outside the vitelline membrane. If the inner semi-opaque zone of *P. nigromaculata* is considered as a separate capsule, then the eggs are virtually identical to those of *P. exspectata*. The eggs of *P. juarezi* apparently lack the semi-opaque zone (soft "D" capsule of Salthe, 1963) observed in the other two species. Again the absence of this zone in the *P. juarezi* eggs may be attributed to developmental stage, i.e., the layer may become less apparent or disappear as the embryo develops.

The eggs of *Pseudoeurycea bellii* resemble those of the other three species in having at least two gelatinous envelopes and no pigment, but differ in that they are not connected in strands, but rather are adherent in groups of three or four (Duellman, 1961). Salthe (1963) saw two capsules in the eggs of *P. bellii* not observed in eggs of *P. juarezi* and one other capsule not observed in the eggs of *P. exspectata* and *P. nigromaculata*.

The eggs of five species of the genus *Bolitoglossa* are best known. Barbour and Cole (1906) mentioned discovery of a single egg of *Bolitoglossa yucatanana* in moist earth near a water trough at Chichén-Itzá, Yucatán, México. Although these authors did not describe the eggs, this is the first report of eggs laid by a tropical plethodontid. Schmidt (1936) reported a clutch and attending female of *Bolitoglossa rostrata* from Guatemala. Additional eggs of this species were mentioned by Stuart (1951). The eggs of *Bolitoglossa rostrata* adhere in clusters and apparently have two capsules surrounding the vitelline membrane (Salthe, 1963).

A clutch of about 30 eggs of *Bolitoglossa platydactyla* was recorded from San Luis Potosí, México, by Taylor and Smith (1945). Smith, Landy, and Underhill (1968), on gross examination, located

what appeared to be two layers external to the vitelline membrane in the eggs of *B. platydactyla*. However, on closer examination the outer envelope was found to consist of two laminae, the outermost of which is thin and hard. Vial (1968) described the eggs of *B. subpalmata* as consisting of two gelatinous envelopes surrounding the vitelline membrane. The eggs are firmly attached to each other and form irregular, grape-like clusters. The number of capsules in eggs of *B. adspersa* is unknown. Valdivieso and Tamsitt (1965) found the eggs in an oblong adhering mass. Nicéforo María (1958) reported six eggs that were a short distance apart, but attached to a small branch of a fern. Among the species of *Bolitoglossa*, eggs apparently are similar in the number of envelopes. The eggs of *Bolitoglossa* lack connecting strands and stalks, but adhere usually in clumps. Apparently *Bolitoglossa* eggs differ from some species of *Pseudoeurycea* in the number of capsules. *Bolitoglossa* eggs also differ from three species of *Pseudoeurycea*, but not *P. bellii*, in lacking gelatinous connecting strands.

Duellman (1959) described the eggs of *Parvimolge townsendi* from a clutch discovered near Huatusco, Veracruz. The eggs are unstalked, adherent, and surrounded by two gelatinous envelopes each enclosed by a membrane. Presumably, the eggs of *Parvimolge* are more similar to the eggs of *Bolitoglossa* and *Pseudoeurycea bellii* than to eggs of the other three species of *Pseudoeurycea*.

Nothing is known about the eggs or reproductive habits of the several species of *Chiropterotriton*, *Thorius*, *Oedipina* or *Lineatriton*.

The eggs of three of the seven species of *Batrachoseps* are known. These eggs are connected by gelatinous strands and have two prominent gelatinous envelopes external to the vitelline membrane (Snyder, 1923; Maslin, 1939; Stebbins, 1949; Davis, 1952). An inner, third layer, probably the capsular cavity, is reported by some (Maslin, 1939; Stebbins, 1962). *Batrachoseps* eggs resemble those of *Pseudoeurycea nigromaculata*, *juarezi* and *expectata* in possessing gelatinous connecting strands and two envelopes. They differ from eggs of *P. juarezi* and *P. expectata* in not being knotted into a cluster.

Gorman (1956) described the eggs of *Hydromantes shastae* in detail. They possess two gelatinous envelopes external to the vitelline membrane and are connected by gelatinous strands. The eggs of two European species, *H. genei* and *H. italicus*, are nearly identical with those of *H. shastae* (Stefani and Serra, 1966; Durand, 1967a). Also, the eggs of *Hydromantes* are similar to those of three species of *Pseudoeurycea* and to those of *Batrachoseps*. They further resemble the egg clutches of *P. juarezi* and *P. expectata* in that the eggs of *Hydromantes* are knotted into a cluster in precisely the same manner. Some of the eggs had only one strand leading to the central

mass; other eggs had two. Although Stefani and Serra (1966) illustrated the central knot in *H. genei*, neither these authors nor Gorman (1956) were able to clearly define how the knot of intertwined strands was formed.

