A Survey of Internal Oral Features of Leptodactyloid Larvae (Amphibia: Anura)

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Introduction

Internal oral features of frog larvae provide information both on morphological adaptations to different larval habitats and on higher taxonomic relationships among frogs (e.g., Wassersug, 1980; Wassersug and Heyer, 1983; Inger, 1983). Larval representatives of many families have now been surveyed; the leptodactyloid frogs of Africa, South America, and Australia are an important exception. The major purpose of this paper is to describe the morphology of internal oral features from a broad spectrum of leptodactyloid larvae, emphasizing the leptodactylids of South America. Our interest in leptodactyloid larval anatomy is threefold: (1) to see whether morphological features correlate with habitat in the same way as demonstrated in other anuran larvae, (2) to determine whether features exist that can be used to elucidate the relationships of the African, South American, and Australian leptodactyloid lineages to each other and to other families of frogs, and (3) to determine whether there are features that can be used to elucidate inter-and intrageneric relationships among the South American leptodactylids.

ACKNOWLEDGMENTS.—Many individuals have provided tadpoles for our studies. These individuals have been most generous, as they donated specimens fully realizing that the specimens would be destroyed in analysis. The following curators have provided specimens from their collections: William E. Duellman, University of Kansas Museum of Natural History (KU); Raymond F. Laurent, Fundacion Miguel Lillo, Tucuman, Argentina (FML); Ronald A. Nussbaum, Museum of Zoology, University of Michigan (UMMZ); Richard G. Zweifel, American Museum of Natural History (AMNH). The following individuals also provided tadpoles: José M. Cei, Argentina; Oswaldo Luiz Peixoto, Universidade Federal Rural do Rio de Janeiro; Rudolfo Ruibal, University of California at Riverside. We have also utilized specimens from the National Museum of Natural History, Smithsonian Institution (USNM).

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Review Chairman: George R. Zug, Smithsonian Institution. Reviewers: Robert F. Inger, Field Museum of Natural History; Roy W. McDiarmid, U.S. Fish and Wildlife Service.

Materials and Methods

South American larvae were assembled that sampled all the major lineages as determined from studies on adults (primarily) (Lynch, 1971; Heyer, 1975) and various habitats utilized by larval leptodactylid frogs. Only one species of the African genus, *Heleophryne*, was sampled. A small sample of Australian genera, including representatives of both myobatrachines and limnodynastine frogs, was included to determine whether there are features that distinguish or unite the leptodactyloid larvae from all three continents.

Larvae were dissected and morphological features recorded

using the methodology presented in Wassersug (1976a; 1984) and Wassersug and Duellman (1984). The larval descriptions were based on light microscopic examination and confirmed with scanning electron microscopy (SEM). All photographs were made with SEM. All line drawings were prepared with camera lucida.

Terminology follows Wassersug (1976a; 1980) for internal features and Altig (1970) for external features; the abbreviations BFA (buccal floor arena), BRA (buccal-roof arena), cb (ceratobranchial), and SVL (snout-vent length) are used throughout. Some comments on pulmonary development are included with the descriptions of internal oral surface features. Detailed descriptions are provided for a representative of each genus.

Where more than one species of a genus was examined, only those features that differ are listed, as appropriate, for the additional species.

The larvae of *Cycloramphus izecksohni* (as *duseni*), *Thoropa miliaris* and *Thoropa petropolitana* were illustrated and described elsewhere (Wassersug and Heyer, 1983). These larvae are not redescribed but are included in the discussion of this paper.

Morphological Descriptions

African Leptodactyloid

Heleophryne natalensis Hewitt

Figure 1

Material.—No number (two specimens dissected, one used for all data except lung development stage 36, SVL 25.3 mm), collected in St. Hilier, South Africa, 25 November 1977, by G. Setaro.

Reference.—Van Dijk (1966) provides information on the external anatomy.

General Remarks.—In a second specimen dissected (stage 25) lungs small, less than 25% length of buccal floor; uninflated.

Ventral Aspect.—*Buccal Cavity:* Buccal floor flask-shaped with a long narrow "neck" extending posterior from lower beak to buccal pockets and with a very wide base between buccal pockets and esophagus. Infralabial papillae organized in 2 parallel ridges per side oriented from anterolateral to posteromedial, smaller simpler anterior ridge capped by larger flap-like posterior ridge; posterior ridge with a free dorsal margin directed anteriorly and medially; each infralabial ridge with 4–6 marginal papillae with secondary pustulation; papillae relatively tall and thin; large gap between the infralabial papillae and the tongue anlage. Two simple, small, lingual papillae. Diamond-shaped BFA with papillae restricted to straight ridges defining BFA posterior margin; 9 papillae on one side, 10 on other, all small and irregular. No prepocket papillae. A few pustulations on each side posterior

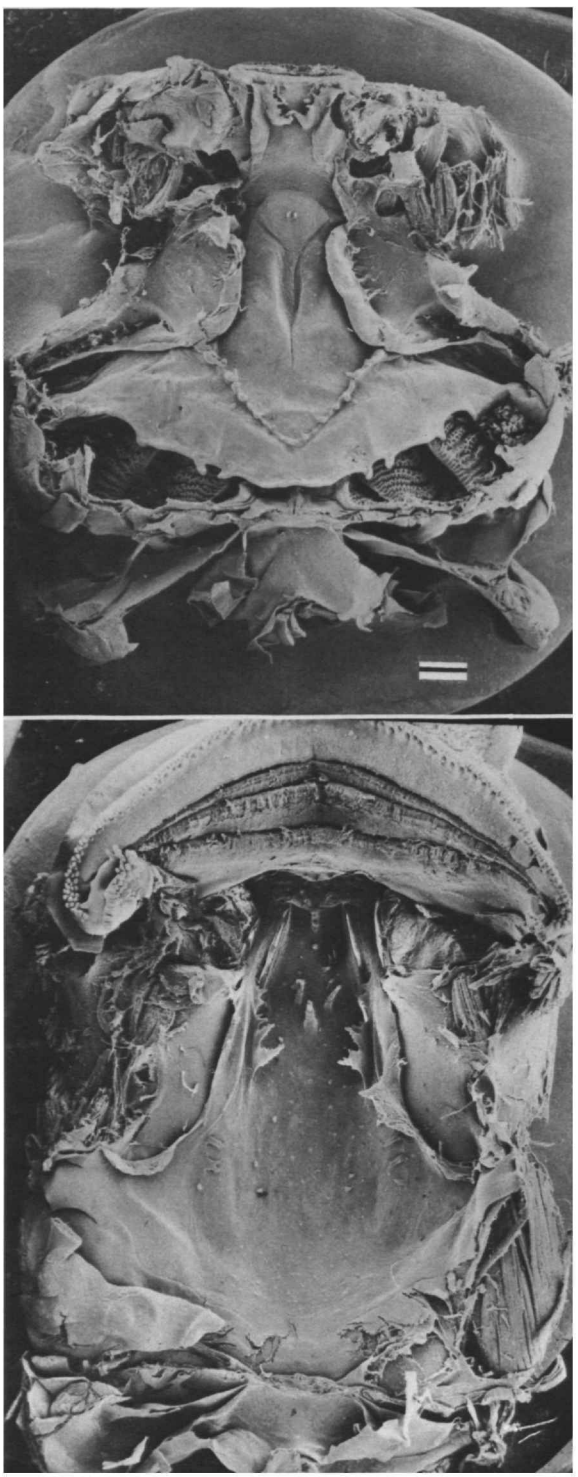


Figure 1.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Heleophryne natalensis;* scale line = 1 mm.

and lateral to BFA and just anterior to middle portion of free velar surface. Very large buccal pockets; oblique conspicuous depressions; apparently perforated. Moderately long, free, velar surface; secretory pits not conspicuous; posterior margin with 3 simple papillae associated with individual filter cavities; papillae absent from medial portion of velar surface; median notch shallow. Secretory pits few and limited to posterior velar margin.

Pharyngeal Cavity: Branchial baskets small, shallow, 25% wider than long; not large for tadpole of this size, but disproportionately large in relation to entire bucco-pharyngeal floor area. Filter cavities narrow, shallow; oriented at 45° from the midline; 3rd filter cavity particularly small and nearly fully capped by 3rd filter plate; 2nd filter plate with straight dorsal margin; 3rd filter plate with upwardly arched dorsal margin; filter plates approximately as long as tall; 3rd filter plate covering about 50% of 3rd filter cavity; cb 1 with 8 filter rows, cb 2 with 8, cb 3 with 8, cb 4 with 7. Filter mesh of extremely low density; numerous secondary folds, tertiary folds rare and short. Filter rows rarely abutting; filter canals large, 20%–40% canopied by filter ruffles. Branchial food traps shallow; no secretory ridges. Apices of secretory cells erupting in random fashion as in *Ascaphus* and *Bombina* (Figure 57*a*). Glottis 50% exposed; small; lips thin; laryngeal disc broad but shallow. Esophageal region very narrow.

Dorsal Aspect.—*Buccal Cavity:* Like floor, roof flask-shaped; elongated and very narrow anteriorly, very broad posteriorly. Nares far forward; median ridge 30% of distance from upper beak to esophagus. Approximately 7 small pustulations in a Y-shaped pattern (arms anterior) in center of prenarial arena; stem of "Y" extending back into space between nares. Nares extremely long; almost parallel; internarial distance large; both anterior and posterior narial walls lacking papillae and pustulations; posterior narial wall 6 times as long as tall. Because of nearly longitudinal orientation of nares, postnarial arena not defined anteriorly. A single, medial, conical papilla with roughened anterior surface just posterior to posterior end of nares, apparently the homologue of median ridge in other tadpoles. A slightly smaller, similarly shaped papilla (homologue of postnarial papilla in other tadpoles?) lying anterolateral to medial ("median ridge") papilla on each side. Two still smaller papillae lying anterior to these "postnarial papillae." A few yet smaller pustulations and papillae scattered between internal nares and prenarial median ridge. Instead of distinct lateral-ridge papillae, 2 parallel long, thin flap-like ridges on each side extending from posterolateral 1/3 of internal nares to a distance as far back as the palatoquadrate-ceratohyal articulation; these ridges with extremely jagged, papillate posterior margin. BRA undelineated; BRA papillae absent; 2–4 small lateral-roof papillae in long rows on each side. Glandular zone with distinct anterior margin except on the midline; no secretory pits; relatively short zone, <10% length of buccal roof; barely continuous on midline; no marginal papillation.

Pharyngeal Cavity: Three pressure cushions per side; most of medial cushion not present in specimen; middle and lateral cushions distinct, small ovals of subequal size. Ciliary groove destroyed in dissection.

South American Leptodactyloids

Adenomera marmorata Fitzinger

Figure 2

Nomenclatural Note.—Fitzinger's otherwise unpublished description of *A. marmorata* was published by Steindachner (1867) so that the proper author indication is *A. marmorata* Fitzinger in Steindachner.

Material.—USNM Field 4497 (one specimen dissected, stage 36, SVL 5.6 mm). Collected from a foam nest under moss on a roadcut at Boracéia, São Paulo, Brazil, 13 December 1976, by W.R. Heyer.

Reference.—The larva is similar to that of *A. hylaedactyla* (Heyer and Silverstone, 1969) in lacking beaks and denticles and in having large yolk stores.

General Remarks.—Lungs moderately large; collapsed, not inflated. Very reduced, short, stubby gill filaments, no particular branching or proliferation.

Ventral Aspect.—*Buccal Cavity:* Floor of mouth oval, about as wide as long. Two pairs of infralabial papillae, 1st pair anterior and medial, simple round knobs; posterior and lateral pair similar in form to first pair but twice as tall with rounded apices (Figure 52*a*). Lingual papillae represented as 2 pustules. BFA not defined; about 20 large round pustulations in middle posterior portion of buccal floor and near medial end of buccal pockets; no other papillae/pustulations on buccal floor. Buccal pockets average size; 5 times as wide as long; oriented 45° from transverse plane; perforations not determinable. Moderate free velar surface, 1/4 length of rest of buccal floor; no visible spicular support; posterior margin gently curved with 3 distinct peaks on each side (excluding median notch), each peak lying above 2nd, 3rd, and 4th filter plates respectively; middle portion with simple, transverse edge; median notch small, sharp slit; no secretory pits.

Pharyngeal Cavity: Branchial baskets transversely oval, 25% wider than long; each basket about 1/5 remaining area of buccal floor; very shallow; 2nd and 3rd filter plates extremely shallow, such that only 1 effective filter cavity. Second filter plate small, 3rd and 4th larger and subequal in size; obliquely oriented from midline; filter plates with simple straight dorsal edges, 5–6 times as wide as tall, not imbricated; cb 1 too short to determine number of filter rows, cb 2 with 5, cb 3 with 5, cb 4 with 4. No filter mesh. Filter rows represented by uneven vermiform ridges, rows narrow, non-abutting; filter canals 2–3 times as wide as filter rows, open. Branchial food traps effectively absent; no secretory ridges. Glottis 60% visible from above, large, occluded; lips thick, not particularly tall; laryngeal disk not conspicuous. Esophageal funnel very broad

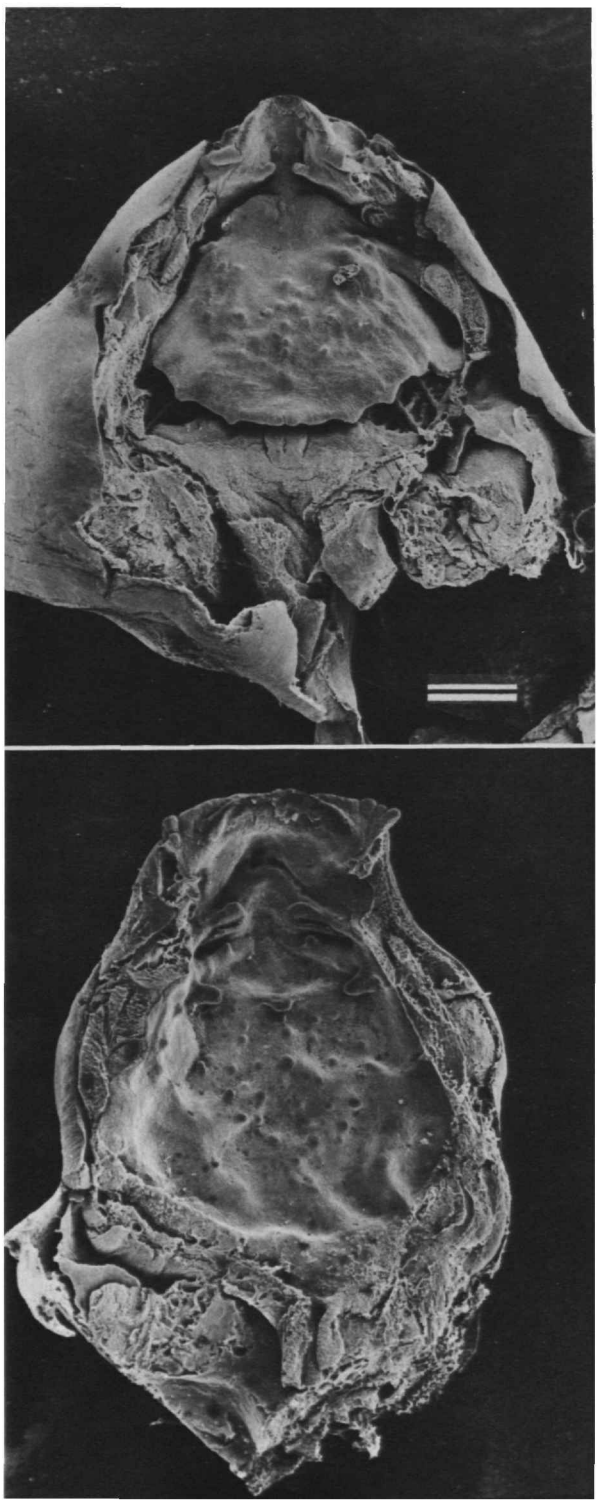


FIGURE 2.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Adenomera marmorata;* scale line = 400 μm.

and large.

DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth an elongated oval, 20% longer than wide; nares about 25% distance from front of mouth to esophagus; median ridge about 40% distance from front of mouth to esophagus. Gently curved, anteriorly directed, V-shaped depression in prenarial arena. Nares of average size; internarial distance about 1/10 length of buccal floor; about 20° orientation from transverse plane; anterior narial wall heavy and thick, particularly medially; no prenarial papillae; posterior narial wall straight, lacking palps or projections. Single, small, blunt, comb-shaped, postnarial papilla on each side located directly posterior to medial third of nares. Median ridge very small trapezoidal flap lacking marginal or surface sculpturing. Lateral-ridge papillae similar in shape to, but slightly larger than, median ridge, blunt, laterally and medially compressed flaps. BRA absent; about 30 pustulations on midportion of buccal roof. No distinct glandular zone; no secretory pits. No dorsal velum.

Pharyngeal Cavity: No pressure cushions. Ciliary groove present, with cilia, but cilia in very narrow, shallow band.

Alsodes monticola Bell

FIGURE 3

MATERIAL.—KU 160574 (two specimens dissected, description based on specimen stage 34, SVL 25.7 mm). Collected from Lago Nahuel Huapi, Neuquén, Argentina.

REFERENCE.—Lavilla, 1983, describes the external morphology.

GENERAL REMARKS.—Only those features that differ from *Alsodes* species (following account) are described. Lungs large, 20% longer than buccal floor, thin, not inflated. Stomach contents largely silt.

VENTRAL ASPECT.—*Buccal Cavity:* BFA bounded by about 50 papillae; papillae smaller and less complex than in *Alsodes* species, only the largest papillae medial to buccal pockets bifurcate; 30–40 simple papillae within arena. Eight prepocket papillae, majority in transverse row, pointing posteriorly over pockets. Buccal pockets smaller than in *Alsodes* species. Spicules in free velar surface slightly smaller than in *Alsodes* species; papillae of posterior margin smaller and not touching large papillae surrounding median notch.

