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# The tadpole of *Pseudis minuta* (Anura: Pseudidae), an apparent case of heterochrony

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**Abstract.** The external morphology, oral disc, and coloration pattern of the larva of *Pseudis minuta* are described. Tadpoles are mostly bottom dwellers that have a small, terminal oral disc with a labial tooth row formula 1(1-1)/(1-1)2. Internal oral anatomy is characterized using scanning electron microscopy, representing the only description available for the family Pseudidae. The coloration pattern of *P. minuta* tadpoles is compared with that of other pseudids. *Pseudis minuta* larvae do not exhibit the ontogenetic coloration change reported for *P. paradoxa*. Considering larval coloration, larval size, and reports of adult size, acceleration or hypermorphosis are suggested as possible heterochronic mechanisms involved in the evolution of *Pseudis*.

**Resúmen.** Se describe la morfología externa, disco oral, y patrón de coloración de la larva de *Pseudis minuta*. Estas larvas nadan en el fondo de los charcos, poseen un disco oral pequeño y terminal con una fórmula dental larval de 1(1-1)/(1-1)2. Se reporta la anatomía oral interna usando microscopía electrónica de barrido. La descripción de la anatomía oral representa la única descripción disponible para la familia Pseudidae. El patrón de coloración de las larvas de *P. minuta* se compara con el de otros pseudidos. *Pseudis minuta* no muestran el cambio de coloración reportado en la ontogenia de *P. paradoxa*. La coloración larval, tamaño larval, e información sobre tamaño de los adultos, sugieren aceleración somática o hiper morfosis como posibles mecanismos heterocrónicos participantes en la especiación de *Pseudis*.

## Introduction

Among Pseudidae, currently three species are recognized in two genera: *Lysapsus limellus* Cope, 1862, *Pseudis minuta* Günther, 1859 "1858", and *Pseudis paradoxa* (Linnaeus, 1758) (Frost, 1985, 1993). The tadpole of *L. limellus* was reported by Kehr and Basso (1990) and that of *P. paradoxa* was described by Kenny (1969). The tadpole of *P. minuta* remained undescribed. In addition to these three taxa, the name *Lysapsus mantidactylus* has been commonly used and appeared several times in the literature on pseudid frogs (Gallardo, 1961, 1964; Barrio, 1965, 1970; Cei, 1980; Gudynas and Rudolf, 1983; Altig and Johnston, 1986; Kehr and Williams, 1990). For example, Fernández and Fernández

(1921) studied the reproductive behavior of *L. mantidactylus* reporting eggs, egg-clutch, and hatching characteristics, and provided a brief description of the external larval morphology. Gallardo (1964) gave additional data on larval stages and Cei (1980) compared the larvae of this species to those of *P. paradoxa platensis*. Emerson (1988) made a few comments on the larvae of *L. mantidactylus* while studying the giant tadpoles of *P. paradoxa*. However, *L. mantidactylus* was synonymised with *P. minuta* by Klappenbach (1985), a move accepted by Duellman (1993). A detailed description and illustration of the tadpole of *P. minuta* are needed; furthermore, comparisons with the limited data reported by Fernández and Fernández (1921) for *L. mantidactylus* may help to confirm the status of this species.

The goals of this work are: first, to provide a description of the larvae of *Pseudis minuta* based on tadpoles from adults that reproduced in captivity. The adults of *P. minuta* bred for this study fully agree with Günther's (1859) description of the species. Furthermore, these specimens did not have expanded anterior terminal digits and possessed prevomerine teeth located between the choanae, features that are diagnostic for the genus *Pseudis* (Savage and Carvalho, 1953). Second, we describe the characteristics of the internal oral anatomy of *P. minuta* using scanning electron microscopy (SEM). Internal oral anatomy has not been characterized for any other species of Pseudidae. Third, to postulate heterochrony as a possible mechanism participating in the evolution of *Pseudis*.