The gill filaments of *Bolitoglossa subpalmata* are simpler than those of *Pseudoeurycea juarezi*, consisting of a single primary branch usually with two short secondary branches (Vial, 1968). The gills of *B. subpalmata* become more filamentous as they are reabsorbed during embryogenesis. Advanced embryos of *B. adspersa* have gills similar to those of *B. subpalmata*, but apparently with fewer branches (von Wahlert, 1965). In advanced embryos of *B. platydactyla* the gills consist of 1 to 3 soft filaments as much as 2 mm in length. The anterior filament is sometimes lacking in well-developed embryos, and the two posterior filaments are fused at their bases. The gill filaments are irregularly branched and adhere closely to the inner surface of the perivitelline membrane (Smith, Landy, and Underhill, 1968). The gills of *Bolitoglossa platydactyla* embryos differ from those of *P. juarezi* in the reduction or absence of the anterior gill filament from the former species.

The gills of *Batrachoseps wrighti* embryos (Stebbins, 1949) resemble those of *Pseudoeurycea juarezi* except that they consist of only two filaments and apparently have more secondary branches. In *B. attenuatus* and *B. major* the gills consist of filaments of which the central one is the longest (Snyder, 1923; Davis, 1952).

The gills of advanced embryos of *Hydromantes shastae* and *H. italicus* are small and weakly lobed (Gorman, 1956; Durand, 1967b). *Plethodon* gill structure is similar to that of *Pseudoeurycea*, some *Bolitoglossa* and *Batrachoseps* in possessing three prominent branches. However, the gills of *Plethodon* exhibit much more secondary branching than found in *Pseudoeurycea* and have an elongated middle filament (Bishop, 1941; Organ, 1960). The gills of *Ensatina* (Stebbins, 1954) and *Aneides* (Miller, 1944) are broadly trilobed and extensively vascularized. As in the gills of *Plethodon*, the middle filament is elongated. The gills of *Ensatina* and *Aneides* differ strikingly from those of *Plethodon* in lacking any secondary branching.

DISCUSSION

Timing of egg deposition, clutch size, clutch type and the presence of attending adults of tropical representatives of the Plethodontidae are summarized in Table 1.

From the limited information available, it appears that species of *Pseudoeurycea* and *Parvimolge* generally deposit their eggs during the drier months. This is not true of *Bolitoglossa*, with the possible exception of *B. platydactyla* and *B. yucatanana*, as egg clutches are deposited in both wet and dry seasons. Valdivieso and Tamsitt

TABLE 1.—Summary of breeding behavior of tropical species of the salamander family Plethodontidae.

Species	Month ¹	Clutch size	Clutch type		Adult attendance
			Adherent	Stranded	
<i>Pseudoeurycea juarezi</i>	Jan.	20		x	♀
<i>nigromaculata</i>	Jan.	19, 20		x	♀, ²
<i>expectata</i>	March, April	24, 21		x	♀
<i>bellii</i>	June	20, 23, 24	x		²
<i>Bolitoglossa adpersa</i>	March, Sept., Oct., Nov.	11, 10, 10, 6	x		♀, ♂, ²
<i>rostrata</i>	Feb., August	36, 20	x		♀
<i>platydactyla</i>	December	ca. 30	x		²
<i>subpalmata</i>	all Months except May	13–38 ³	x		♀, ♂
<i>yucatanana</i>	March	?	?		♀
<i>Parvimolge townsendi</i>	March	12	x		♀

¹ Time eggs found, not necessarily time of laying.

² Indicates no attending adult.

³ $\bar{x} = 22.5$, $N = 31$.

(1965) and Vial (1968) pointed out that reproduction in *Bolitoglossa adpersa* and *B. subpalmata* is nonseasonal and apparently acyclic.

The deposition of eggs during the dry season by individuals of *Pseudoeurycea* and *Parvimolge* would at first seem to be disadvantageous in terms of coping with desiccation. However, if the duration of embryonic development is 4 or 5 months, as in *Bolitoglossa subpalmata* in Costa Rica (Vial, 1968), then the eggs would hatch near the beginning of the rainy season, a period more suitable to the hatchlings. Incomplete data concerning egg deposition suggest that laying depends upon the climatic conditions of the inhabited area. The critical factor is not the timing of egg deposition with equitable climatic conditions (rainy season), but rather the timing of laying so that hatching takes place at the beginning of or during the wet season. There is some precipitation in southeastern México (Veracruz and eastern Oaxaca) during the dry season, but little or no precipitation during the same period in western and northern México. This may account for the relative success of plethodontids in the former area and may be more important for success of the

eggs than previously suspected. In any event, egg laying in the dry season assures that hatchlings will not be subjected to extremely arid conditions. In addition, food will be more abundant at a time when it is critical for normal growth and development. The growth rate for *Bolitoglossa subpalmata* is greatest from hatchling size to 20 mm (Vial, 1968) indicating the need for abundant food at this time.