Pharyngeal Cavity: Cb 1 with 6 filter rows, cb 2 with 7, cb 3 with 8, cb 4 with 6. Filter rows closer than in *Alsodes* species, but not abutting. Filter canals fully exposed, largest subequal to width of filter rows. Glottis dorsally oriented, 80% exposed; laryngeal disk not visible.

DORSAL ASPECT.—*Buccal Cavity:* Anterior narial wall simple, lacking projections; posterior narial wall simpler than in *Alsodes* species. Postnarial arena defined by 2 papillae on each side, anteromedial pair larger with terminal rugosities, located midway between medial margin of nares and median ridge, second pair directly posterolateral to 1st pair, smaller and simpler. Lateral-ridge papillae similar in shape but much

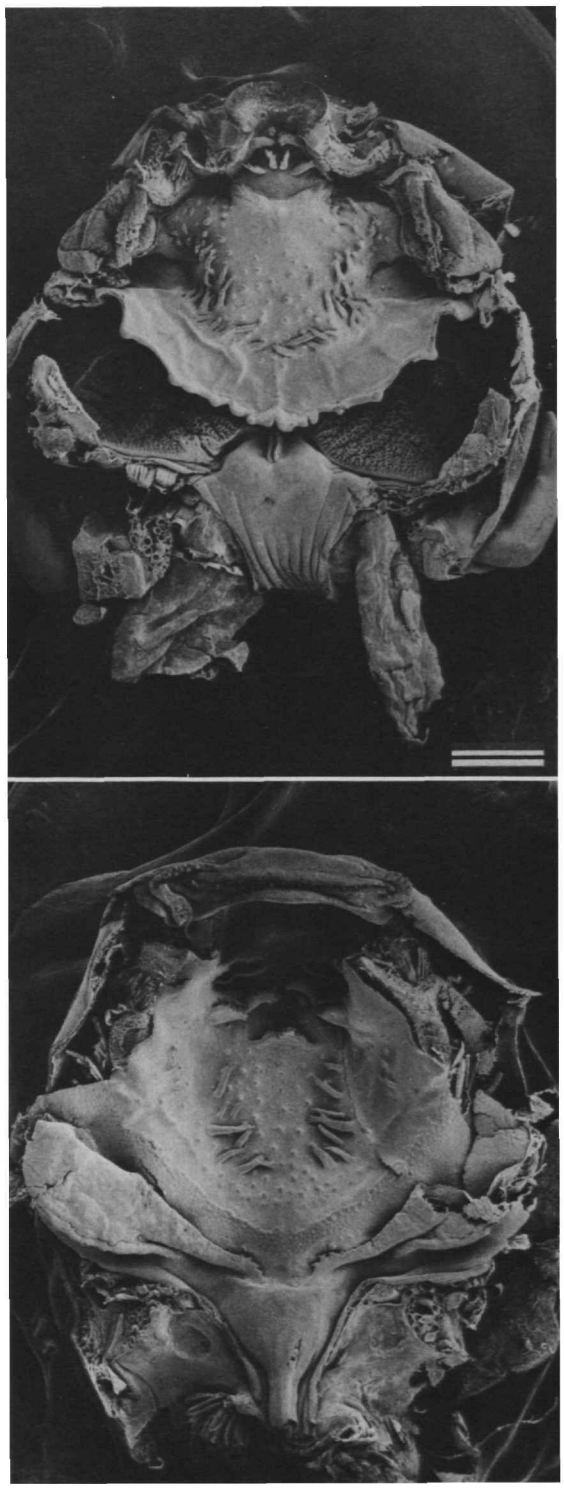


FIGURE 3.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Alsodes monticola;* scale line = 1 mm.

smaller than in *Alsodes* species, in proportion more similar to other tadpoles, 4 papillae per side. BRA defined by 10–15 papillae on each side (Figure 63*a*).

Alsodes species

MATERIAL.—KU 162244 (one specimen dissected, stage 37, SVL 28.6 mm.) Collected from Parque Nacional Nahuelbuta (Cabrerías), 1030 m, Malleco, Chile. Specimen disintegrated prior to illustration.

REFERENCE.—Formas (1981b) indicated that the Kansas series of specimens from Cabrerías represents a new species being described by Alberto Veloso, who is presumably describing the external morphology of the tadpole.

GENERAL REMARKS.—Lungs about 20% longer than buccal floor: inflation indeterminable.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth pentagonal, broad, length and width equal. Four subequal infralabial papillae, 2 anteromedial, 2 posterolateral; simple, cylindrical, with irregular apices, posterior pair bifurcated. Four lingual papillae arranged in slight arc; simple, medial 2 largest. BFA a broad U-shaped; arena bounded by about 40 BFA papillae, 20 per side with the following unusual features—dense cluster of rather large attenuate papillae along posterior limit of BFA; more than usual papillae in anterior portion of BFA; largest BFA papillae (those immediately medial to buccal pockets) laterally compressed, huge pinwheel-like structures with long pointed apices; within arena about 60 cylindrical simple papillae of subequal size. Dense cluster of 8–10 prepocket papillae; attenuate; sizes various. Pustulations within buccal floor largely limited to posterior and lateral margins of BFA or to region directly anterior to buccal pockets; relatively few pustulations on buccal floor proper. Buccal pockets large; about 4 times as wide as long; transversely oriented; not perforated. Free velar surface long, total surface about 1/4 area of remainder of floor; conspicuous spicular support; spicular tips flattened; posterior velar margin gently arching except where interrupted by distinct round marginal papillae, smallest papillae directly over opening of 2nd filter plate, next largest papilla anterior and medial to esophagus, last pair largest, directed medially halfway between 2nd pair and median notch and touching large papillae surrounding median notch; median notch very deep, bounded by single large papilla on each side; very large secretory pits on marginal papillae.

Pharyngeal Cavity: Branchial baskets in shape of right triangles with hypotenuses running anterolaterally to posteromedially; baskets as wide as long; total area of both baskets about 50% buccal floor area; baskets shallow. First filter cavity about 50% of branchial basket in dorsal view with 2nd filter cavity almost as large, 3rd filter cavity exceptionally small, completely obscured from dorsal view by 3rd filter plate and ventral velum; 2nd and 3rd filter plates horizontally oriented, 2nd filter plate with weak medial peak, 3rd filter plate free edge arching medially following posterior and medial edge of

branchial basket, length and width about equal for 2nd and 3rd plates, filter plates extremely imbricate; cb 1 with 8 filter rows, cb 2 with 10, cb 3 with 8, cb 4 with 7. Filter mesh density low; on 2nd and 3rd filter plates some very wide filter rows with quaternary folds, but few rows abutting and many separated by space equalling row itself; filter mesh on 1st and 4th plates narrow and lacking tertiary folds. Filter canals mostly exposed, some wider than filter rows, less than 20 to more than 80% canopied. Branchial food traps large; largely limited to ventral surface of ventral velum; secretory ridges conspicuous, large, straight, uniform (see Figure 59 for *A. monticola*). Glottis vertically oriented, open, fully exposed; small but distinct lips; poorly defined but broad laryngeal disk. Esophageal funnel broad and large.

DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth same shape as floor; nares about 25% distance from front of mouth to esophagus; median ridge about 40% distance from front of mouth to esophagus. Single, simple, posteriorly directed papilla in prenarial arena; no other topographic features in prenarial arena. Nares of average size; large internarial space, about equal to length of one naris; 40° orientation from transverse plane; anterior narial wall shallow, with gently curved anteromedial projection and distinct cylindrical papilla extending from anterior wall directly posterior over middle of nares; posterior narial wall with wavy margin; no distinct narial-valve projection. Postnarial arena very elongate; defined by 5 papillae on each side, papillae with predominantly transverse orientation posteriorly and rostrocaudal orientation anteriorly; largest papillae more posterior, compressed and curved with rugose anterior free edges; all postnarial papillae fairly far posterior such that space between postnarial papillae and nares larger than postnarial arena itself; smooth within arena proper. Median ridge small; triangular; thick with bifurcate apex; some pustulation on most anterior surface. Lateral-ridge papillae gargantuan, about 5 times size of median ridge; laterally compressed flaps with 3 attenuate pointed fingers on one side, 4 on other. BRA wedge-shaped; BRA defined by about 15 papillae on each side; all simple, relatively attenuate papillae, largest lateral. Many small papillae within BRA and few pustulations concentrated more posteriorly in arena. Glandular zone short; large secretory pits of low density except directly in front of esophagus; pits extending onto pressure cushions. Dorsal velum average length but extremely shallow and dorsoventrally compressed; medial gap about as wide as dorsal velum on each side; no marginal papillation.

Pharyngeal Cavity: Single, extremely shallow pressure cushion. Ciliary groove extremely shallow.

Atelognathus patagonicus (Gallardo)

FIGURE 4

MATERIAL.—KU 160469 (one specimen dissected, stage 37, SVL 27.5 mm). Collected from Laguna Blanca, 1275 m, Neuquén, Argentina.

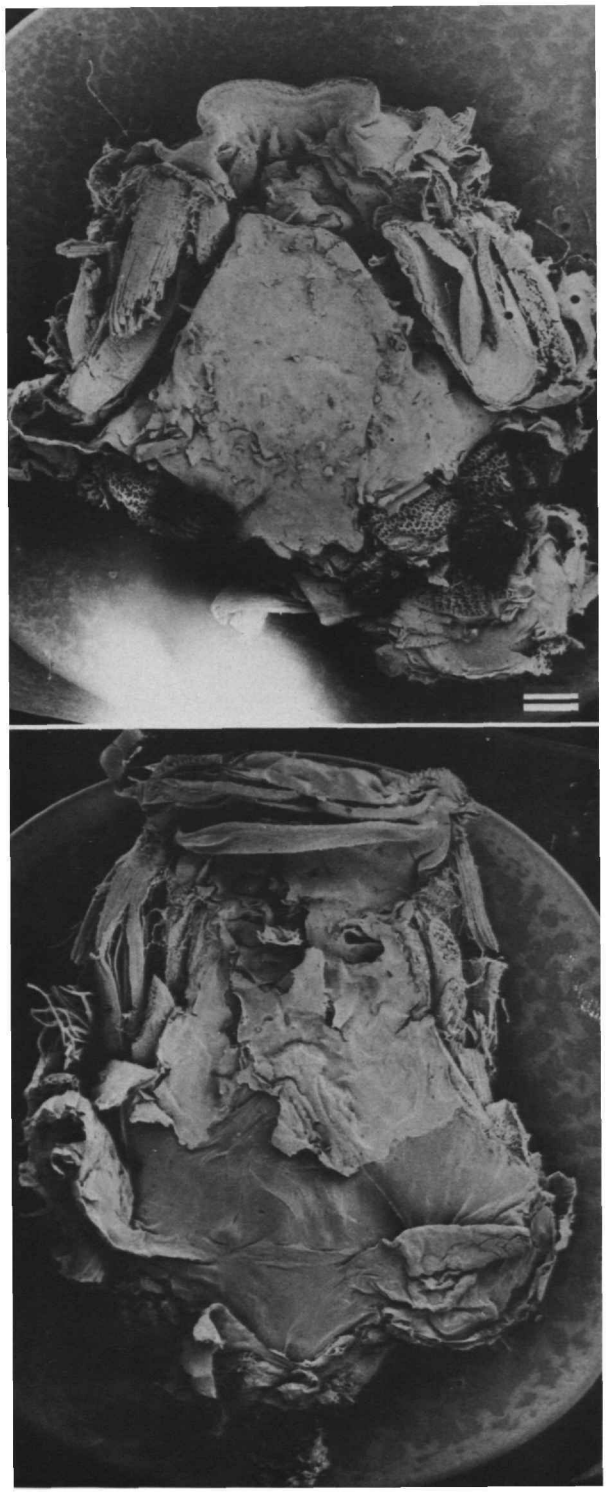


FIGURE 4.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Atelognathus patagonicus;* scale line = 1 mm.

REFERENCE.—Lavilla, 1983, described the external morphology.

GENERAL REMARKS.—This specimen was partially damaged in dissection; only those features that can be discerned are compared and these are stated only if different from those of *Atelognathus reverberii* (following account).

VENTRAL ASPECT.—*Buccal Cavity:* Infralabial papillae subequal in size. About 20 BFA papillae on each side; not bifurcate. Less than 6 prepocket papillae. About 6 papillae in posterior 1/2 of BFA. Cb 1 with at least 6 filter rows, cb 2 with 11 or 12, cb 3 with at least 10, cb 4 with at least 8.

DORSAL ASPECT.—*Buccal Cavity:* Postnarial arena papillae smaller than in *A. reverberii.* Median-ridge base just more than 1/2 height. Both edges of lateral-ridge papillae serrate, lateral-ridge papillae smaller than median ridge.

Atelognathus reverberii (Cei)

FIGURE 5

MATERIAL.—USNM 204798 (one specimen dissected, stage 34, SVL 23.0 mm). Collected from Somuncura Plateau, Laguna Raimunda, Rio Negro, Argentina, 20 December 1967, by J.M. Cei.

REFERENCE.—Cei (1980) described and figured the tadpole (as *Telmatobius reverberii*).

GENERAL REMARKS.—Lungs long and thin, 10% longer than length of buccal floor; not inflated.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth triangular, length about equal width. Four infralabial papillae in transverse line; compressed cones with rugose margins; medial pair 50% size of lateral pair; medial pair pointing dorsally, lateral pair medially; none bifurcate; none abutting on midline. Four lingual papillae in an anteriorly directed arch; all simple, attenuate papillae; anterior medial pair with knobby apices, twice size of lateral pair. BFA an elongate oval bounded by about 25 papillae on each side; BFA papillae sickle-shaped, larger ones with knobby, bifurcate apices. Cluster of at least 6 very small papillae anteromedial to buccal pockets merging with BFA papillae. Few small papillae immediately posteromedial to buccal pockets merging with more posterior BFA papillae; at least 10 simple, attenuate papillae of unequal size in posterior 1/2 of BFA and equal number of pustulations scattered among them. Buccal pockets short, about as wide as long; shallow; obliquely oriented at about 45° from transverse plane; perforated. Free velar surface of average length (Figure 56*a*); thin spicular support; posterior margin gently curved with very distinct marginal cusps just over dorsal free edges of 2nd, 3rd, and 4th filter plates; median notch average size with rounded symmetrical cusps on each side; secretory pits faint, largely limited to peaks on free velar margin.

Pharyngeal Cavity: Branchial baskets as long as wide, irregularly oval; large; each branchial basket more than 70% remaining buccal floor area; very deep; 1st filter cavity about equal in size to 2nd; 3rd 50% smaller (Figure 56*a*). Second

FIGURE 5.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Atelognathus reverberii;* scale line = 1 mm.

filter plate with slightly bowed-down edge, 3rd filter plate dorsal edge arching upward slightly; 2nd filter plate 2–3 times as long as high, 3rd filter plate about as long as high; moderately imbricate with 3rd filter plate covering about 50% of 3rd filter cavity, tipped about 45° from vertical; cb 1 with 10 filter rows, cb 2 with 12, cb 3 with 10, cb 4 with 8. Filter mesh moderate to dense; many quaternary and higher order folds (Figure 56*a*). Filter rows of varying width, more posterior and lateral rows in 1st and 2nd filter cavities exceptionally wide; slightly separated. Filter canals less than 1/3 width of rows; 80%–100% canopied. Branchial food traps with distinct secretory ridges. Glottis open; 50% visible; small; narrow lips; laryngeal disk not well defined. Esophageal funnel of average dimensions.

DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth anteriorly truncated diamond-shape, length about equal to width; nares about 25% distance from front of mouth to esophagus; median ridge about 40% distance from front of mouth to esophagus. Prenarial arena with faint pustulations scattered in a relatively transverse arrangement posteriorly. Nares of small to average size; internarial distance large, about 70% or more naris length; transversely oriented; anterior narial wall globose medially, otherwise prenarial papillae absent; posterior wall thin, lacking distinct narial-valve projection. Two postnarial arena papillae on each side in a relatively transverse row; larger and more medial pair very elongate cones with roughened anterior surfaces and pointed apices almost abutting anteromedially; 2nd pair much smaller, simple, conical. Median ridge an exceptionally tall trapezoid with the base just less than 1/2 height; free edge with pustulations; 2 pustulations in sagittal plane of posterior surface. Lateral-ridge papillae laterally compressed with smooth posterior edges and serrate anterior edges, each papilla terminating in a point; as tall as median ridge, but base not as broad. BRA egg-shaped; defined by about 10 papillae on each side; all BRA papillae simple, straight or slightly curved conical structures with pointed apices. Couple of very small papillae between median ridge and postnarial papillae; 2 or 3 papillae isolated in most lateral portion of buccal roof; about 20 small papillae and pustulations randomly scattered in BRA. Glandular zone long, of medium-sized, densely packed, secretory pits; front edge with simple V-shape. Dorsal velum of short to average length; broadly interrupted on midline; very smooth free edge.

Pharyngeal Cavity: Pressure cushions very faint, 2 per side. Ciliary groove shallow, average width.

Batrachyla taeniata (Girard)

FIGURE 6

MATERIAL.—KU 162052 (one specimen dissected, stage 34, SVL 13.7 mm). Collected from Parque Nacional Nahuelbuta, Malleco, Chile.

REFERENCE.—Cei (1980, fig. 109e,f) described and figured the tadpole.