## Material and methods

A total of 108 *Pseudis minuta* individuals were studied. Larvae were preserved in 10% formalin from commercial grade solution throughout development and staged using Gosner's table of normal development (Gosner, 1960). These specimens range from developmental stage 28 through metamorphosis and include ten postmetamorphic juveniles. Larvae were raised from "naturally induced" (= non hormone injected) clutches obtained in the laboratory from one female (USNM 498369) and three male *Pseudis minuta* collected in Laguna del Cisne, Salinas, Departamento de Canelones, Uruguay, 27 October 1994, by A. Olmos and R. de Sá. Individuals exhibited breeding activity at the time of collection; the female and one of the males were in amplexus, while the other two males were calling among vegetation on flooded pastures surrounding the lake. Tadpoles were raised in 40 l aquaria, at a density of 25 tadpoles per aquarium to standardize density dependent variation and were fed *ad libitum* with commercial fish food. Voucher specimens are deposited in the National Museum of Natural History, Washington D.C. (USNM).

The description of larval external morphology is based on 10 specimens in stages 31-35 (2 specimens in each stage, USNM 498370-75 and USNM 498377-80). The tadpole illustration corresponds to USNM 498376. Morphometric descriptors are those suggested by Lavilla and Scrocchi (1986). Measurements were taken to the nearest 0.01 mm with a Mitutoyo dial caliper and micrometric ocular in a Wild M3C stereomicroscope. All

**Table 1.** Measurements of *Pseudis minuta* tadpoles (values in mm). Abbreviations given in text.

Tadpole #	1	2	3	4	5	6	7	8	9	10
TL	39.2	39.3	37.6	38.1	41.4	40.7	35.7	37.7	45.5	42.5
BL	13.4	12.6	13.6	13.6	13.5	12.4	12.4	12.7	14.8	14.2
TaL	25.8	26.7	24	24.5	27.9	28.3	23.3	25	30.7	28.3
BW	7.8	7.9	8.1	8.1	7.9	7.6	7.7	8	9.2	8.9
BWE	7.8	7.9	8.1	8.1	7.9	7.6	7.7	8	9.2	8.9
BWN	5.3	5	5.1	5.4	4.9	4.8	5.3	5.2	5.4	5.3
BH	7.8	7.8	7.9	8.2	7.8	7	7.4	6.7	8.6	8.9
TMH	3.2	3.2	3.4	3.2	3.4	2.73	2.68	2.97	3.8	3.7
FH	9.1	8.6	10.6	10.6	9.8	9.5	7.4	8.6	10	10.5
RSD	8.3	8.5	8.9	9.3	9.1	8.6	8	8.6	10.1	10
FN	2.18	2.15	2.29	2.42	2.29	2.5	1.89	2.17	2.45	2.36
NO	2.71	2.82	2.9	2.92	2.71	2.74	2.36	2.86	3.1	2.98
IN	2.12	2.28	2.22	2.39	2.4	2.31	2.34	2.27	2.56	2.42
IO	5.3	5.2	5.4	5.1	5.4	5.1	5	4.9	6	5.7
EN	3.3	3.2	3.3	3.4	3.4	3.2	3.2	3.1	3.7	3.6
EO	7.8	7.9	8.1	8.1	7.9	7.6	7.7	8	9.2	8.9
E	1.65	1.65	1.77	1.77	1.89	1.91	1.9	1.84	2.05	1.92
N	0.64	0.52	0.53	0.65	0.66	0.49	0.66	0.47	0.71	0.54

measurements are given in table 1; values given in the text accompanying the description correspond to mean values ( $n = 10$ ). Measurements are abbreviated as follows: TL (total length), BL (body length), TaL (tail length), BW (body maximum width), BWE (body width at eyes), BWN (body width at nostrils), BH (body maximum height), FH (fin height), TMH (tail muscle height), RSD (rostrum-spiracular distance), FN (frononasal distance), NO (naso-ocular distance), N (nostril diameter), E (eye diameter), EN (extranarial distance), IN (internarial distance), EO (extraorbital distance), IO (interorbital distance). Drawings were made with the aid of a camera lucida attached to the stereomicroscope.