These assumptions find some support in the timing of egg deposition recorded for four species of *Pseudoeurycea*. Specimens of *P. juarezi*, *P. nigromaculata*, and *P. exspectata* (well-developed embryos) from localities where there is some precipitation during the dry season and where the rainy season may begin in late May, apparently deposit their eggs earlier than do specimens of *P. bellii* from localities where the dry season is drier and the rainy season begins somewhat later (late June or July). In areas where there is no marked wet-dry season or where local conditions (cloud cover or fog) provide a relatively uniformly moist climate, the species should deposit their eggs throughout the year. This apparently is what happens with *Bolitoglossa adspersa* and *B. subpalmata* (Table 1).

Pseudoeurycea bellii is widespread in México. The dry season is more severe and the rainy season somewhat later at localities in the northern and western portions of its range. If our hypothesis concerning time of egg deposition is correct, clutches of *P. bellii* from localities throughout its range should show temporal spacing correlated with the beginning of the rainy season. Additional information would also indicate whether or not the timing of egg deposition is uniform for the species from localities throughout its range or whether the timing of egg deposition is the result of selection by environmental factors that are different at each locality, as predicted by our hypothesis.

Much more data on the dates of egg deposition in tropical plethodontids are needed to indicate the extent that latitude affects the timing of laying. Plethodontid species from areas near the equator apparently deposit their eggs year around, but the North American temperate zone plethodontids exhibit seasonal cycles (Bishop, 1941; Organ, 1960; Highton, 1962).

Clutch size seems to be consistent among species of *Pseudoeurycea*, but varies among species of *Bolitoglossa*. Perhaps clutch size for species of *Bolitoglossa* is more consistent among closely related species or species of similar size. The available information (Table 1) suggests that clutch type, either adherent or stranded, also generally is consistent within a genus. Three of the four species of *Pseudoeurycea* have eggs connected by strands. *Pseudoeurycea bellii* has unconnected eggs and, in this character, is more similar to species of *Bolitoglossa* and *Parvimolge* than other *Pseudoeurycea*.

Clutches from other species of *Pseudoeurycea* may clarify this difference. Vial's observations (1968) of the egg-aggregating behavior of female *Bolitoglossa subpalmata* illustrate the method whereby eggs of *Bolitoglossa* and probably *Parvimolge* are clustered into adherent clutches. The single egg of *Bolitoglossa yucatanana* probably represents only part of a clutch; we presume that eggs of this species also are adherent. How the eggs of some *Pseudoeurycea* are knotted together is not known, although continual movement of the eggs by the female probably accounts for the tangled nature of the cluster. Only eggs of *P. juarezi* and *P. exspectata* (FMNH 68750) containing well-developed embryos, had the peculiar knotted cluster. The eggs of *P. nigromaculata* were not clustered and apparently recently laid, as indicated by their early developmental stages. Apparently the female had not yet begun to manipulate the egg string.

Attendance of egg clutches, usually by females, is characteristic of most tropical plethodontid species and may be crucial to the development of the embryos (Vial, 1968).

Finally, the eggs of *Pseudoeurycea juarezi*, *P. nigromaculata* and *P. exspectata* are morphologically similar, but show some differences from the eggs of *P. bellii*, *Bolitoglossa* and *Parvimolge*. They are also remarkably similar to the eggs of *Hydromantes* and *Batrachoseps*. Wake (1966) has shown that the latter two genera are more closely related to tropical plethodontids than to other temperate species. The similarities of their eggs with some species of the genus *Pseudoeurycea* are additional evidence of this relationship.

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LITERATURE CITED

- BARBOUR, T., AND L. J. COLE. 1906. Vertebrata from Yucatan. Reptilia, Amphibia, and Pisces. Bull. Mus. Comp. Zool. 50(5):146-159.