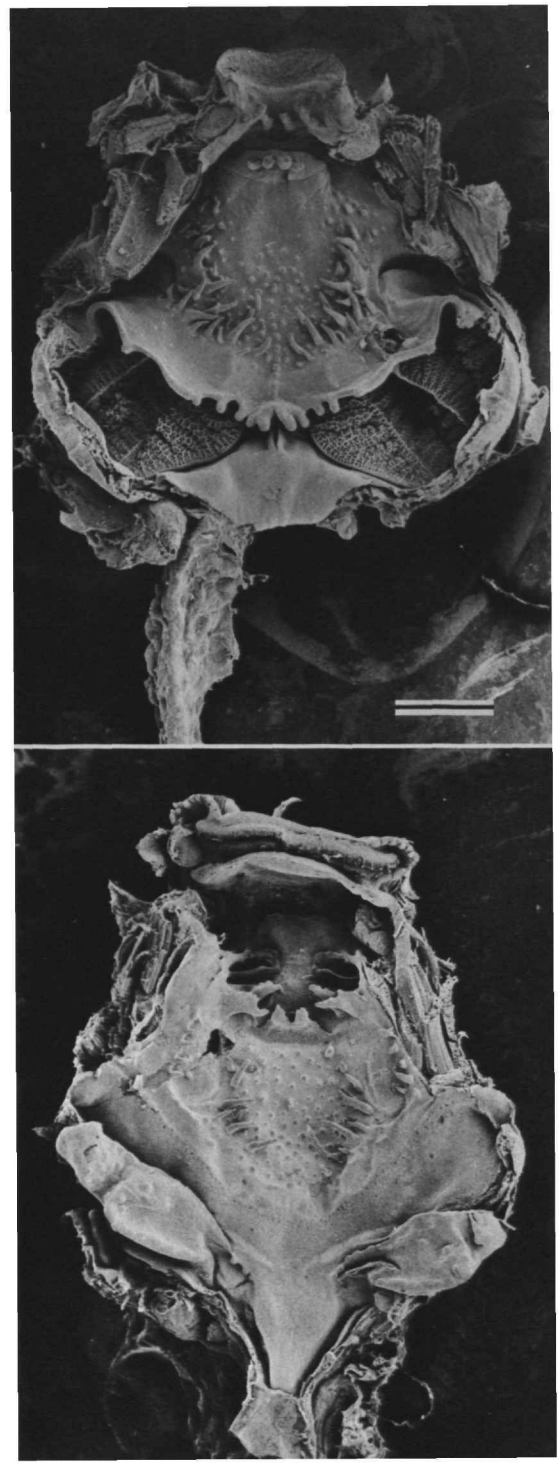


FIGURE 6.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Batrachyla taeniata;* scale line = 1 mm.

GENERAL REMARKS.—Well-developed gill filaments. Lungs large, thin, 10% longer than buccal floor.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth triangular, of about equal length and width. Four infralabial papillae in a transverse row; 2 near midline directed dorsally, 2 more lateral directed anteromedially; papillae about equal in size, slightly compressed anteroposteriorly, with roughened anterior surfaces. Four quite tall and distinct lingual papillae in a transverse row, medial pair slightly larger than lateral pair, larger ones with terminal rugosities. BFA an elongate oval defined by 20–25 papillae on each side; largest BFA papillae medial to buccal pockets arising as a pair from a common base, rest of BFA papillae simple. About 6 small prepocket papillae positioned anteromedial to buccal pockets. Many pustules on posterior 1/2 of BFA. Buccal pockets of average size, twice as wide as long; oriented transversely; perforated. Free velar surface of average length; total area about 1/3 rest of buccal floor; velum supported by long spicules; posterior velar margin semicircular with 5 round marginal papillae not counting papillae surrounding median notch, most lateral papilla on each side over edge of 2nd filter plate, rest of papillae clustered near median notch; median notch distinct, deep, surrounded by rounded papillae; broad zone of secretory pits along entire free edge and completely covering marginal papillae.

Pharyngeal Cavity: Branchial baskets oval, almost round; fairly large, each branchial basket about 1/2 remaining buccal floor area; 60% as deep as wide. Only 2 filter cavities per side, subequal in size—dorsal margin (top) of 3rd filter plate abutting directly with ventral margin (bottom) of 4th filter plate, therefore no filter rows on medial side of 3rd filter plate, nor any 3rd filter cavity; branchial baskets obliquely oriented from midline; dorsal edges of 2nd and 3rd filter plates slightly curved downward, dorsal edge of 4th filter plate arching acutely upward towards glottis; filter plates twice as long as high, no imbrication; cb 1 with 8 filter rows, cb 2 with 11, cb 3 with 11, cb 4 with 9. Filter mesh dense; intricately folded with tertiary and higher order folds. Filter rows of average width, 80%–100% abutting; filter canals narrower than filter rows, 80%–100% canopied. Well-developed branchial food traps, extending 1/3 distance into front of filter cavities; secretory ridges numerous, narrow, occasionally discontinuous, of uniform width. Glottis 100% visible from above; open; lips narrow; laryngeal disk not visible. Esophageal funnel relatively narrow.

DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth elongate, trapezoid-shaped; nares 20% distance from front of mouth to esophagus; median ridge 40% distance from front of mouth to esophagus. Prenarial arena with transversely oriented shelf, shelf with rounded lateral edges in mid-arena. Nares large; internarial distance just less than width of naris; nares oriented transversely; anterior narial wall not thickened, but with jagged free edge; no prenarial papillae; posterior narial wall a thin flap with a weak narial-valve projection. Postnarial arena a triangular-shaped zone bounded by 3 papillae along anterior and lateral edges and by median ridge posteriorly; postnarial papillae conical with flattened and roughened anterior edges, largest papilla the most posterolateral on each side. Median ridge a moderately large, triangular flap with a deeply forked apex. Lateral-ridge papillae in a line with postnarial papillae and directly lateral to median ridge; papillae small, laterally compressed flaps with distinct apex and regular anterior free edges. BRA a narrow elongate oval defined by 6–8 relatively uniform, simple, attenuate papillae on each side. An even, dense field of pustulations within BRA and a small papilla in middle of arena; five papillae in an anteromedial to posterolateral row on lateral edge of buccal roof on each side. Glandular zone with distinct and relatively smooth, V-shaped, anterior edge with apex directed posteriorly; near midline, zone about 1/8 length of buccal roof and twice that laterally; large and dense secretory pits along anterior edge of glandular zone. Dorsal velum broadly interrupted medially, with faint papillae just along medial terminus; otherwise velum with smooth, straight edge.

Pharyngeal Cavity: Two nearly oval-shaped pressure cushions per side; more anterior and lateral pressure cushion smaller, more posterior and lateral pressure cushion 2–3 times as large. Ciliary groove of average dimensions.

Caudiverbera caudiverbera (Linnaeus)

FIGURE 7

MATERIAL.—KU 162056 (one specimen dissected, stage 39, SVL 45.0 mm). Collected from 19 km S. Parral (Río Perquilauquen), Linares, Chile.

REFERENCE.—Cei (1962) described and figured the larva (as *Calyptocephalella gayi*).

GENERAL REMARKS.—Internal anatomy not well preserved, precluding evaluation of certain features. Keratinized mouthparts fell off during specimen examination. Fresh water clam shell in gill filaments. Lungs moderate-sized, about 30% longer than length of buccal floor; inflated.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth triangular with rounded margins, wide, 30% wider than long. Four infralabial papillae; 1 pair anterior and medial, 2nd pair posterior and lateral, papillae equidistant; papillae small but tall, cylindrical with irregular margins, blunt to finely pointed. Four simple lingual papillae in straight transverse row. BFA an elongate oval, open anteriorly; BFA defined by 10–15 papillae on each side; BFA papillae small, thin, conical; larger papillae with some curvature and rugosities, not bifurcate. No prepocket papillae. Dense field of pustulations in posterior 1/3 of BFA and anterior to buccal pockets. Buccal pockets small, 4 times as wide as long; oriented about 30° from transverse plane; perforated. Free velar surface of typical tadpole proportions, total area about 30% rest of buccal floor; conspicuous spicular support; spicules relatively thin; posterior velar margin gently curved except medially where disrupted by irregular papillae; small irregular peaks over filter cavities,

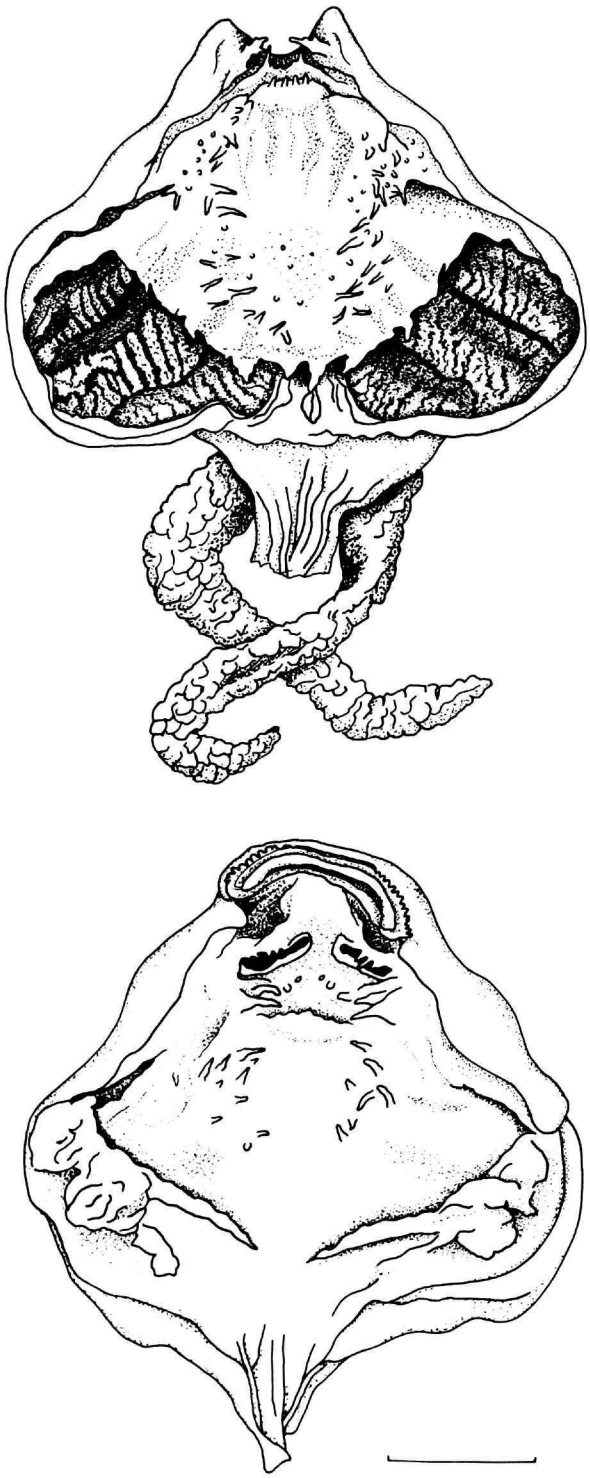


FIGURE 7.—Camera lucida drawings of floor (above) and roof (below) of oral cavity of *Caudiverbera caudiverbera;* scale line = 5 mm.

3 projections per side including those bounding median notch; median notch deep, surrounded by 2 conical projections; secretory pits present, pattern indeterminate due to poor preservation.

Pharyngeal Cavity: Branchial baskets about as long as wide, round, large, each about 70% buccal area, almost as deep as wide. Filter cavities subequal in size. Second dorsal plate with straight dorsal margin, 3rd dorsal plate with upwardly arched dorsal margin, 2nd plate twice as long as tall, 3rd plate 30% longer than tall; slightly imbricated; cb 1 with 12 filter rows, cb 2 with 12, cb 3 with 12, cb 4 with 11. Filter mesh relatively dense; filter rows not abutting; rows complexly folded, some very wide; filter canals 2/3 width of rows, 50%–80% canopied. Branchial food traps present, details indeterminable due to poor preservation; secretory ridges wide and ill-defined. Glottis small but open; fully exposed; lips indistinct; vaguely definable laryngeal disk. Esophageal funnel relatively narrow.

DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth triangular, slightly wider than long; nares about 20% distance from front of mouth to esophagus; median ridge about 30% distance from front of mouth to esophagus. Small, vague, anteriorly directed V-shaped swelling descending ventrally from prenarial arena. Nares large; internarial distance relatively short, about 60% length of naris; 45° orientation from transverse plane; anterior narial wall thin with series of 3 or 4 small, simple, posteriorly directed papillae arising from midportion of anterior wall; posterior narial wall with slight narial-valve projection. Postnarial arena poorly defined triangular area bounded by 3 papillae on one side, 2 on other and a few pustulations; small and simple postnarial papillae located 1/2 distance between median ridge and nares. Median ridge with arched free edge; very wide, about 3 times as wide as tall; very faint sculpturing on free ventral edge; anterior surface relatively smooth. Lateral-ridge papillae conical, slightly compressed laterally with pointed apices each 1/3 size of median ridge. BRA vague, poorly defined U; about 6–10 BRA papillae on each side, papillae all small, simple, irregular. Few pustulations lateral and posterior to BRA. Glandular zone indeterminate due to poor preservation. Dorsal velum of average length; average-sized midline gap; margin lacking papillae.

Pharyngeal Cavity: Two distinct, round, subequal pressure cushions. Ciliary groove very broad.

Ceratophrys aurita (Raddi)

FIGURE 8

MATERIAL.—USNM 241298 (one specimen dissected, stage 31, SVL 16.3 mm). Collected from a temporary pond at Fazenda do Veado, Serra da Bocaina, São Paulo, Brazil, 3 January 1977, by W.R. Heyer.

REFERENCE.—The external morphology of this tadpole has not been described previously. Briefly: spiracle sinistral; anus median, separate from tail fin, lying to left or right of fin;

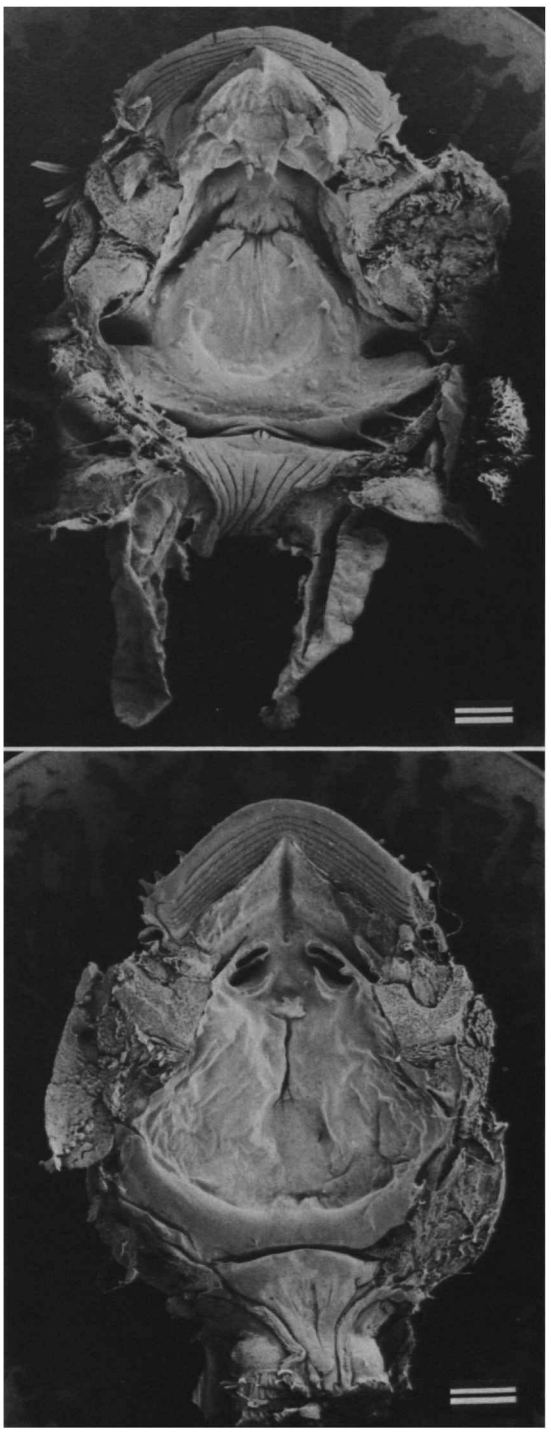


FIGURE 8.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Ceratophrys aurita;* scale lines = 1 mm.

mouthparts anteriorly directed; oral disk not emarginate, single row of marginal papillae interrupted anteriorly; denticle formula 7–8 (5–8)/8–9 (1–6); overall habitus stout, that of pond dwelling carnivorous tadpole (Orton, 1953).

GENERAL REMARKS.—Extensive, luxuriant gill filaments. Lungs of average size, almost equal in length to maximum width of mouth.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth bell-shaped, narrow anteriorly, 10% longer than wide. Three flattened infralabial papillae; 1 papilla transversely oriented on midline with a V cut into its free edge; other 2 papillae anterolateral to this median papilla, lateral papillae obliquely oriented triangular flaps with jagged anterior edges. Two small, simple, lingual papillae. BFA oval; defined by 5 evenly spaced, small, conical papillae with constricted apices, papillae of similar size. Three or four tiny prepocket papules. No papillae or pustulations elsewhere on buccal floor. Buccal pockets small, shallow, horizontally oriented, not perforated. Free velar surface short, largely limited to area over 1st filter cavity; no spicular support; posterior margin smooth, lacking sculpturing/papillation; medial 2/3 of ventral velum margin thickened and curved dorsally; median notch extremely broad, 1/4–1/5 width of entire velar surface; no secretory pits.

Pharyngeal Cavity: Branchial baskets extremely small, comma-shaped, only covered by ventral velum laterally, 30% wider than long; each branchial basket approximately 1/8–1/10 remaining area of buccal floor in dorsal view, no depth to medial 2/3 of branchial baskets. First filter cavity 6 times as wide as deep; straight dorsal edge on filter plates; cb 1 with 3 filter rows on one side, cb 2 with 5, cb 3 with 3, cb 4 with 3. Filter folds not developed beyond irregular ridge; some secondary but no tertiary folds; no filter rows abutting; filter canals fully exposed, canals equal to or wider than filter rows; gill filaments visible dorsally, coming up through gill slits in 2nd and 3rd gill cavities. No branchial food traps. Glottis fully exposed; small but distinct; antero-posteriorly directed; open, with small but distinct lips on a very wide but ill-defined laryngeal disc. Esophageal funnel of average profile, but esophagus very wide in diameter.