A tadpole in stage 36 was dissected for SEM analysis, two additional tadpoles (stage 37) were dissected, stained with methylene blue, and observed under a stereomicroscope to verify SEM observations. Morphological features were recorded using the methodology presented by Wassersug (1976) and Wassersug and Heyer (1988). The specimen for SEM was prepared as follows: ultrasonically cleaned for 15 minutes, fixed in 3-4% solution of glutaraldehyde for 2 h at room temperature (rt), followed by three 15 minute washes with 0.1 M phosphate buffer, post fixed for 2 h in a 1% solution of osmium tetroxide (rt), three 15 minute washes in 0.1 M phosphate buffer were repeated. Subsequently, samples were dehydrated using 15 minute changes of the following graded ethanol series: 35, 50, 70, 80, 95%, and three 100% changes. Specimens were critical point dried in CO<sub>2</sub>, mounted on aluminum stubs and sputter coated with gold/palladium, 22 nanometers thick, using a Hummer VII sputtering system. Internal oral anatomy was examined in a Hitachi S-2300 scanning electron microscope at 15 kV, 20 kV and 25 kV and photographed using Polaroid 55 positive/negative film.

## Results

### *Description of larvae*

*Pseudis minuta* larvae in developmental stages comparable to those of Gosner stages 31-35 with a total length between 35.7 and 45.5 mm ( $n = 10$ ). Body height almost equal to the maximum body width (BH/BW = 0.99-1.19;  $\bar{x} = 1.04$ ,  $s = 0.057$ ), maximum body width at the level of eyes coinciding with extraocular distance. Overall, body ovoid without lateral constrictions, snout rounded in lateral and dorsal views (fig. 1), nostrils dorsolateral (EN/BWN = 0.60-0.68;  $\bar{x} = 0.64$ ;  $s = 0.031$ ), oval, and non-protruding on body surface; nostrils located nearer snout than eyes (FN/NO = 0.76-0.91;  $\bar{x} = 0.80$ ;  $s = 0.053$ ). Eyes lateral and of medium size (E/BWE = 0.21-0.25;  $\bar{x} = 0.23$ ;  $s = 0.015$ ).

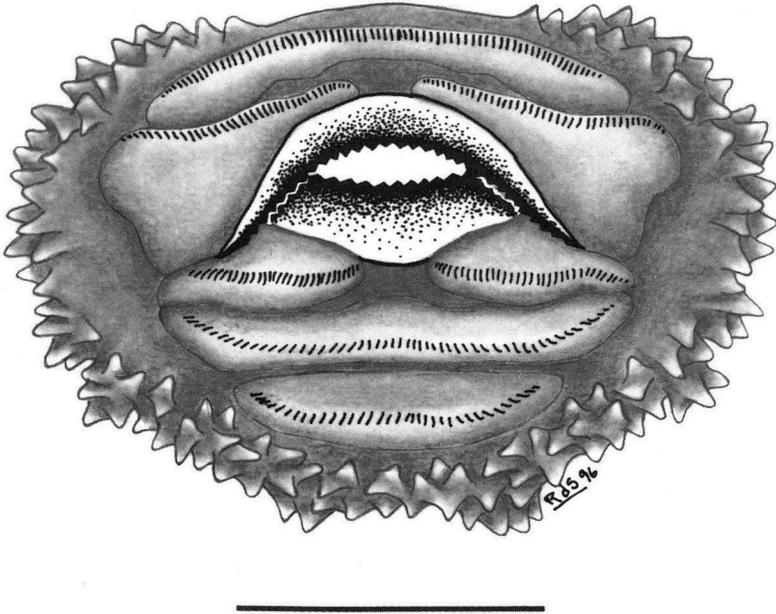
Oral disc small (OD/BW = 0.21-0.33;  $\bar{x} = 0.31$ ;  $s = 0.012$ ), terminal, and visible dorsally, lacking lateral folds even while closed (fig. 2). Multiple rows of well-developed marginal papillae bordering oral disc, marginal papillae interrupted by a rostral gap, about 40% of width of oral disc (range from 36-45%;  $s = 2.6$ ), submarginal papillae forming infraangular lateral patches, not reaching mental region. Upper and lower beaks serrated and approximately 20-30% keratinized (as suggested by pigmentation), upper beak broadly concave and lower beak U-shaped, labial tooth row formula 1(1-1)/(1-1)2. All tooth rows approximately equal in length, except distal row in posterior labium which is noticeably shorter.