- BISHOP, S. C. 1941. The salamanders of New York. New York State Mus. Bull. 324:1-365.
- BRAME, A. H., JR., AND D. B. WAKE. 1963. The salamanders of South America. Contr. Sci. Los Angeles Co. Mus. 69:1-72.
- DAVIS, J. 1952. Observations on the eggs and larvae of the salamander *Batrachoseps pacificus major*. Copeia 1952:272-274.
- DUELLMAN, W. E. 1959. The eggs and juveniles of the plethodontid salamander *Parvimolge townsendi* Dunn. Herpetologica 15:35-36.
- . 1961. The amphibians and reptiles of Michoacán, México. Univ. Kansas Publ. Mus. Natur. Hist. 15(1):1-148.
- DURAND, J. 1967a. Sur la reproduction d'*Hydromantes italicus strinatii* Aellen (Urodèle, Plethodontidae). Comptes Rendus Acad. Sci. Paris ser. D. 264:854-856.
- . 1967b. Sur l'ontogenèse d'*Hydromantes italicus* Dunn (Urodèle, Plethodontidae). Comptes Rendus Acad. Sci. Paris ser. D. 265:1533-1535.
- GORMAN, J. 1956. Reproduction in plethodont salamanders of the genus *Hydromantes*. Herpetologica 12:249-259.
- HIGHTON, R. 1962. Geographic variation in the life history of the slimy salamander. Copeia 1962:597-613.
- MASLIN, T. P., JR. 1939. Egg-laying of the slender salamander (*Batrachoseps attenuatus*). Copeia 1939:209-212.
- MILLER, L. 1944. Notes on the eggs and larvae of *Aneides lugubris*. Copeia 1944:224-230.
- NICÉFORO MARÍA, H. 1958. Sección herpetologica. Bol. Inst. La Salle, Bogotá 45(198):1-16.
- ORGAN, J. A. 1960. Studies on the life history of the salamander, *Plethodon welleri*. Copeia 1960:287-297.
- PETERS, W. 1863. Fernere Mittheilungen über neue Batrachier. Monatsber. Akad. Wiss. Berlin 1863:445-470.
- POSADA ARANGO, A. 1909. Nueva especie de salamandrido. Estudios Científicos, p. 125.
- RUTHVEN, A. G. 1922. The amphibians and reptiles of the Sierra Nevada de Santa Marta, Colombia. Misc. Publ. Mus. Zool. Univ. Michigan 8:5-69.
- SALTHE, S. N. 1963. The egg capsules in the Amphibia. J. Morphol. 113(2):161-171.
- SCHMIDT, K. P. 1936. Guatemalan salamanders of the genus *Oedipus*. Zool. Ser. Field Mus. Natur. Hist. 20(17):135-166.
- SMITH, H. M., M. J. LANDY, AND D. K. UNDERHILL. 1968. Some characteristics of the eggs and embryos of a Mexican plethodontid salamander. Herpetologica 24:67-72.
- SNYDER, J. O. 1923. Eggs of *Batrachoseps attenuatus*. Copeia 1923:86-88.
- STEBBINS, R. C. 1949. Observations on laying, development, and hatching of the eggs of *Batrachoseps wrighti*. Copeia 1949:161-168.
- . 1954. Natural history of the salamanders of the plethodontid genus *Ensatina*. Univ. California Publ. Zool. 54(2):47-124.
- . 1962. Amphibians of Western North America. Univ. California Press, Berkeley and Los Angeles, 539 p.
- STEFANI, R., AND G. SERRA. 1966. L'oviparità in *Hydromantes genei* (Temme Schl.). Bol. Zool. Italiana 33(2):283-291.
- STUART, L. C. 1951. The herpetofauna of the Guatemalan Plateau, with special reference to its distribution on the southwestern highlands. Contr. Lab. Vert. Biol. Univ. Michigan 49:1-71.
- . 1954. Descriptions of some new amphibians and reptiles from Guatemala. Proc. Biol. Soc. Washington 67:159-178.

- TAYLOR, E. H., AND H. M. SMITH. 1945. Summary of the collections of amphibians made in México under the Walter Rathbone Bacon Traveling Scholarship. Proc. U. S. Nat. Mus. 95(3185):521-613.
- VALDIVIESO, D., AND J. R. TAMSITT. 1965. Reproduction in a neotropical salamander *Bolitoglossa adspersa* (Peters). Herpetologica 21:228-236.
- VIAL, J. L. 1968. The ecology of the tropical salamander, *Bolitoglossa subpalmata*, in Costa Rica. Rev. Biol. Trop. 15(1):13-115.
- VON WAHLERT, G. 1965. Molche und Salamander. Kosmos, Ges. Natur. Franckh'sche Verlagshandlung Stuttgart, 71 p.
- WAKE, D. B. 1966. Comparative osteology and evolution of the lungless salamanders, family Plethodontidae. Mem. S. California Acad. Sci. 4:1-111.

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