DORSAL ASPECT.—*Buccal Cavity:* Nares far anterior; median ridge about 30% distance from front of mouth to esophagus. Prenarial arena small, bare. Nares large, oblique; anterior wall of average height, slightly thickened both anteromedially and posterolaterally, with some marginal sculpturing, but no distinct papillae; posterior narial wall as tall as wide with a deep sulcus posterior to it; posterior wall thin, with small medial projection on each side. Single postnarial papilla about halfway between midline and posterior limit of nares, conical, slightly flattened in antero-posterior plane with 1 major and 1 minor cusp; apices directed anteriorly. Median ridge small, but tall, crescent with a jagged free margin; largely smooth anterior surface. No lateral-ridge papillae. No BRA papillae. Scattered pustulations medially on buccal roof; pustulations and papillae absent elsewhere on buccal roof. No

glandular zone. Dorsal velum effectively absent, definitely absent on midline.

Pharyngeal Cavity: Two elongate but very shallow pressure cushions associated with 1st and 2nd filter cavities. Ciliary groove very shallow and narrow, cilia present.

Crossodactylodes species

FIGURE 9

MATERIAL.—USNM 241308 (one specimen dissected, stage 30, SVL 7.8 mm). Collected from an arboreal bromeliad at Santa Tereza, Espírito Santo, Brazil, 9 October 1980, by E. Izecksohn and O.L. Peixoto.

REFERENCES.—Peixoto (1981) described and figured the external morphology and provided habitat data for this species as *C. pintoi*. Later, Peixoto (1983) determined that the description pertains to either *C. bokermanni* or *izecksohni*, not *pintoi*.

GENERAL REMARKS.—Lungs short, unequal in size, smallest about 2/3 length of buccal floor, largest about equal in length to buccal floor; expanded, sac-like, lacking obvious septation except at caudal end.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth triangular, about 20% wider than long. Three small, conical, short infralabial papillae in a transverse row on each side far anterior; 1 large, hand-like papilla posterior to smaller papillae on each side with long, wrist-like base and short, stubby, finger-like terminal bifurcations, "fingers" touching on midline; at least 2 more papillae anterior to base of larger, more posterior pair. Four tall, thin, lingual papillae arranged in an anteriorly directed arc with medial pair larger than lateral pair. BFA V-shaped; 10 BFA papillae per side, all relatively simple, tall, thin, attenuate, slightly curved, medially directed, some shorter, but mostly uniform in size, not bifurcate. No prepocket papillae. Extensive pustulation within BRA and directly lateral to it both anteriorly and posteriorly. Buccal pockets shallow, less than 50% wider than long, transversely oriented, perforated(?). Free velar surface short; no spicular support; posterior margin recurved; no marginal peaks; weak median notch; scattered, small, secretory pits.

Pharyngeal Cavity: Branchial baskets slightly wider than long, transversely oval; each branchial basket about 50% remaining area of buccal floor; as deep as long; 2nd and 3rd filter cavities forming single common cavity subequal in size to other filter cavity. Dorsal edge of abutting 2nd and 3rd filter plates bowed down sharply; 2nd filter plate 3 times as long as tall, 3rd filter plate 5–6 times as long as tall; 2nd plate tipped 45°, lateral portion of 3rd plate horizontal, medial portion vertical; cb 1 with at least 11 filter rows, cb 2 with 14, cb 3 with 9, cb 4 with 8. Filter mesh slight; secondary folds barely developed, no higher order folds. Filter rows very narrow, filter canals wider than rows; no filter rows abutting, all filter canals exposed. Secretory cells oriented longitudinally but not organized into distinct secretory ridges. Glottis open; 50%

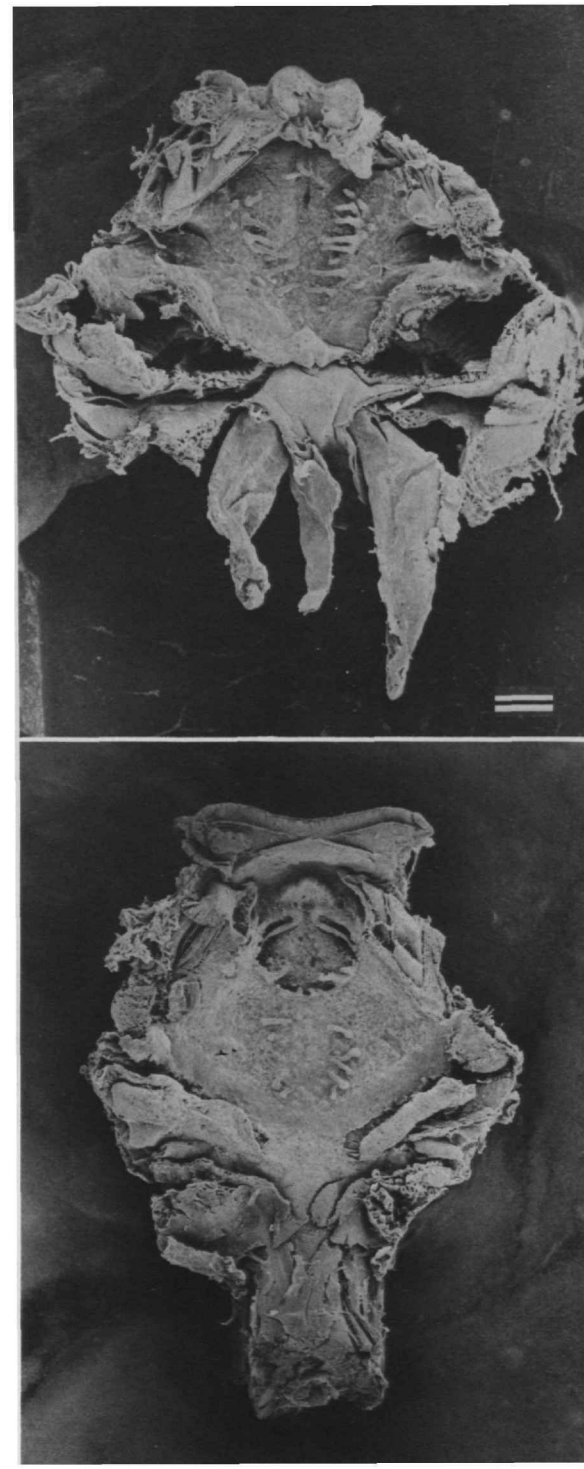


FIGURE 9.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Crossodactylodes* species; scale line = 400 μm.

covered by ventral velum; very slight lips on broad laryngeal disk. Esophageal funnel of average proportions.

DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth diamond-shaped, 20% wider than long; nares about 25% distance from front of mouth to esophagus; median ridge 40%–50% distance from front of mouth to esophagus. Anteriorly bowed, shallow ridge with irregular ventral margin descending from prenarial arena. Nares very large, internarial distance very small, less than 1/5 length of naris; 45°–50° orientation from transverse plane; anterior and posterior narial walls unusual in lacking projections. Postnarial arena an equilateral triangle bounded by row of 2 or 3 very small, postnarial arena papillae plus row of pustulations in line with them anteriorly; half dozen pustulations scattered about postnarial arena. Median ridge very shallow and wide, extending on each side laterally to base of lateral-ridge papillae; 4 times as wide as tall; with sculptured free edge and 2 particularly distinct marginal papillae near midline. Two lateral-ridge papillae per side in direct transverse line with median ridge; medial papilla on each side larger, with irregular rugose surface, not bifurcate; lateral papilla on each side simple, attenuate cone. BRA elongate, U-shaped; bounded by 4 simple, attenuate papillae on one side, 5 on other; BRA papillae relatively uniform in size, most posterior smallest, not bifurcate. Pustulations scattered rather evenly within entire BRA; few pustulations extending just lateral to posterior end of BRA. Glandular zone ill-defined with scattered secretory pits. Dorsal velum of average length; broadly interrupted on midline; no marginal papillation.

Pharyngeal Cavity: Two pressure cushions per side, lateral larger and more oval, medial smaller and poorly defined. Ciliary groove broad and shallow.

Crossodactylus gaudichaudii Duméril and Bibron

FIGURE 10

MATERIAL.—USNM 241310 (one specimen dissected, stage 38, SVL 17.7 mm). Collected from São Gonçalo, Paraty, Rio de Janeiro, Brazil, 7 April 1979, by E. Izecksohn, C.A.G. da Cruz, and O.L. Peixoto.

REFERENCE.—The external morphology has apparently not been described or figured. The larva is externally very similar to that of *C. dispar* (see "Reference" for *C. schmidti*).

GENERAL REMARKS.—Entrance to mouth narrow; jaws strongly serrate, overlapping. Lungs of unequal size; longer one about equal in length to buccal floor, shorter one about 70% length of buccal floor; not inflated.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth triangular, length about equal to width. Four infralabial papillae; 2 anterolateral papillae elaborate branching structures with many long, rugose, attenuate fingers; fingers abutting on midline and pointing anteriorly out of oral cavity; more posterior pair simple, straight blunt papillae lacking rugosity and bifurcations, pointing dorsally and abutting on midline (Figure 52*b*).

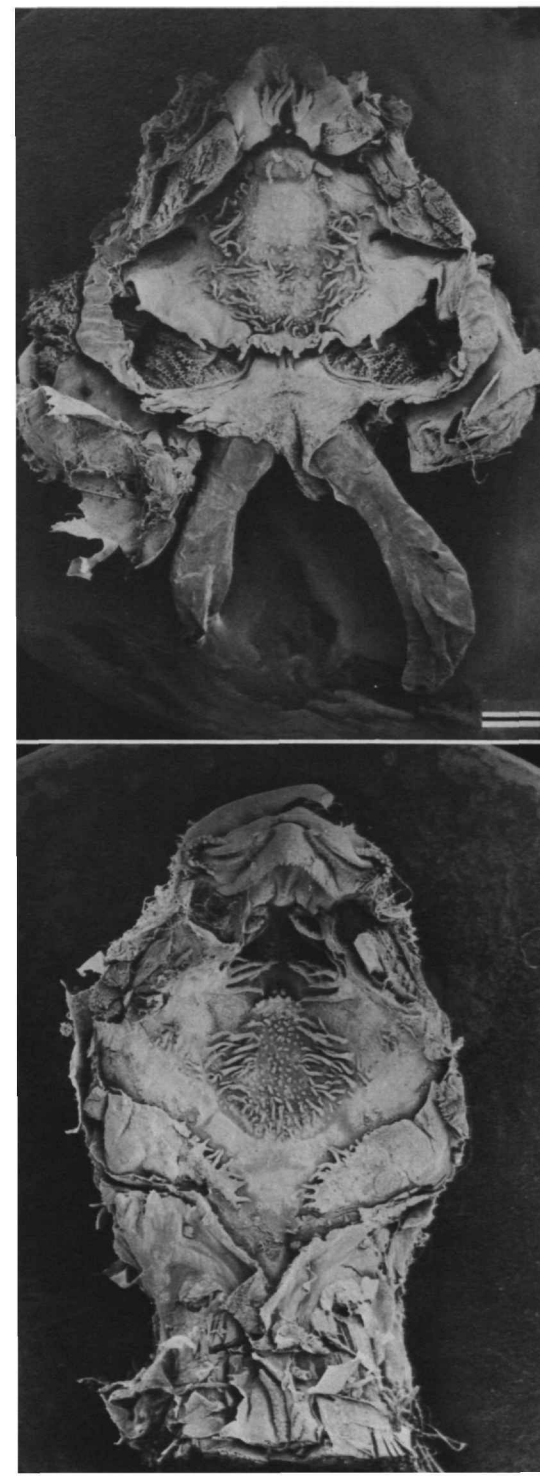


FIGURE 10.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Crossodactylus gaudichaudii;* scale line = 1 mm.

Four lingual papillae arranged in forward-arching row; subequal, bifurcate, attenuate, with knobby apices. BFA an elongate oval defined by 30–40 tall papillae on each side extending forward to tongue anlage; BFA papillae mostly having attenuate, pointed apices, largest 2 papillae arising from common base directly medial to buccal pockets, not bifurcated; very dense posteriorly. Cluster of about 6 pustulations or papillae directly anterior to buccal pockets. At least a dozen papillae in medial portion of BFA continuous with rows of BFA papillae; cluster of 5 or 6 papillae posteromedial to buccal pockets. Buccal pockets relatively small, 3 times as wide as long; transversely oriented; perforated. Free velar surface long; conspicuous spicular support; posterior margin semicircular with small peak far laterally over edge of 2nd filter plate directed posterolaterally, larger peak over free edge of 3rd filter plate directed posteromedially, remaining midportion very extensively but irregularly sculptured with many knobby processes; median notch broad but shallow; secretory pits conspicuous on marginal papillae of ventral velum but between papillae limited to thin posterior band.

Pharyngeal Cavity: Branchial baskets triangular in shape, about as long as wide; each branchial basket equal to slightly more than 50% of remaining buccal floor area; branchial baskets very shallow, deepest part located laterally, depth 1/5 width of branchial basket; 2nd filter cavity largest; 1st 50% size of 2nd, 3rd barely visible under free edge of ventral velum and 3rd filter plate about 1/10 size of 2nd. Second filter plate with straight dorsal edge; edge of 3rd filter plate arching up gently, but largely hidden by ventral velum; 2nd and 3rd filter plates about twice as long as tall, tipped more than 45° from vertical; cb 1 with 9 filter rows, cb 2 with 10, cb 3 with 8, cb 4 with 5. Filter mesh not particularly dense; abundant secondary and some tertiary folding, little higher order folding. Filter rows not abutting, very uneven in size, of particularly low density medially. Filter canals ranging from less than 60% width of filter rows and about 80% canopied to twice width of filter rows and 80%–90% exposed. Branchial food traps shallow; well-developed secretory ridges in straight, even rows. Glottis open; 60% covered by ventral velum; small; lips narrow, thin; laryngeal disk broad but faintly defined. Esophageal funnel very broad, average size.

Dorsal Aspect.—*Buccal Cavity:* Roof of mouth diamond-shaped, 15%–20% longer than wide; nares about 25% distance from front of mouth to esophagus; median ridge about 40% distance from front of mouth to esophagus. Prenarial arena with some faint longitudinal folding, but no distinct depressions or projections. Nares long; internarial distance short, about 30% length of naris; nares oriented 45° from midline; anterior wall simple although a tall, anteriorly pointing, curved, rugose papilla arising just ventral to midpoint of narial wall on each side; posterior narial wall curving gently downward, but no distinct narial-valve projection. Postnarial arena defined by dense row of 10–15 papillae on each side beginning as simple structures anteriorly and increasing in size posteriorly, rows running longitudinally to point about 1/2 distance between nares and median ridge, then papillar rows turning sharply lateral extending as far as base of lateral-ridge papillae; larger postnarial papillae with serrated anterior margins. Median ridge of average size; very serrated free edge; rugose surfaces. Lateral-ridge papillae elaborate laterally compressed flaps with long, finger-like projections pointing medially; 4 per side; some with terminal, attenuate bifurcations. Field of pustulations just lateral to anterior clusters of postnarial papillae; 2 small, blunt, subequal papillae in transverse row in front of median ridge in postnarial arena. BRA elongate rectangle defined by 30–40 attenuate, tall papillae of varying size on each side; a particularly dense cluster of small papillae defining posterior limit of BRA; many BRA papillae with twisted apices and rugosities, only 1 or 2 bifurcate. Continuous dense field of pustulations and small, conical, blunt papillae within BRA; at least half dozen attenuate papillae on lateral limit of buccal roof on each side, continuous as band posterolaterally merging with most posterior BRA papillae. Glandular zone of average length; well defined along anterior edge; medially with large secretory pits of unusually low density, continuing onto ventral surface of dorsal velum. Dorsal velum of average length; broadly interrupted medially; medial margins curving posteriorly towards esophagus; middle half of dorsal velum on each side with dorsoventrally flattened papillate fringe.

Pharyngeal Cavity: Pair of weakly defined pressure cushions, more lateral about 3 times size of more medial. Ciliary groove very broad and very shallow.

Crossodactylus schmidti Gallardo

Figure 11

Material.—USNM 253671 (one specimen dissected, stage 33, SVL 20.9 mm). Collected from a stream at Hotel El Tirol, 19.5 km by road NNE Encarnación, Itapuá, Paraguay, 14 November 1976, by Mercedes S. Foster.

Reference.—Cei (1980) described the tadpole and stated that it was very similar to the species he illustrated, *C. dispar*.

General Remarks.—Only those features that differ from *C. gaudichaudii* are described. Lungs smaller than in *C. gaudichaudii*.

Ventral Aspect.—*Buccal Cavity:* Smaller, more medial pair of infralabial papillae with rugosities. Medial pair of lingual papillae about twice as large as lateral pair, simpler than in *C. gaudichaudii*, lacking knobby apices. BFA with 25–35 papillae on each side. About 3 or 4 pustulations/papillae directly anterior to buccal pockets. Midportion of posterior margin of free velar surface jagged, with longer peaks than in *C. gaudichaudii;* median notch very deep; posterior velar margin on each side of median notch overlapping.