Spiracle single, sinistral, dorsally visible, located laterally on posterior half of the body (RSD/BL = 0.62-0.70,  $\bar{x} = 0.67$ ;  $s = 0.015$ ), most of spiracular tube attached to body wall, only most distal tip free; vent large and triangular, lying and opening along ventral midline. In preserved specimens vent is variably folded. Tail length about 66% of total length (range from 64-69%,  $s = 1.5$ ), tail height greater than body height (FH/BH = 1.00-1.36;  $\bar{x} = 1.21$ ;  $s = 0.107$ ), tail fins about equal in height and about 1.3 × tail musculature height. Margin of dorsal fin uniformly curved, whereas that of ventral fin resembling an italicized and elongated *S*. Dorsal fin extending onto posterior half of body, ventral fin continuous with vent, tail tip slightly flagelliform.

*Coloration of preserved specimens.* Dorsum and flanks with pale brown reticulations and a more or less continuous white stripe laterally, extending from posterior angle of oral disc to antero-ventral margin of eye; stripe present throughout development. Dorsally, two whitish stripes extend from tip of snout posteriorly, for about one-quarter of body length, and slightly past the posterior margin of the nostrils; antero-ventral body coloration brown with two white stripes running posteriorly across throat area. Postero-ventral and ventrolateral body skin transparent, intestinal coils visible through skin. Ventral and dorsal whitish stripes clearly defined in early larval stages but less distinct in later development (stages 35-36 on). External wall of vent tube transparent with few small, subcircular brown spots, internal wall of vent tube uniformly brown,



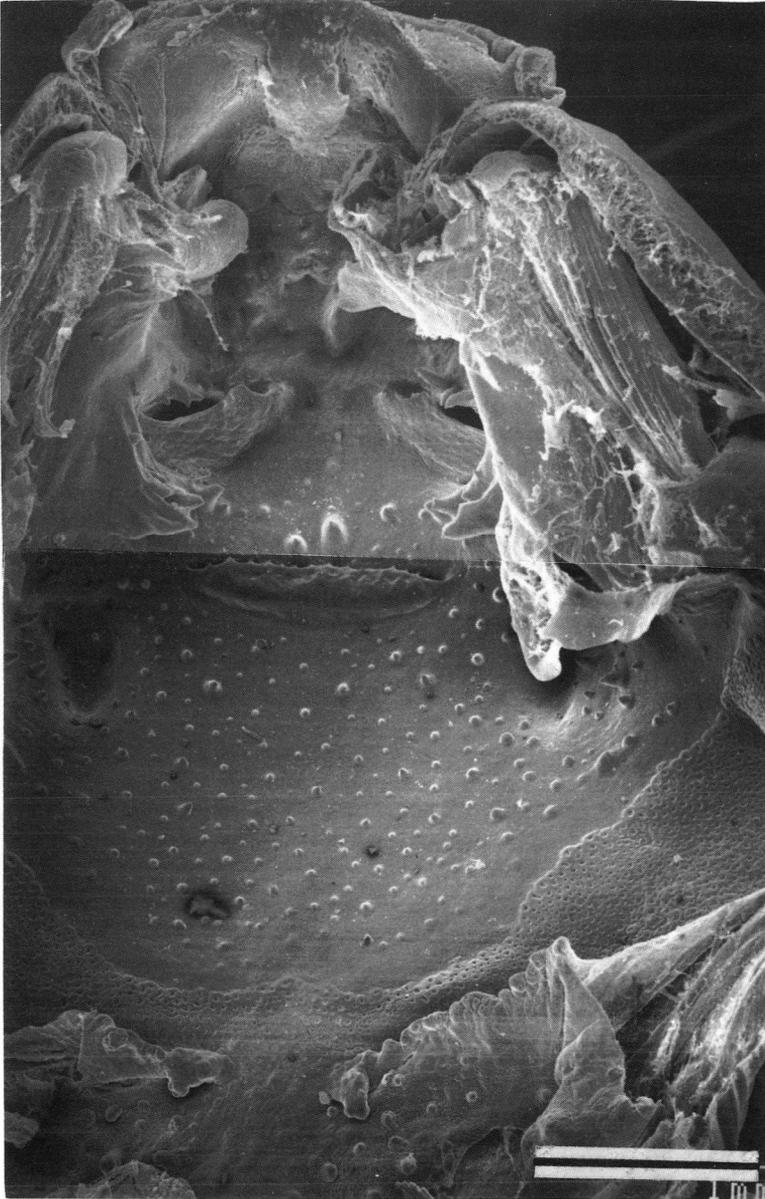
Figure 1. Lateral view of *Pseudis minuta* tadpole, USNM 498376, Gosner's Stage 32. Bar = 1.0 mm.