Pharyngeal Cavity: Second filter plate with slightly curved-downward, dorsal edge; 2nd and 3rd filter plates not as horizontal as in *C. gaudichaudii;* cb 1 with 10 filter rows, cb 2 with 10, cb 3 with 9, cb 4 with 6. Filter mesh denser, abundant tertiary folding. Some filter rows abutting ventrally, rows of more or less even size. Filter canals more canopied

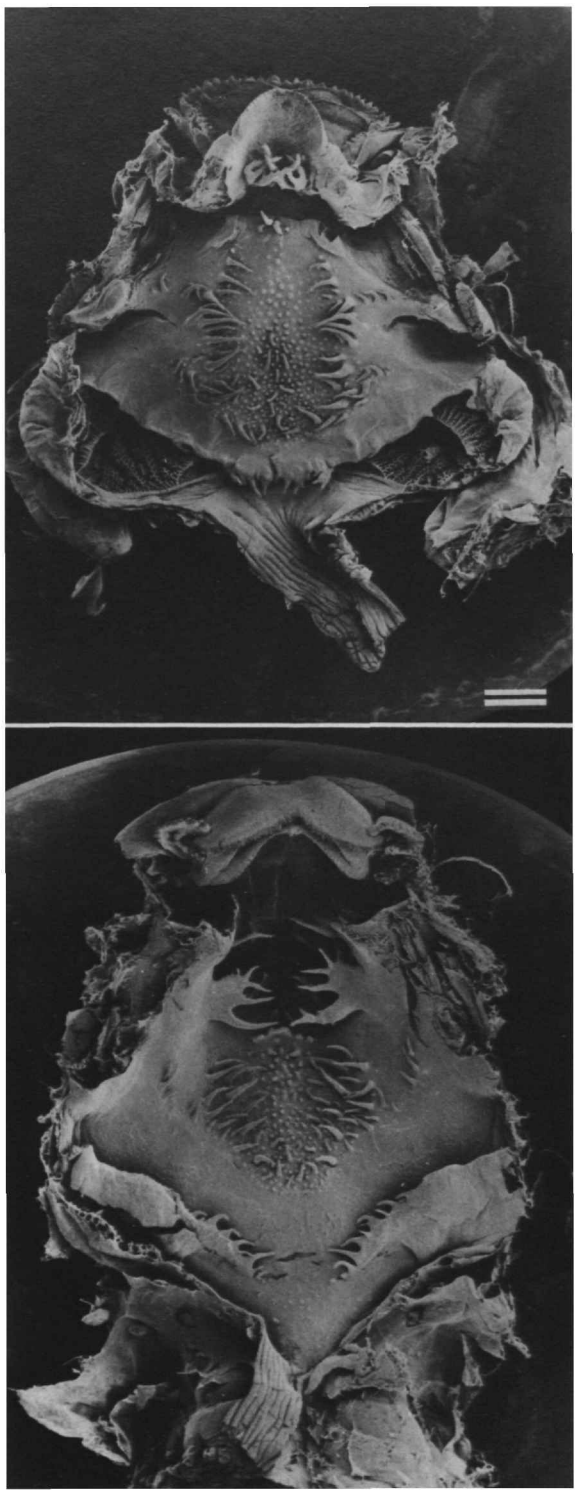


FIGURE 11.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Crossodactylus schmidti;* scale line = 1 mm.

than in *C. gaudichaudii.* Glottis fully covered by ventral velum.

DORSAL ASPECT.—*Buccal Cavity:* Median ridge about 50% distance from front of mouth to esophagus. Anterior narial wall with 1 large attenuate papilla plus small papilla anterior to large papilla. Lateral-ridge papillae with 4–6 long, finger-like projections with apices closer on midline than in *C. gaudichaudii.* Double row of postnarial papillae running parallel to oblique nares on each side, largest papillae posterior and lateral, grading into pustulations anteriorly, most medial row with largest papillae, approximately total of 9 papillae on either side in addition to 3 papillae in a more posterior triangular array directly in front of median ridge. BRA defined by 20–30 papillae on each side. BRA papillae simpler than in *C. gaudichaudii,* not as rugose, none bifurcate. About 4 papillae on lateral limit of buccal roof, isolated from BRA papillae. Dorsal velum shorter than in *C. gaudichaudii;* medial margins not curving as greatly towards esophagus.

Pharyngeal Cavity: Two pair of roundish pressure cushions, medial cushion 50% larger than lateral cushion.

Crossodactylus species

FIGURE 12

MATERIAL.—USNM 241309 (one specimen dissected, stage 36, SVL 16.3 mm). Collected from São Gonçalo Paraty, Rio de Janeiro, 7 April 1979, by E. Izecksohn, C.A.G. Cruz, and O.L. Peixoto.

GENERAL REMARKS.—This larva is like that of *C. dispar,* but adult *dispar* were not collected at this locality (Peixoto, pers. comm.). Only those features that differ from *C. gaudichaudii* are described. Lungs smaller than in *C. gaudichaudii;* longer of the two lungs about 40% length of buccal floor.

VENTRAL ASPECT.—*Buccal Cavity:* More posterior pair of infralabial papillae not as simple, with more rugose tips than in *C. gaudichaudii.*

Pharyngeal Cavity: Ceratobranchial 1 with 11 filter rows, cb 2 with 11, cb 3 with 10, cb 4 with 5.

DORSAL ASPECT.—*Buccal Cavity:* Median ridge wider than in *C. gaudichaudii.*

Cycloramphus stejnegeri (Noble)

MATERIAL.—USNM 209370 (one specimen dissected, stage 31, SVL 7.5 mm). Collected from under a log beside a stream with an attendant female near Teresópolis, Rio de Janeiro, Brazil, 10 December 1977. The specimen disintegrated during preparation for SEM; no figure is available.

REFERENCE.—The external morphology and ecological habitat were described by Heyer and Crombie, 1979 (as *Craspedoglossa stejnegeri*).

REMARK.—*Cycloramphus stejnegeri* has terrestrial, non-feeding larvae (Heyer and Crombie, 1979).

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth slightly wider than long. Large, globose, infralabial papillae with

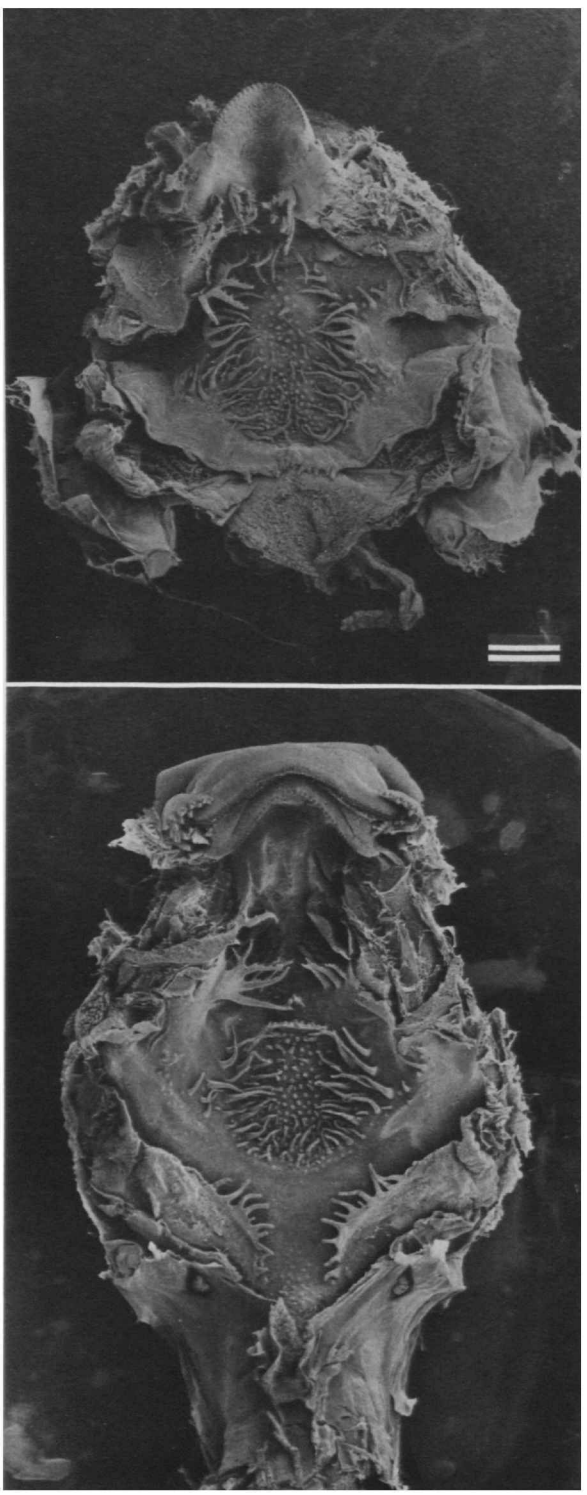


FIGURE 12.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Crossodactylus* species; scale line = 1 mm.

elevated anteriorly directed edge; 1 on each side. One pustulation on each side in position of lingual papilla. BFA tear-drop shaped; no BFA papillae, but several pustulations defining the arena; 2 largest pustulations anterior to buccal pockets. No prepocket papillae. Rest of buccal floor lacking papillae or pustulations. Very shallow buccal pockets, about twice as long as wide; obliquely oriented; not perforated. Free velar surface relatively long, about 20%–25% area of rest of buccal floor; no spicules visible in free velar surface; posterior margin of ventral velum wavy, lacking distinct peaks over filter cavities; very shallow median notch. Thickened epithelium with buff-like texture on posterior margin of ventral velum characteristic of glandular tissue, but individual secretory pits not visible under light microscopy.

Pharyngeal Cavity: Branchial baskets small, round in dorsal profile; total branchial basket area about 40% of buccal area; branchial baskets extremely shallow, 1 small common filter cavity. Filter plates with straight dorsal edges, filter plates 2–3 times as long as tall with slight imbrication; cb 1 with 1–3 filter rows, cb 2 with 4, cb 3 with 4, cb 4 with 3. Filter mesh reduced; filter rows consisting of single simple knobs; no filter folds; no filter rows abutting. Branchial food trap area extensive, but no filter ridges evident under light microscopy. No glottis evident. Esophageal funnel narrow; esophagus huge.

DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth triangular, about 20% longer than wide; nares lying about 20% distance from front of mouth to esophagus; presumed median ridge (present as a pustule only) midway between front of mouth and esophagus. Prenarial arena lacking papillae, pustules, or ridges. Nares small, very close to each other on midline; nares obliquely oriented from transverse plane; anterior narial wall shallow, poorly defined, lacking papillae; postnarial wall about 5 times as long as wide; no narial-valve projection. No postnarial papillae. Single median pustulation in median-ridge position. One short, squat, unbifurcated, lateral-ridge papilla on each side. BRA absent; no BRA papillae; few scattered pustulations over medial and posterior portion of buccal roof. No obvious glandular zone or concentration of secretory tissue characteristic of a glandular zone. Dorsal velum short; broadly interrupted; lacking marginal papillation.

Pharyngeal Cavity: Single, small, oval, pressure cushion arising from dorsal velum. No obvious ciliary groove.

Eleutherodactylus species

FIGURE 13

MATERIAL.—No number (one specimen dissected, stage 37, total length 4.3 mm). No data, gift from University of Southern California.

GENERAL REMARKS.—Small lung buds present.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth an elongate oval. All buccal floor and roof papillation, as well as branchial food traps and gill filters and other such structures

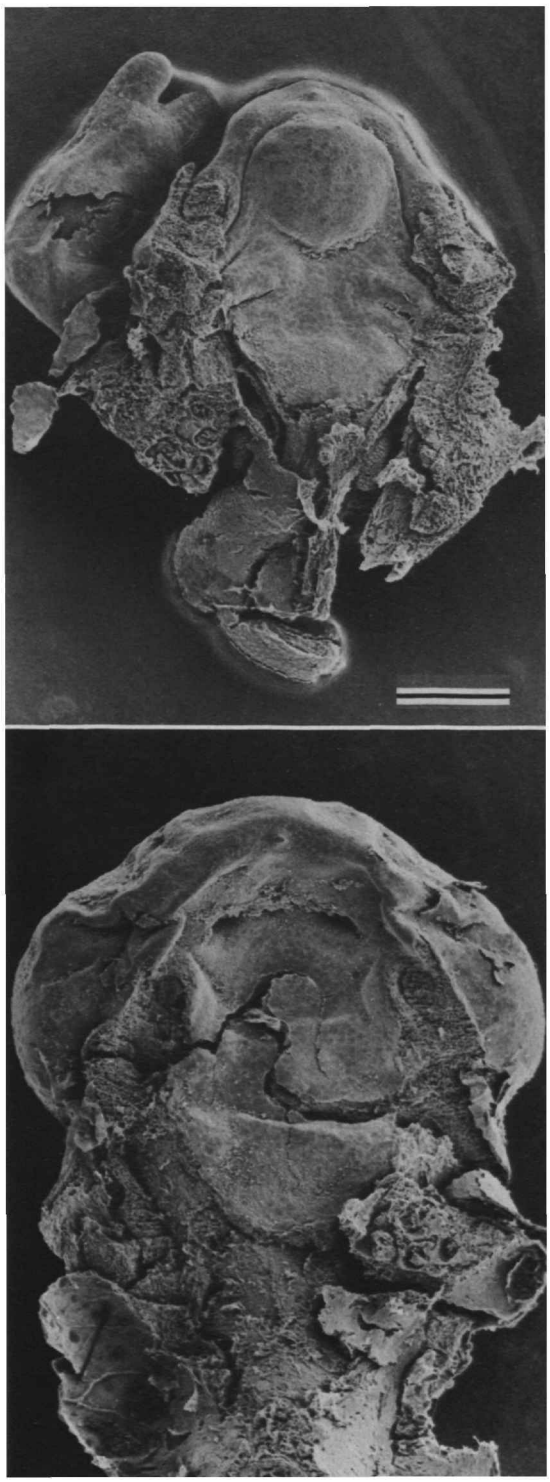


FIGURE 13.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Eleutherodactylus* species; scale line = 400 μm.

associated with a larval way of life, absent. Mouth wide and arch of jaw filled with developing tongue.

Pharyngeal Cavity: Three naked gill slits visible. No glottis visible. Esophageal funnel broad, esophagus of broad diameter.

DORSAL ASPECT.—*Buccal Cavity:* Single medial egg tooth visible on upper jaw. Internal nares oblique elongate ovals lacking valves. Rest of buccal roof smooth, free of topographic relief.

Eupsophus roseus (Duméril and Bibron)

FIGURE 14

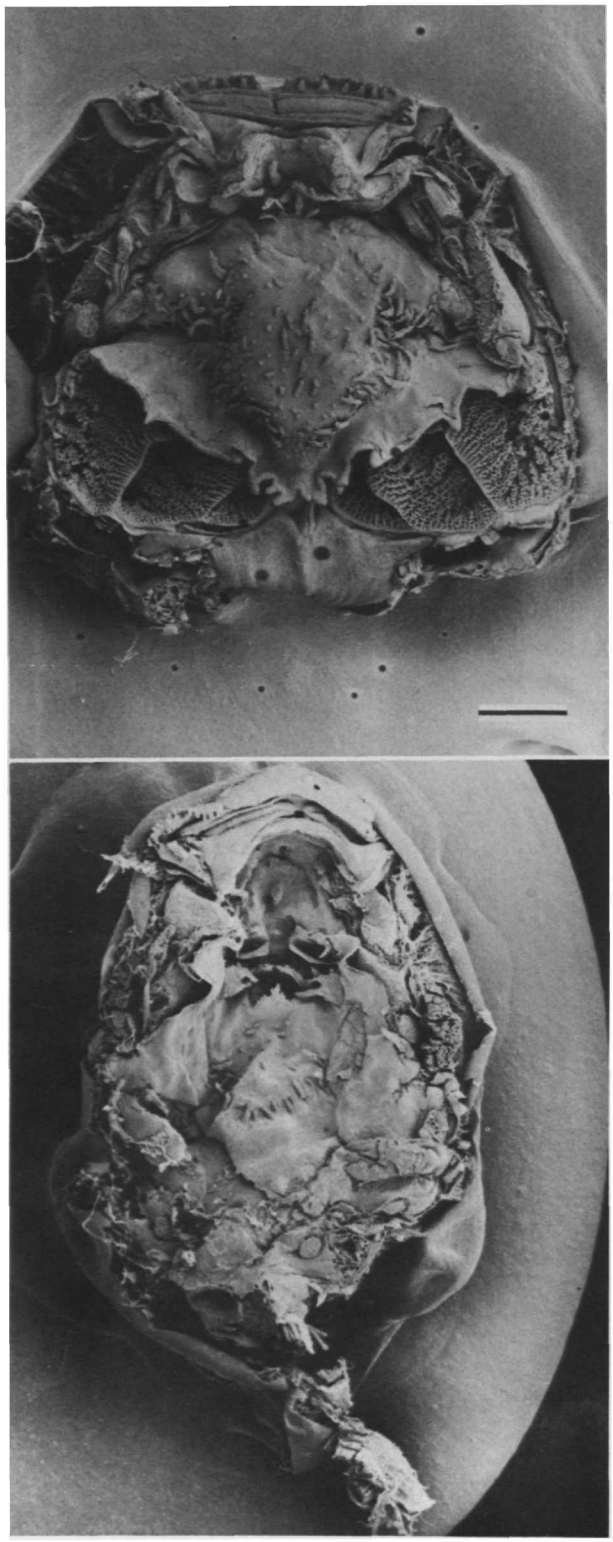
MATERIAL.—KU 162057 (one specimen dissected, stage 29, SVL 14.9mm). Collected from 11 km W Angol (Arroy Los Lleulles), 710 m, Malleco, Chile.

REFERENCE.—Cei (1980:283, fig. 111 I,J) described the larva.

GENERAL REMARKS.—Beaks torn off in dissection.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth roundish. Four infralabial papillae in a transverse row; subequal in size; lateral pair anteroposteriorly flattened; all papillae with rugose anterior surfaces. Four tall, attenuate, lingual papillae in transverse arch; anteromedial pair twice as long as posterolateral pair. BFA V-shaped, defined by 20–30 papillae on each side; BFA papillae small to medium in size, attenuate. Large cluster of 8–12 prepocket papillae merging medially with row of BFA papillae. Cluster of 10–12 cylindrical, blunt, subequal papillae in middle of buccal floor. Buccal pockets very wide, about 5 times as wide as long, moderately deep; pockets transversely oriented (no perforation data available). Free velar surface of average extent, each side about 20% rest of buccal floor area; velum with spicular support; posterior margin with broad V-shape overall, but extensively crenulate with distinctive peaks over the top of each filter plate; median notch asymmetrical, broad; small secretory pits visible in uniform, thickened band along margin of velum.

Pharyngeal Cavity: Branchial baskets transverse ovals, about 20% wider than long; each branchial basket about 60% remainder of buccal floor area, 1/2 as deep as wide. First and 2nd filter cavities subequal, 3rd 1/2 size of first two; oriented obliquely; dorsal edge of 2nd filter plate relatively straight, dorsal edge of 3rd filter plate curving upward and covering about 1/3 of the 3rd filter cavity; 2nd filter plate about 30% longer than tall, 3rd filter plate as long as tall; filter plates tipped about 45° from horizontal plane; cb 1 with 8 filter rows, cb 2 with 10, cb 3 with 11, cb 4 with 10. Filter mesh very dense with many tertiary folds; filter row width variable, not particularly wide; filter rows all abutting or nearly so; filter canals almost as wide as filter rows, nearly to fully canopied. Branchial food traps distinct with well-developed, narrow, secretory ridges of uniform width. Glottis open; fully exposed; lips tall but thin; laryngeal disk small and indistinct. Esophageal funnel broad.



DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth relatively narrow oval; nares 25% distance from front of mouth to esophagus; median ridge 40% distance from front of mouth to esophagus. Single, large, medial papilla descending from prenarial arena; some irregular pustulations lateral to medial prenarial papilla. Nares large; internarial distance 1/4 that of naris length; nearly transverse orientation; anterior narial wall slightly thickened and rugose medially; distinct, tall, posteriorly directed papilla rising from middle 1/3 of anterior narial wall; posterior narial wall a thin flap with a weak narial-valve projection. Three postnarial papillae in an oblique line approximately parallel to nares on each side; postnarial papillae conical, pointed, with rugose anterior margins; most medial on each side larger than more lateral papillae. Median ridge a triangular flap with jagged anterior surface and free edge. Lateral-ridge papillae laterally compressed flaps with 2–4 marginal projections, approximately equal in size to median ridge. BRA U-shaped, defined by approximately 10 small, cylindrical, subequal papillae on each side, none bifurcate. About 12 pustulations and 6 papillae randomly scattered about BRA. Glandular zone present with distinct secretory pits, poorly defined on midline. Dorsal velum of average length, interrupted on midline, with some light sculpturing on free medial edge.

Pharyngeal Cavity: Dorsal pharynx region destroyed in dissection.

Hylodes cf. *asperus* (Müller)

FIGURE 15

MATERIAL.—USNM 241311 (one specimen dissected, stage 31, SVL 22.7 mm). Collected from a stream at Tijuca, Rio de Janeiro, Brazil, 17 November 1978, by O.L. Peixoto.

REFERENCE.—The *Hylodes asperus* group is in need of systematic revision. The tadpoles at hand differ in details of shape and coloration from those described and figured by Bokermann (1963), but are similar in all other aspects.

GENERAL REMARKS.—Guts containing sandy material. Beaks narrow, very extensively sculptured with distinct sharp serrations; a distinctly large median cusp on upper beak with a thickening of the beak at base of median cusp. Lung buds present but small, about 1/2 length of buccal floor; not inflated. Luxuriant gill filaments.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth broadly triangular, 30% wider than long. Two pair of infralabial papillae in a transverse row; more medial pair small, simple, thin; lateral pair complex, multiple-branched structures completely filling space at entrance of mouth, projecting primarily medially. Two tall, thin, pointed, lingual papillae. BFA pentagonal, much longer than wide; 25–30 BFA papillae on

FIGURE 14.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Eupsophus roseus;* scale line = 1 mm.

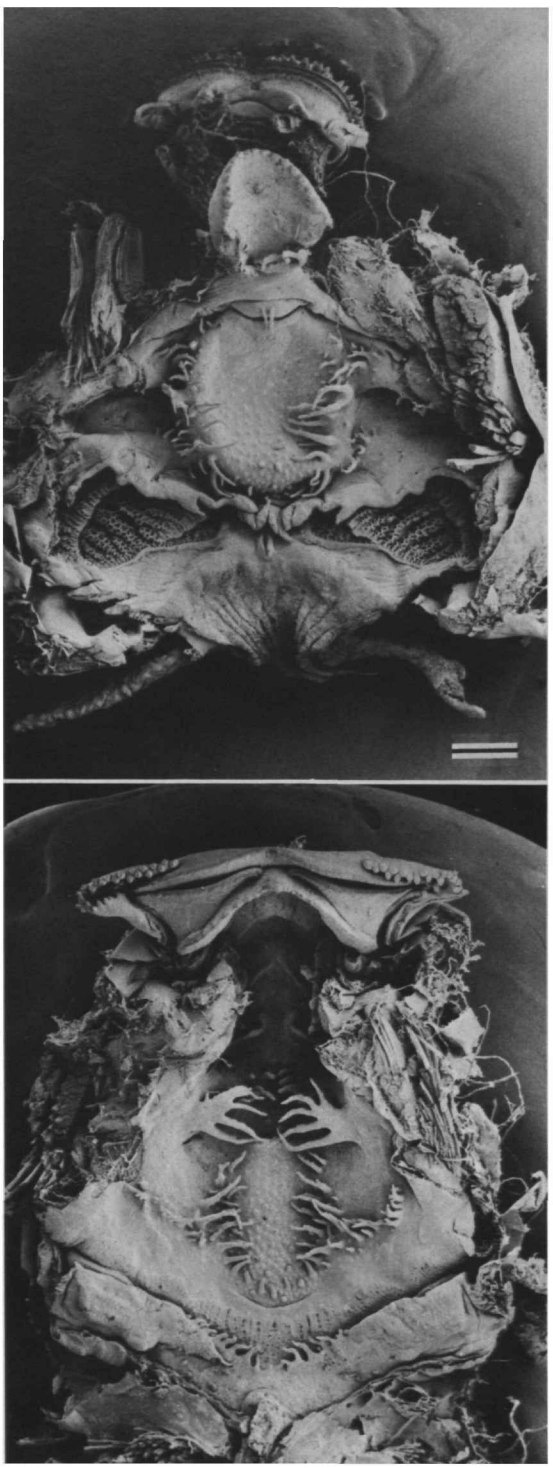


FIGURE 15.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Hylodes* cf *asperus;* scale line = 1 mm.

each side defining arena; BFA papillae characteristically tall, thin, taller papillae curved; largest BFA papillae (those directly medial to buccal pockets) distinctly bifurcate, others with rugosities on anterior surfaces, but not bifurcate. Four or five prepocket papillae of various sizes on each side, like BFA papillae, curved, attenuate, pointed, with rugose anterior margins. Papillae between posterior portion of BFA and buccal pockets extending as a field laterally behind medial portion of buccal pockets; 6 papillae on each side grading into BFA papillae; pustulations everywhere on buccal floor except along posterior margin of velum and anterior to tongue anlage. Buccal pockets shallow; very long and wide, about twice as wide as long; transversely oriented; perforated. Free velar surface with irregular, very wavy, posterior margin; conspicuous spicular support, spicules thin; free velar surface with small cusp directed laterally over 2nd filter plate, larger posterolaterally directed cusp over 3rd filter plate, fringe of 7 thick papillae along midportion over larynx; median notch asymmetrical; abundant secretory pits along whole free edge of velum.

Pharyngeal Cavity: Branchial baskets 50% wider than long, shaped like isosceles triangle with small longitudinally oriented base; each branchial basket about equal to 1/3 remaining area of buccal floor; baskets shallow, 5–6 times as wide as deep; 1st and 2nd filter cavities continuous, collectively 8–10 times 3rd filter cavity. Dorsal edge of 2nd plate curved downward, 3rd convex; 2nd filter plate twice as long as tall, 3rd 1 1/2 times as long as tall; 3rd filter cavity largely obscured in dorsal view by dorsal edge of 3rd filter plate and ventral velum; filter plates extremely tipped; cb 1 with 11 filter rows, cb 2 with 13, cb 3 with 10, cb 4 with 5. Filter mesh denser in more lateral portions of branchial baskets; larger rows with tertiary and higher order folds. Filter rows of uneven width; lateral rows tending to abut, medial rows not tending to abut. Filter canals smaller than filter rows laterally, larger than filter rows medially; 20%–100% canopied. Branchial food traps with uneven, faint secretory ridges. Glottis 40% covered by ventral velum; large; lips thin but of uniform thickness; no laryngeal disk. Esophageal funnel extremely broad.

DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth triangular, same shape as floor; nares about 30% distance from front of mouth to esophagus; median ridge about 50% distance from front of mouth to esophagus. V-shaped shallow ridge with thickened walls pointing anteriorly in roof of prenarial arena. Nares large, close together, internarial distance about 1/4 length of naris; 45° orientation from transverse plane; anterior wall simple with 2 small prenarial papillae on middle 1/3 on one side, 3 on other side; posterior wall with weak narial-valve projection. Multiple rows of papillae oriented in an anteromedial to posterolateral direction defining sides of triangular postnarial arena; more medial and posterior postnarial papillae largest, those more anterior smallest, largest papillae all curved, pointing medially or posteromedially with serrated anterior

margins, postnarial papillary rows grading into pustulations anteriorly; couple of small blunt papillae within posteromedial portion of postnarial arena proper. Median ridge very small triangular structure; very gently sculptured free edge. Lateral-ridge papillae gargantuan, hand-like flaps, compressed laterally, with 5 very attenuate, finger-like projections pointing medially. BRA elongate, almost rectangular-shaped; bounded by 15–25 BRA papillae per side; BRA papillae thin, tall, with jagged margins; BRA papillae of widely varying size, 2 or 3 largest distinctly bifurcate. Distinct row of papillae on lateral portion of buccal roof on each side oriented on line running anterolaterally to posteromedially, merging posteriorly with more caudal BRA papillae; lateral-roof rows with 12–15 small very irregularly shaped papillae; dense field of pustulations within BRA proper. Glandular zone with very abrupt, wavy, anterior margin, medial secretory pits extremely large and elongated to form comb-like secretory zone, pits in this comb-like zone elongated along rostro-caudal axis, more lateral pits smaller, denser, and more randomly arranged. Dorsal velum very short, maximum length about 1/10 length of buccal roof; slightly interrupted on midline; medial portion extensively papillate.

Pharyngeal Cavity: Very faint swellings in pressure cushion area. Ciliary groove narrow, laterally expanding into broad funnel.

Hylorina sylvatica Bell

FIGURE 16

MATERIAL.—KU 162054 (one specimen dissected, stage 36, SVL 24.4 mm). Collected from 25 km NE Parqua, 70 m, Llanquihue, Chile.

REFERENCE.—Cei (1980:286, fig. 111K) described and illustrated the tadpole.

GENERAL REMARKS.—Filamentous gills fine, sparse. Description prepared from SEM specimen that had some damage in preparation. Lungs of a second wet specimen about equal to length of buccal floor.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth diamond-shaped in dorsal view, about 20% wider than long. Two pairs of infralabial papillae in transverse row; medial pair smaller with rugose apices and anterior surfaces, more lateral pair larger and anteroposteriorly flattened. Four lingual papillae in slightly forwardly arched transverse row, medial pair larger. BFA elongate egg-shaped, bounded by 25–35 papillae on each side; BFA papillae relatively simple, attenuate, conical; largest 2 or 3 papillae on each side (immediately medial to buccal pockets) arising from common ridge-like base. Prepocket area with 10–15 scattered papillae of uneven size; all simple, conical. Region of 10–15 papillae posteromedial to buccal pocket and directly lateral to BFA, merging posteriorly with BFA papillae; about 6 anteriorly directed, conical papillae in posteromedial portion of BFA; about 100 pustulations scattered about posterior 1/2 of BFA. Buccal pockets long, deep,

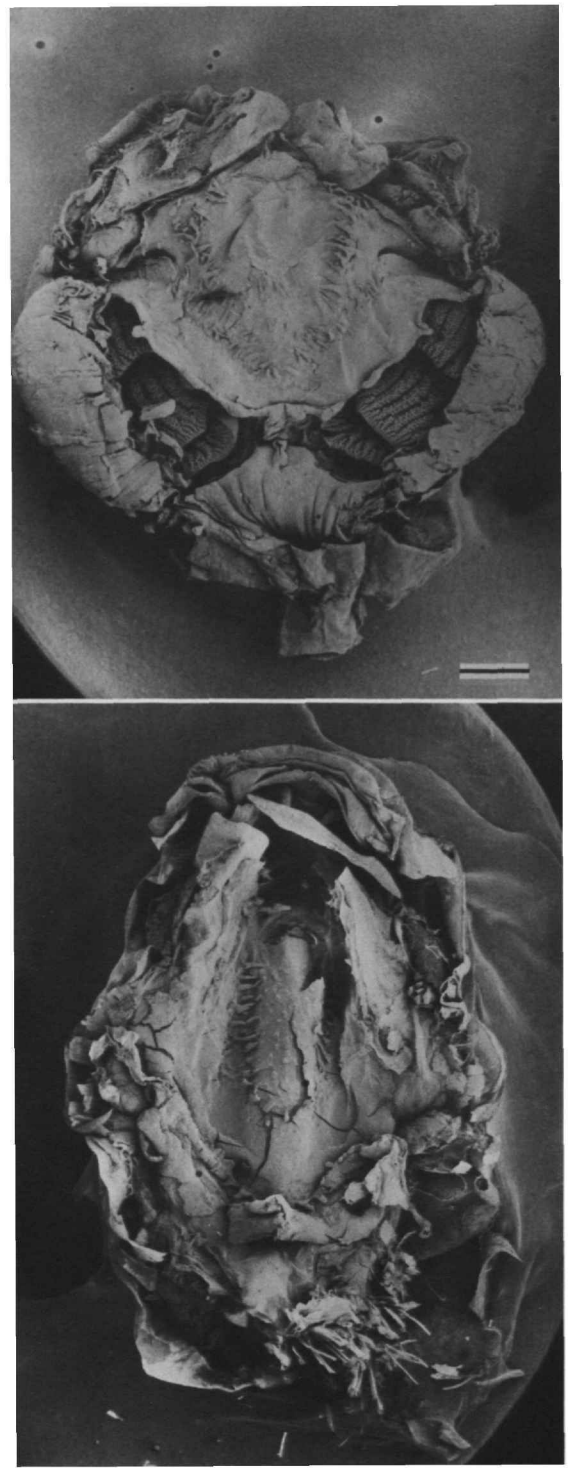


FIGURE 16.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Hylorina sylvatica;* scale line = 1 mm.

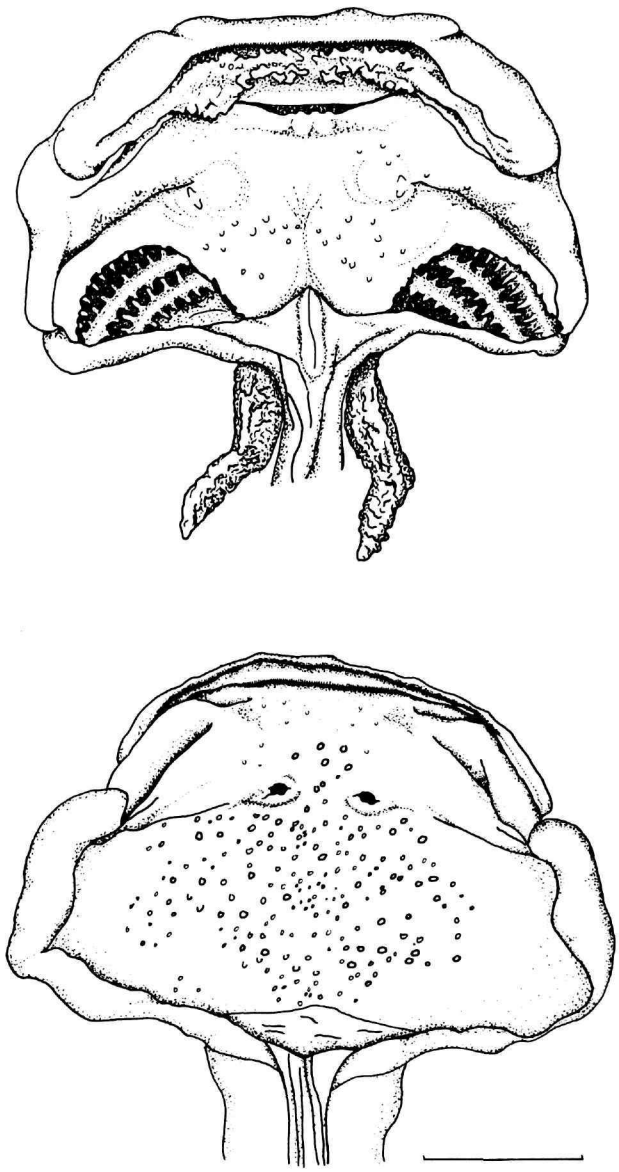


FIGURE 17.—Camera lucida drawings of floor (above) and roof (below) of oral cavity of *Lepidobatrachus laevis;* scale line = 5 mm.

3 times as wide as long; oriented 20° from transverse plane; perforation data unobtainable from specimen. Free velar surface of average length; well supported by spicules; bow-shaped edge with 3 distinct peaks on each side over 2nd, 3rd, and 4th filter plates respectively; broad, distinct, median notch bounded on each side by rounded cusp; no additional sculpturing on edge; secretory pits along margin and cusps.