**Figure 2.** Opened oral disc of *Pseudis minuta* tadpole, USNM 498376. Bar = 1.0 mm.

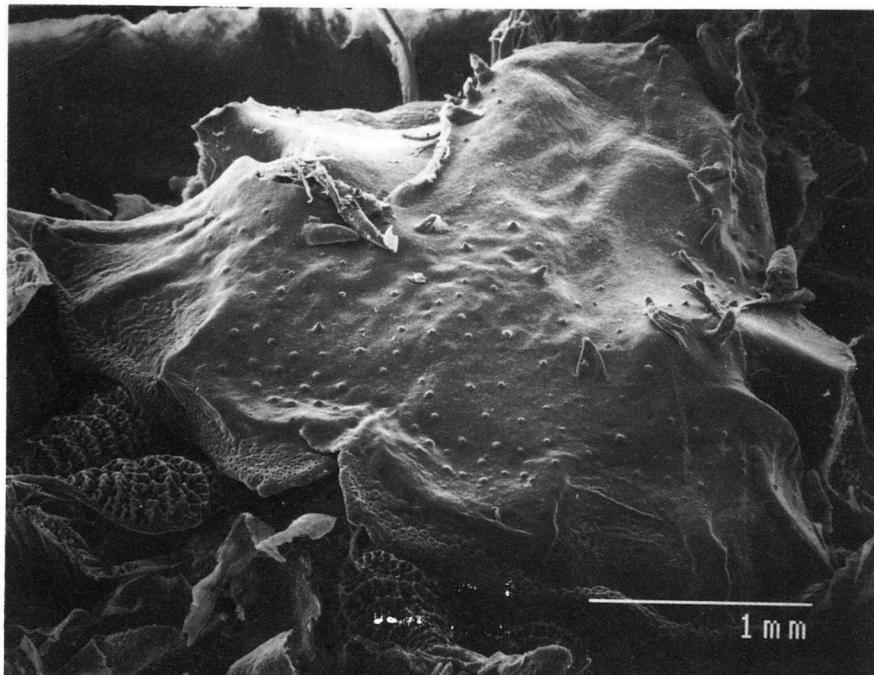
visible through external wall. Tail with three vertical, dark brown stripes, alternating with more or less transparent regions of fins; most anterior stripe at junction of tail musculature and body, extending from external margin of dorsal fin onto tail musculature; second dark brown stripe present at about level of anterior one quarter of tail musculature, extending across dorsal fin, variably interrupted by whitish spots on tail musculature, and continuing across ventral fin; a third, less defined, and lighter brown stripe found about half the length of tail musculature, extending across dorsal and ventral fins and variably continuous with lighter brown reticulum on posterior half of tail fins. Caudal musculature brown with large, irregular, and variably fused white spots that in some specimens form longitudinal white stripes along the edges of the tail musculature.