Pharyngeal Cavity: Branchial baskets as long as wide, long axis anterolateral to posteromedial; each branchial basket about 50% remaining buccal floor area; branchial baskets about as deep as wide. Second filter cavity about 25% larger than 3rd, about 45° orientation from midline. Second filter plate with relatively straight dorsal edge, 3rd filter plate with slightly upward curving dorsal edge; 1st, 2nd, and 4th filter plates 30% longer than tall, 3rd filter plate as long as tall; 3rd filter plate almost lying on side, other filter plates tipped at 45°; cb 1 with 8 filter rows, cb 2 with 11, cb 3 with 12, cb 4 with 8. Filter mesh relatively dense; quaternary folds on larger filter rows; filter rows relatively wide and of uniform thickness; filter rows separated but almost abutting; filter canals narrow, <50% width of largest rows, 50% or more canopied. Branchial food traps present, well developed, with narrow, even secretory ridges (Figure 57*c*), more medial food trap descending well into front of 3rd filter cavity. Glottis distinct, fully exposed, open, with average-sized lips; broad, round and distinct laryngeal disk. Esophageal funnel narrow; esophageal diameter broad.

DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth distorted in preparation; nares 25% distance from front of mouth to esophagus; median ridge 40% distance from front of mouth to esophagus. Prenarial arena with transverse ridge with single anteroposterior cusp on each side of midline (cusps not visible in Figure 16). Nares of average size; internarial distance 50% length of naris; nares at 45° from midline; anterior narial wall with knobby anteromedial edge and single, small, posteriorly directed, prenarial papilla along lateral third; posterior narial wall a thin flap with no distinct narial-valve projection. Several small conical papillae posterior to nares defining the postnarial arena; pustulations scattered within arena (actual pattern of structures cannot be determined because of distortion of specimen during SEM preparation). Median-ridge and lateral-ridge papillae destroyed in dissection. BRA an elongate "U" defined by 15–20 simple, conical, slightly medially and anteriorly curved papillae on each side. Two or three small, lateral-roof papillae; pustulate ridge running from lateral-roof papillae posteromedially to BRA; more than 100 pustulations scattered about roof of BRA. Glandular zone distinct, of uniform width; secretory pits fairly dense. Dorsal velum relatively large, almost continuous across midline, with moderately papillate medial ridge on each side.

Pharyngeal Cavity: Pressure cushions and ciliary groove destroyed in dissection.

Lepidobatrachus laevis Budgett

FIGURE 17

MATERIAL.—USNM 241344 (one specimen dissected, stage 38, SVL 31.2 mm). Adults collected from Filadelfia, Boqueron, Paraguay; larvae raised in laboratory of Rudolfo Ruibal.

REFERENCE.—Cei (1968) described and figured the external morphology of *Lepidobatrachus asper* and *llanensis*. The larva of *laevis* is very similar to the larvae of *asper* and *llanensis*.

GENERAL REMARKS.—Very large fields of filamentous gills. Lungs small, about 3/4 length of buccal floor; uninflated.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth extremely broad, especially anteriorly, almost rectangular, 25% wider than long. Floor of mouth lacking many features found on other tadpoles. Infralabial region poorly defined. Irregular collection of pustules immediately posterior to denticle tooth row; immediately behind pustules a transversely oriented low ridge running width of mouth but interrupted medially; near midline and posterior to ridge, 2 short, knobby, conical papillae with very broad bases. Tongue anlage very small, 3 tiny lingual papillae and a pustulation in a transverse row. BFA not defined. No prepocket papillae. Only distinct papilla isolated just posterior to medial end of buccal pockets; some pustulations scattered in prepocket area and many in posterior 1/2 of buccal floor. Buccal pockets very long, curved, 8 times as wide as long; deep; oriented 40% from transverse plane; perforations not visible under light microscopy. Almost no free velar surface, area of free velar surface less than 3% rest of buccal floor; velum divided, middle 1/3 of velum absent; spicules absent; free velar margin on each side a single arch with slightly irregular jagged margin; secretory pits absent.

Pharyngeal Cavity: Branchial baskets isosceles triangle-shaped with transverse base, 20% wider than long; area of both branchial baskets equalling about 25% area of remainder of buccal floor. No filter cavities. No filter plates; small projections on dorsal surface of some gill bars probably vestiges of filter rows; cb 1 with 9 filter row vestiges, cb 2 with 8, cb 3 with 7, cb 4 with 6; gill filaments visible through gill bars. No filter mesh. Branchial food traps absent. Glottis fully exposed, large, dorsally directed; lips well developed; glottis on triangular laryngeal disk; esophageal funnel narrow, esophagus diameter large.

DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth very broad, particularly anteriorly; nares about 30% distance from front of mouth to esophagus. No median ridge. Roof of mouth lacking many features found in other tadpoles. Small, distinct, randomly distributed pustulations of uneven size scattered about entire buccal roof. Nares small transverse ovals, internarial distance 1/4 width of buccal roof; flap arising from posteromedial margin of internal nares covering less than 1/2 of narial orifice and as such incompetent as a valve. BRA not defined. No glandular zone. No dorsal velum.

Pharyngeal Cavity: No pressure cushions. No ciliary groove.

Leptodactylus chaquensis Cei

FIGURE 18

MATERIAL.—USNM 241322 (one specimen dissected, stage 37, SVL 18.1 mm). Collected from a pond in the city of Embarcación, Salta, Argentina, 31 December 1971.

REFERENCE.—The external morphology of the *L. chaquensis* larva has been reported and illustrated by Cei (1980:351, fig. 148).

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth triangu-

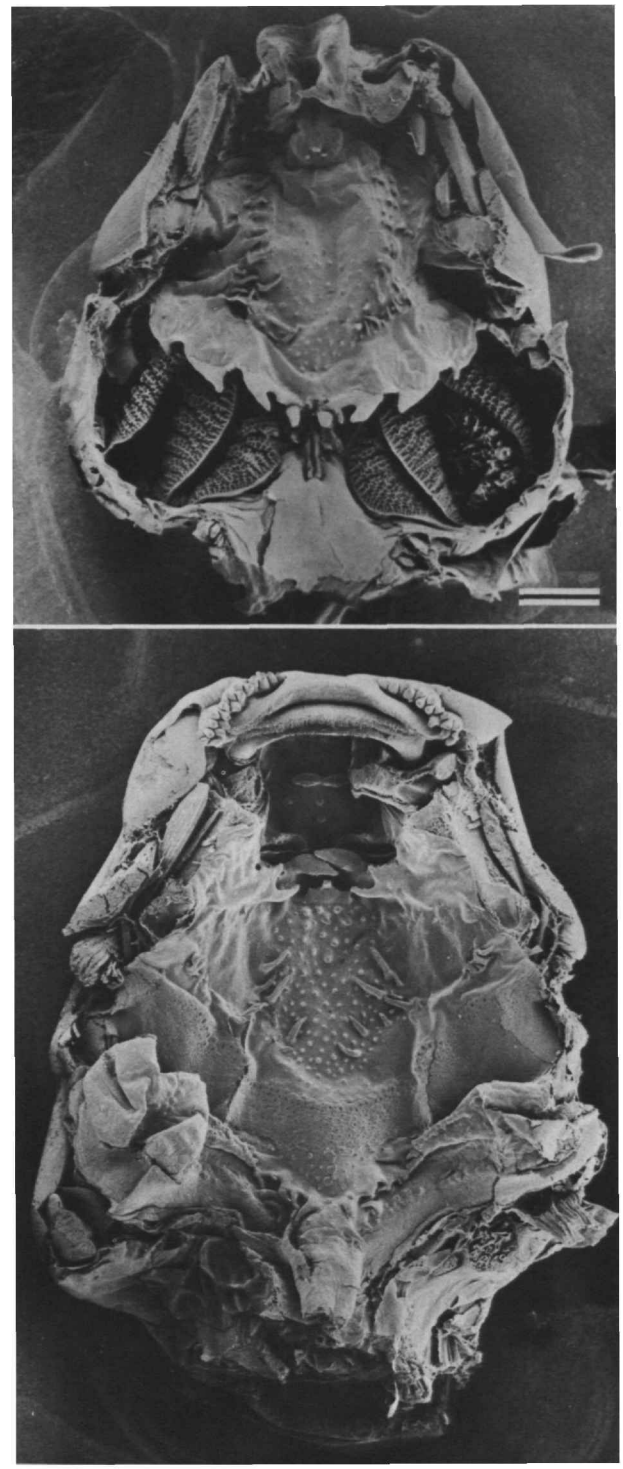


FIGURE 18.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Leptodactylus chaquensis;* scale line = 1 mm.

lar, length about equal width. Two infralabial papillae on each side, 1 pair near midline, much larger pair directly lateral to medial pair; papillae with rough knobby margins; 2 or 3 pustulations anterior to infralabial papillae. Three anteriorly to posteriorly flattened lingual papillae; large one on midline, bifurcated at tip, smaller two lingual papillae posterolateral to larger median one. BFA broadest anteriorly, narrowing gradually posteriorly, then abruptly near posterior limit; 10–15 BFA papillae on each side; largest BFA papillae medial to buccal pockets; most thin and conical, some with bifurcated tips. No prepocket papillae. Five or six papillae lateral to BFA just posterior to medial edge of pockets. Buccal pockets large; transverse; not perforated. Free velar surface of slightly longer than average length; spicular support obvious through epithelium of buccal floor; spicules long, thin, and stiff; posterior edge of ventral velum with 3 long, distinct, posteromedially directed, marginal projections on each side directly above the tops of the 2nd, 3rd, and 4th filter plates and 2 short papillae on either side of median notch; median notch large; very conspicuous secretory pits densely distributed on margin and marginal projections of velum.

Pharyngeal Cavity: Branchial baskets oval, almost round, with long axis from anterolateral to posteromedial; area of both branchial baskets about equal to rest of buccal floor area; branchial baskets deep; filter cavities about same size, 2nd less than 25% larger than 1st and 3rd. Two medial filter plates with gently upwardly curved dorsal edges; more lateral filter plates with straight dorsal margins; filter plate length about equal to height; slightly imbricate; cb 1 with 12 filter rows, cb 2 with 12, cb 3 with 12, cb 4 with 9. Filter mesh dense; extensively branched with conspicuous tertiary folds. Filter rows wide, abutting. Filter canals not as wide as rows, fully canopied. Branchial food traps of average size with conspicuous secretory ridges. Glottis entirely exposed when viewed from above, small with tall, thin lips; no laryngeal disc. Esophageal funnel narrow, but esophagus relatively large.

Dorsal Aspect.—*Buccal Cavity:* Mouth relatively narrow, roof 20% longer than wide; long prenarial area, nares about 25% distance from front of mouth to esophagus; median ridge located about 40% distance from front of mouth to esophagus. Prenarial arena with 5 or 6 random pustulations plus a transverse median ridge with a gently curved, biconcave margin and a medial cleft. Nares of moderate size, transversely oriented; anterior narial wall thick, not exceptionally high, ending medially with a medially directed papilla; narial valves thin, 5 times as long as tall, no distinctive projection. Postnarial arena with few pustulations and 1 irregular, short, pustulate papilla on each side. Median ridge triangular, ending in 1 truncate papilla; anterior surface pustulate. Lateral-ridge papillae complex, large, elkhorn-shaped, far lateral and slightly anterior to median ridge. One to four small lateral-roof papillae. BRA triangular, relatively narrow; 5 attenuate, simple BRA papillae on 1 side, 8 on other; 30–40 pustulations scattered evenly about BRA. Glandular zone with distinct anterior margin of secretory pits; zone of uniform anterior to posterior dimension, about 1/10 length of roof of mouth. Free medial 1/2 of dorsal velum pustulate and papillate, larger and more medial papillae pointing posteriorly; dorsal velum narrowly interrupted on midline.

Pharyngeal Cavity: Pressure cushions distinct; lateral cushions irregular in shape, more medial cushion oriented in anteromedial to posterolateral plane; medial cushion large, vaguely pyramid in shape. Ciliary groove shallow and wide.

Leptodactylus fuscus (Schneider)

Figure 19

Material.—USNM 241294 (one specimen dissected, stage 37, SVL 15.3 mm). Collected from a 3 by 10 m pond in an open situation near Teresópolis, Rio de Janeiro, Brazil, 4 December 1977.

Reference.—Lescure (1972) described and illustrated the external larval morphology.

General Remarks.—Only those features that differ from *L. chaquensis* are described. Lungs large, about length of floor of mouth. Dense mesh of gill filaments.

Ventral Aspect.—*Buccal Cavity:* Three infralabial papillae in a transverse row, all relatively small, blunt, stubby; medial papilla with deeply bifurcate apex. Four lingual papillae, subequal in size in an approximately transverse row; simple and attenuate. BFA more an open, simple "U" than in *L. chaquensis;* few BFA papillae with jagged tips. One or two very small, prepocket papillae. Two or three papillae lateral to BFA just posterior to medial edge of pockets.

Pharyngeal Cavity: Three most medial filter plates with upwardly curved dorsal margins; cb 1 with 10 filter rows, cb 2 with 11, cb 3 with 10, cb 4 with 7 or 8. Filter canals 90%–100% canopied. Glottis lying mostly under ventral velum, 80% exposed through median notch proper.

Dorsal Aspect.—*Buccal Cavity:* Fewer prenarial pustulations, median ridge not deeply cleft. Anterior narial wall rugose, lacking papillae. Postnarial arena with 4 papillae; larger pair more anterior and medial, smaller pair more posterior and lateral. Median ridge with serrate apex (Figure 61*a*). Lateral-ridge papillae not as branched as in *L. chaquensis*. BRA U-shaped, 4 or 5 BRA papillae on each side.

Pharyngeal Cavity: Medial pressure cushion oval-shaped.

Leptodactylus gracilis (Duméril and Bibron)

Figure 20

Material.—USNM 241234 (one specimen dissected, stage 38, SVL 14.1 mm). Collected from a small temporary pond in a vacant lot in Santo Amaro da Imperatriz, Santa Catarina, Brazil, 19 November 1979.

Reference.—Fernandez and Fernandez (1921) described and figured the external larval morphology.

General Remarks.—Only those features that differ from

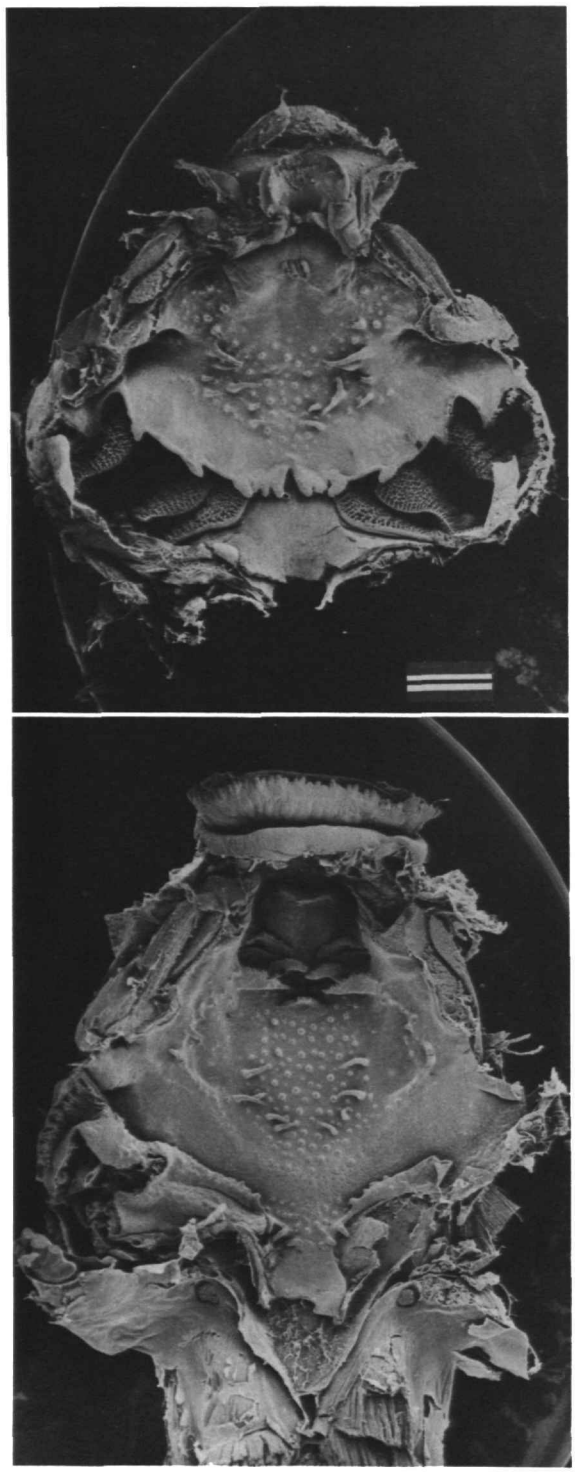


FIGURE 19.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Leptodactylus fuscus;* scale line = 1 mm.

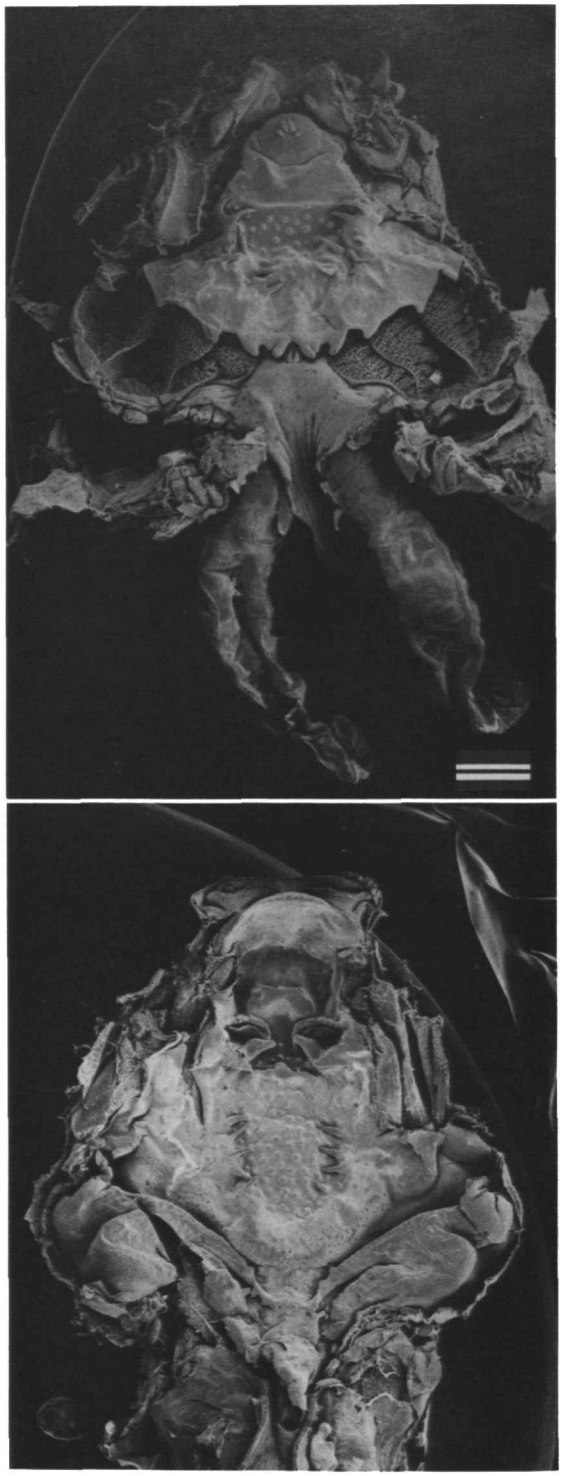


FIGURE 20.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Leptodactylus gracilis;* scale line = 1 mm.