*Internal oral anatomy.* Oral roof semicircular, with a narrow and semicircular prenarial arena. Nares about one-third way back on buccal roof, oriented transversely (fig. 3). Four or five prenarial papillae present at anterior edge of each naris. Narial valve well developed, posteriorly convex and rugose, with a clearly visible narial projection. Post-narial area complex. Postnarial papillae absent; 3-4 conical secondary papillae present on each side on the anterior surface of the lateral ridge papillae. A single and conspicuous lateral ridge papilla anterior to and on each side of median ridge. Median ridge positioned about half way back on buccal roof; crescentic with a rugose ventral margin and uniformly convex posterior surface. Buccal roof arena (BRA) broad, U-shaped, with numerous pustulations, but no BRA papillae. Four-five lateral roof papillae occur



**Figure 3.** SEM micrograph of roof of oral cavity of *Pseudis minuta*; scale line = 1 mm.

at most lateral edges of BRA. A distinct glandular zone with clearly visible secretory pit occurs posterior to the BRA, maximum length of glandular zone found laterally and covers about 25% of buccal roof. Glandular zone extending onto dorsal velum. Dorsal



**Figure 4.** SEM micrograph of floor of oral cavity of *Pseudis minuta*.

velum with a clear gap at midline and possessing marginal papillae at either side of the gap for about half its length.

Buccal floor triangular, about 1 1/4 wider than long (fig. 4). Four infralabial papillae present, the most anterior pair consisting of columnar, conical, and blunt ended apices, with second pair posterolateral, larger, and with jagged apices. Scattered pustulations occur on each side of lower jaw. Three lingual papillae present in a triangular arrangement; pustulations present in vicinity of lingual papillae. Buccal floor arena (BFA) bounded by a row of 12 conical, blunt ended, papillae on each side. These rows of BFA papillae run posteriorly, parallel to each other from a point behind and lateral to the lingual papillae, for about half the length of the BFA. Posterior half of BFA with scattered pustulations, anterior half free of pustulations. Velar surface free and long, about one sixth length of buccal floor. Posterior margin of velum glandular with well developed secretory pits. Marginal projections absent except for a pair of globose papillae bounding an inverted V-shaped and deep median notch.

## Discussion

Considering *Lysapsus mantidactylus* as a junior synonym of *Pseudis minuta* Günther, 1859 (Klappenbach, 1985; Duellman, 1993) implies that the larvae described here, ob-

tained from adults breeding in captivity that fully agree with the diagnostic characteristics for *P. minuta* (Günther, 1859; Savage and Carvalho, 1953), must overall agree with the brief reports for the larvae of *L. mantidactylus* (Fernández and Fernández, 1921; Gallardo, 1964). Indeed, the external morphology and coloration pattern presented here for *P. minuta* agree with previous reports for *L. mantidactylus*. The lack of available information on the internal oral anatomy of other species of pseudids preclude us from drawing comparisons within the family. However, the overall characteristics of the internal morphology of *P. minuta* match those predicted for ecologically typical pond tadpoles (Wassersug, 1980; Wassersug and Heyer, 1988). Based on oral characteristics, *P. minuta* can be best described as an omnivorous larva with generalized external structures and an internal oral anatomy for suspension feeding on microscopic particles.

Once the tadpole of *Pseudis minuta* was described, comparisons with the larvae of other pseudids resulted in three interesting observations. First, black tail tips have been reported for larvae of *Lysapsus limellus* (Kehr and Basso, 1990) and early stages of *P. paradoxa* (Dixon et al., 1995). Previous work on the relationship between predation and tadpole coloration showed that black tail tips help to increase survivorship (Caldwell, 1982, 1986) and vertical bands may function as disruptive coloration (Altig and Channing, 1993). In *P. paradoxa*, an overall darker tail results from darkening of the tail from the black tail tip forward as the tadpole grows in length and weight. Dixon et al. (1995) suggested that the pattern of disruptive coloration may only be needed in smaller tadpoles, that is until the tadpoles reach certain limits of differential predation. *Pseudis minuta* does not have a black tail tip. However, the vent of the tadpoles of *Pseudis minuta* tadpoles is unusually large, triangular, and with dark brown pigmentation accumulated on its internal wall, but with no pigmentation on its external surface. This pigmentation on the vent duct looks like a continuation of the most anterior stripe across the dorsal fin. Visually, this results in the tail having three dark stripes across its length. If this pattern of tail coloration in *P. minuta* is playing an ecological/defensive role, e.g. disruptive or cryptic coloration, as suggested for the smaller tadpoles of *P. paradoxa*, then the unusual accumulation of pigments on the vent duct may be the result of natural selection and it may help *P. minuta* tadpoles to avoid, at least some, predators.

Second, *Pseudis paradoxa* is characterized by its "gigantic" tadpole stage (maximum length recorded = 230 mm, Kenny, 1969). Long-term exposure to prolactin has been suggested as a key factor in larval gigantism (Emerson, 1988). Specimens reaching up to 102 mm have been reported in overwintering larvae of *P. minuta* (= *L. mantidactylus*, Gallardo, 1964). Among our specimens, raised in captivity under semi-controlled conditions, we did not observe these large specimens; the maximum length recorded was 63.2 mm at stage 42. This suggests that overwintering (= longer exposure to prolactin) is required for *P. minuta* larvae to reach large sizes; however, *P. minuta* larvae never reach the gigantic sizes of *P. paradoxa* tadpoles.

Third, the resemblance between the coloration patterns of *Pseudis minuta* and early developmental stages of *P. paradoxa* is remarkable. Kenny (1969) and Dixon et al.

(1995) described *P. paradoxa* larvae and reported a change in coloration during development. Kenny (1969) described a *P. paradoxa caribensis* tadpole of about 60 mm in length that is almost identical to the one reported here for *P. minuta*. However, Kenny reported that larger specimens (about 230 mm) are “uniformly dark brown, with bluish rosette-like spotting on back, flanks and tail” (Kenny, 1969, fig. 31). Dixon et al. (1995) documented the same ontogenetic pattern of coloration change in populations of *P. paradoxa* from northeastern Argentina. Tadpoles of *Pseudis minuta* do not undergo this dramatic ontogenetic change in coloration. Furthermore, to our knowledge, melanistic tadpoles have never been collected or reported in *P. minuta*, even among overwintering individuals, or *L. limellus*. Ontogenetic changes in coloration have been reported for other anuran species (Altig and Channing, 1993). However, the presence of melanic tadpoles in *P. paradoxa* provides a unique opportunity to address the evolutionary origin of melanism within a single lineage of Pseudidae.

Evolutionarily these observations are interesting and may suggest that a shift in developmental timing, i.e. a heterochronic mechanism, may have been involved in the evolution of the genus *Pseudis*. We suggest that the coloration pattern of *Pseudis minuta* larvae is similar to the one in the ancestral stock of *Pseudis*. No data are available on the timing of sexual maturity of *Pseudis*; consequently we can only suggest that acceleration or hypermorphosis (sensu Gould, 1977) may have participated in the speciation of *Pseudis*. Acceleration, the speeding up of somatic growth, resulting in tadpoles that reach metamorphosis climax faster in *P. minuta*, or hypermorphosis, the phyletic extension of larval ontogeny, resulting in larger and melanic tadpoles in *P. paradoxa*, could have resulted in the diversification of *Pseudis*.

The original description of *P. minuta* Günther (1858, p. 6) stated: “This species agrees in nearly all its characters with *P. paradoxa*, but is at once distinguished by its much smaller size. . .”. This statement could also be re-interpreted if heterochrony played a role in *Pseudis* speciation. Previous work has showed a correlation between larval and adult sizes, species that obtained larger sizes during larval stages reach larger adult sizes (Alberch et al., 1979; Hanken, 1992). Speciation coupled with alteration of the duration of the larval stage could explain sister lineages that are significantly differing in size, but morphologically very similar, as exemplified by the genus *Pseudis*.

A final systematic consideration is in order. The synonymization of *Lysapsus mantidacytlus* with *Pseudis minuta* (Klappenbach, 1985) leaves *Lysapsus* as a monotypic genus unless some of the geographical variation reported for *L. limellus*, currently identified as subspecies, is proven to represent independently evolving lineages. *Pseudis* is represented by two lineages, *P. minuta* and the *P. paradoxa* complex (*P. fusca*, Caramaschi and Cruz, 1996; other species can be recognized within *P. paradoxa*, Caramaschi, pers. com.). Males of *P. minuta* are unique among pseudids in having paired vocal sacs; this character should be interpreted as an autoapomorphy of *P. minuta* and does not warrant recognition of a separate genus from *Pseudis*.

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