L. chaquensis are described. Lungs well developed, about length of floor of mouth; partially inflated. Filamentous gills present.

VENTRAL ASPECT.—*Buccal Cavity:* Medial pair of infralabial papillae fused on common base; papillae smaller and less elaborate than in *L. chaquensis;* prenarial arena without additional pustulations (Figure 53*a*). Four lingual papillae in forwardly arching row; all simple and attenuate. BFA V-shaped; 8–10 papillae on each side; all thin and conical, lacking bifurcations. One or two small prepocket papillae. Three or four papillae lateral to BFA just posterior to medial edge of pockets. Buccal pockets perforated. Single papilla on either side of median notch.

Pharyngeal Cavity: Branchial baskets slightly smaller than in *L. chaquensis.* Tops of filter plates slightly more tipped than in *L. chaquensis;* cb 1 with 9–10 filter rows, cb 2 with 11, cb 3 with 9 or 10, cb 4 with 7. Filter mesh with quaternary folds. Filter canals 90% canopied. Glottal lips thicker than in *L. chaquensis;* faint laryngeal disk.

DORSAL ASPECT.—*Buccal Cavity:* Anterior narial wall pustulate, without distinct papilla. Small, posterolateral, secondary papillae in postnarial arena; larger pair of papillae not as large as in *L. chaquensis* and not abutting on midline. Median ridge broader than in *L. chaquensis.* Lateral-ridge papillae non-branching. Four or five BRA papillae on each side. Free medial margin of dorsal velum more pustulate and less papillate than in *L. chaquensis.*

Leptodactylus knudseni Heyer

FIGURE 21

MATERIAL.—USNM field 44780 (one specimen dissected, stage 39, SVL 18.9 mm). Collected from forest pond at Reserva Biologica Rio Trombetas, Pará, Brazil, 9 February 1979, by Ronald I. Crombie.

REFERENCE.—The larval external morphology is being described by Ronald I. Crombie (pers. comm.). The habitus is very similar to that of *L. labyrinthicus* or *L. pentadactylus.*

GENERAL REMARKS.—Only those features that differ from *L. chaquensis* are described. Lungs average size; left lung larger than right, left lung about same length as buccal floor, right 20% smaller; not inflated.

VENTRAL ASPECT.—*Buccal Cavity:* Five infralabial papillae as two tiny knobs far forward, third one posteromedial on midline in form of anteriorly cupped palp with deep anteromedial cleft; last pair posterolateral and largest, consisting of multiangular knobby palp-like structures; no infralabial papillae touching, all well separated from each other (Figure 53*b*). BFA a bit more open posteriorly than in *L. chaquensis;* up to 10 BFA papillae on each side; no BFA papillae with bifurcations, not as tall or attenuate as in *L. chaquensis.* Two or three tiny prepocket papillae. Only 1 or 2 papillae lateral to BFA just posterior to medial edge of pockets. Buccal pockets perforated. Marginal papillae on ventral velum shorter than in

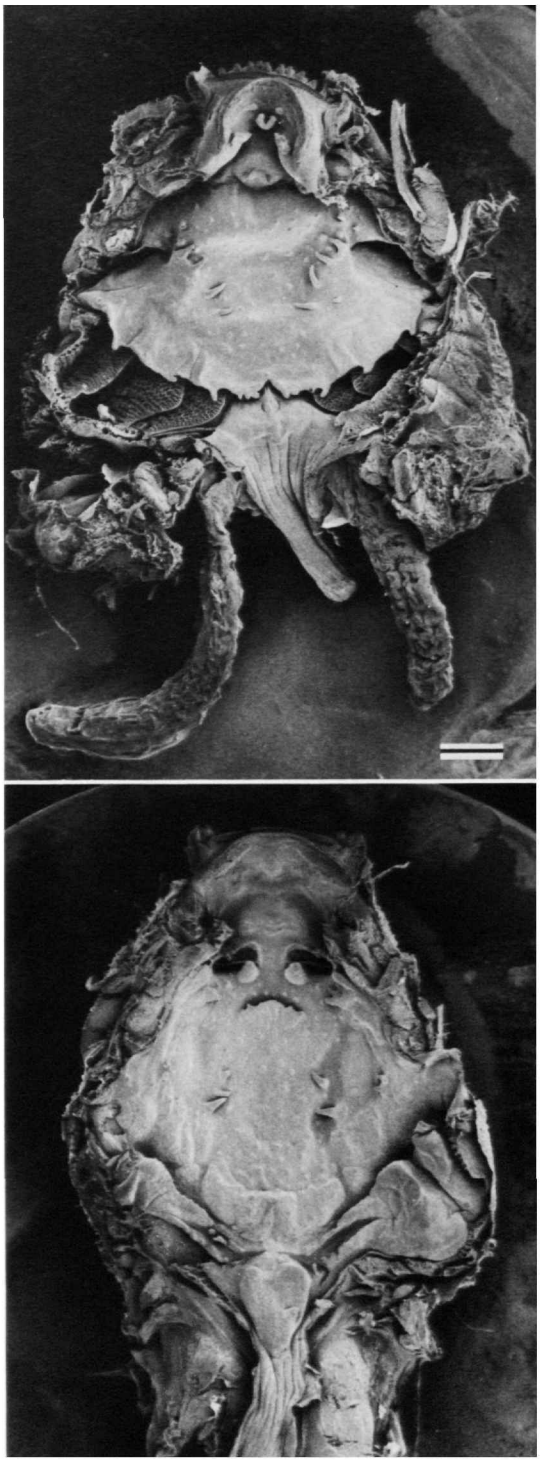


FIGURE 21.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Leptodactylus knudseni;* scale line = 1 mm.

L. chaquensis; secretory pits not as conspicuous as in *L. chaquensis.*

Pharyngeal Cavity: Branchial baskets wider than long by 20%; irregularly oval. Third and fourth filter plates with distinct upward curving peaks; 2nd filter plate with straight dorsal margin; 3rd filter plate overlapping 4th more extensively than in *L. chaquensis;* cb 1 with 11 filter rows, cb 2 with 12, cb 3 with 12, cb 4 with 7.

DORSAL ASPECT.—*Buccal Cavity:* Prenarial arena with faint posteriorly directed broad V-shaped notch on midline flanked directly laterad by 1 or 2 pustulations. No papillae on prenarial wall; single, large, globose, postnarial papilla directly posterior to median half of nares with completely smooth surface. Median ridge broader than in *L. chaquensis,* with serrate lateral edges; no distinct terminal papilla; anterior surface smooth (Figure 61*b*). Lateral-ridge papillae small, simple, triangular structures with rugose margins; each about 1/4 size of median ridge. BRA triangular, poorly defined by 2 or 3 papillae on each side; about 3 dozen pustulations scattered about BRA and postnarial arena. Anterior margin of ventral velum smooth.

Leptodactylus mystacinus (Burmeister)

FIGURE 22

MATERIAL.—USNM 241303 (single specimen dissected, stage 37, SVL 12.2 mm). Collected from a temporary pond in a clearing at Fazenda do Veado, Serra da Bocaina, São Paulo, Brazil, 3 January 1977.

REFERENCE.—Sazima (1975) described and figured the external larval morphology.

GENERAL REMARKS.—Only those features that differ from *L. chaquensis* are described. Lungs well developed, 80%–90% length of buccal floor; not inflated. Filamentous gills present.

VENTRAL ASPECT.—*Buccal Cavity:* Medial pair of infralabial papillae fused to common base. Four lingual papillae in a transverse row; tall, simple, subequal in size. Seven or eight BFA papillae on each side; no papillae with bifurcate tips; largest 2 BFA papillae rising from common base. No papillae lateral to BFA posterior to medial edge of pockets. Buccal pockets perforated.

Pharyngeal Cavity: Branchial baskets wider than in *L. chaquensis.* Third and 4th filter plates curving upward more extensively and abruptly than in *L. chaquensis;* 3rd filter plate slightly taller and more imbricate than in *L. chaquensis;* cb 1 with 10 filter rows, cb 2 with 10, cb 3 with 10, cb 4 with 8. Filter rows not as abutting as in *L. chaquensis.* Filter canals 80% canopied.

DORSAL ASPECT.—*Buccal Cavity:* Roof about as long as wide. Prenarial arena with transverse ridge broadly V-shaped; rest of prenarial arena featureless. Anterior narial walls simpler than in *L. chaquensis,* lacking papillae. Small, posterolateral, secondary papillae in postnarial arena; larger pair of papillae not as large as in *L. chaquensis* and not abutting on midline.

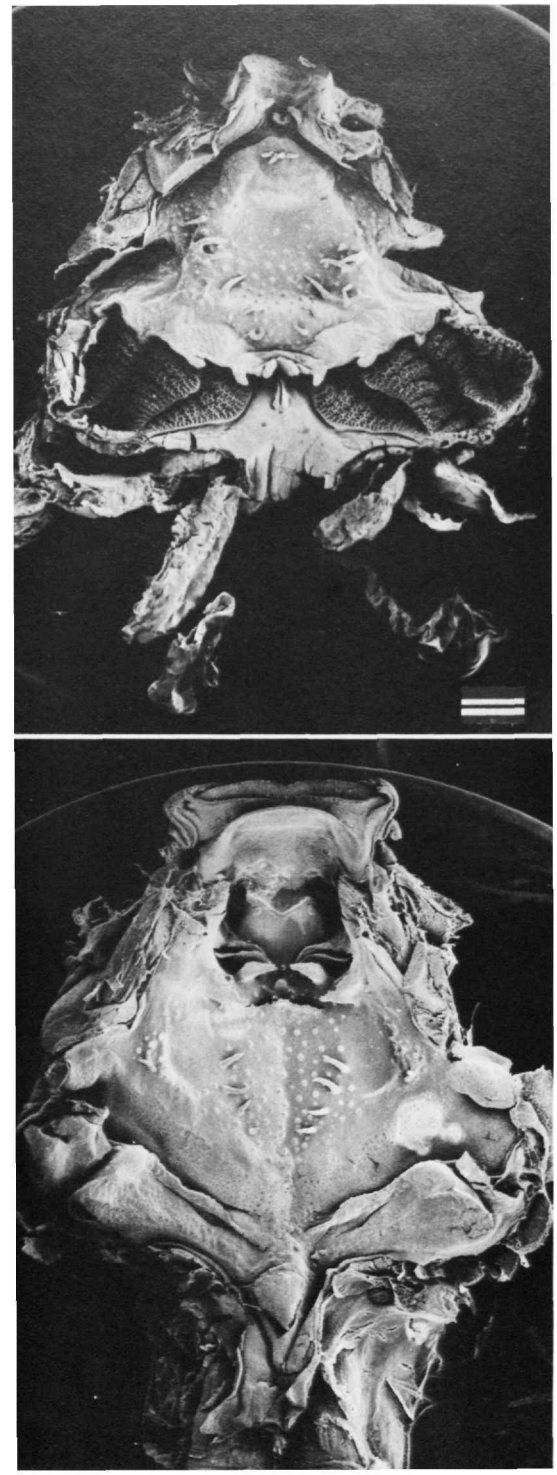


FIGURE 22.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Leptodactylus mystacinus;* scale line = 1 mm.

Anterior surface of median ridge smooth, median ridge broader than in *L. chaquensis*. Lateral-ridge papillae smaller than in *L. chaquensis*, lacking terminal branches, with jagged terminal edges. Four BRA papillae on each side. Free medial margin of dorsal velum slightly pustulate, lacking papillae.

Leptodactylus pentadactylus (Laurenti)

MATERIALS.—USNM uncatalogued (single specimen dissected, stage 34, SVL 18.4 mm). Collected from 6 km west of Turrialba, Cartago, Costa Rica. Specimen subsequently destroyed in SEM preparation.

REFERENCES.—External descriptions are in Heyer (1970, 1979). Discussions of ecology, habitat occurrence, and facultative carnivory are found in Heyer, McDiarmid, and Weigmann (1975) and Muedeking and Heyer (1976).

GENERAL REMARKS.—Only those features that differ from *L. chaquensis* are described.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth relatively wide anteriorly. Four infralabial papillae, 2 fused at midline; the 2 lateral infralabial papillae simple, round palps with single, medially directed, apical projection; all infralabial papillae relatively small but distinct and anteriorly-posteriorly flattened. Three lingual papillae; medial papilla anteriorly-posteriorly flattened, distinctly bifurcate; other 2 lingual papillae simple, attenuate, posterolateral to medial one. Elongate oval BFA, not distinctly defined anteriorly; 6 BFA papillae on one side, 5 on other, simple attenuate cones; no pustules or bifurcations. Randomly scattered pustulations anterior to buccal pockets and on posterior half of BFA. Buccal pockets long, not as wide as in *Leptodactylus chaquensis;* transversely oriented; distinctly perforated. Posterior margin of ventral velum crenulate, peaks over filter cavities relatively small, but distinct; median notch wide and jagged; secretory pits of velar surface very conspicuous, but limited to free margin of velum; secretory pits densest medially, except right in front of median notch.

Pharyngeal Cavity: Area of both branchial baskets about 80% of buccal floor area. Second filter plate largest, 40% larger than 1st or 3rd; 3rd filter plate imbricating 3rd filter cavity covering 1/2 the filter cavity; cb 1 with 9 filter rows, cb 2 with 11, cb 3 with 10, cb 4 with 9. Filter mesh moderately dense with tertiary and higher order folds present. Filter rows moderately wide, intermittently abutting, but filter canals exposed; filter canals about 1/4 width of filter rows. Glottis small with tall, moderately thick lips.

DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth wide, trapezoidal, almost as wide as tall; nares located about 1/4 distance from front of mouth to esophagus. Weak, posteriorly directed, wide, V-shaped elevation in middle of prenarial arena, located about 2/3 distance from upper beak to nares, otherwise no other structures (pustulations or papillae) in prenarial arena. Nares large; transversely directed; anterior narial wall thick, short, lacking papillae. Postnarial arena with 2 short, stout, postnarial papillae with rounded apices together with a few small pustulations in the postnarial region. Median ridge small, rounded, but with slightly jagged ventral margin; median ridge lacking any secondary papillae or pustulations. Lateral-ridge papillae small, stout, with jagged apices, located far lateral and slightly anterior to median ridge. BRA poorly defined, with only 1 or 2 small attenuate papillae on each side; BRA papillae not bifurcate. Several dozen randomly distributed pustulations on buccal roof; fewer pustulations laterally. Glandular zone wide and smooth; secretory pits dense, not distinct under light microsope. Dorsal velum short; interrupted medially; with a slightly rough medial margin on each side.

Pharyngeal Cavity: Destroyed in dissection.

Leptodactylus wagneri (Peters)

FIGURE 23

MATERIAL.—USNM 241307 (two specimens dissected, stage 37, SVL 10.8 mm; stage 38, SVL 9.9 mm). Collected from pond at Curuçá, Amazonas, Brazil, 9 November 1975.

REFERENCE.—Kenny (1969) described the external anatomy (as *Leptodactylus podicipinus petersi*).

GENERAL REMARKS.—Only those features that differ from *L. chaquensis* are described. Lungs long, about length of buccal floor, uninflated. Dense gill filaments.

VENTRAL ASPECT.—*Buccal Cavity:* Three infralabial papillae, one on midline bifurcate. No lingual papillae. Zero to three prepocket papillae. Posterior edge of ventral velum symmetrically sculptured, small papillae irregularly spaced on edge; median notch average size.

Pharyngeal Cavity: Cb 1 with 9 filter rows, cb 2 with 10, cb 3 with 11, cb 4 with 6. Filter rows mostly not abutting. Filter canals 80% canopied. Glottis 80% exposed when viewed from above; glottal lips thicker than in *L. chaquensis*.

DORSAL ASPECT.—*Buccal Cavity:* Prenarial arena lacking pustulations and ridge less relief than in *L. chaquensis*. Anterior narial papilla a knob-like structure. Postnarial arena with second small papillae between medial papilla and lateral-ridge papilla. Lateral-ridge papillae simpler structures than in *L. chaquensis*. About 6 BRA papillae on each side. Glandular zone less distinct than in *L. chaquensis*. Papillae on free velar margin smaller than in *L. chaquensis*.

Macrogenioglottus alipioi Carvalho

FIGURE 24

MATERIAL.—USNM 200456 (one specimen dissected, stage 31, SVL 17.7 mm). Collected from a forest pond near Santa Teresa, Espírito Santo, Brazil, 15 April 1971, by James F. Jackson, Jr.

REFERENCE.—Abravaya and Jackson (1978) described and figured the larva and discussed the reproductive behavior of the species.

GENERAL REMARKS.—Beaks weakly cornified. Very slight

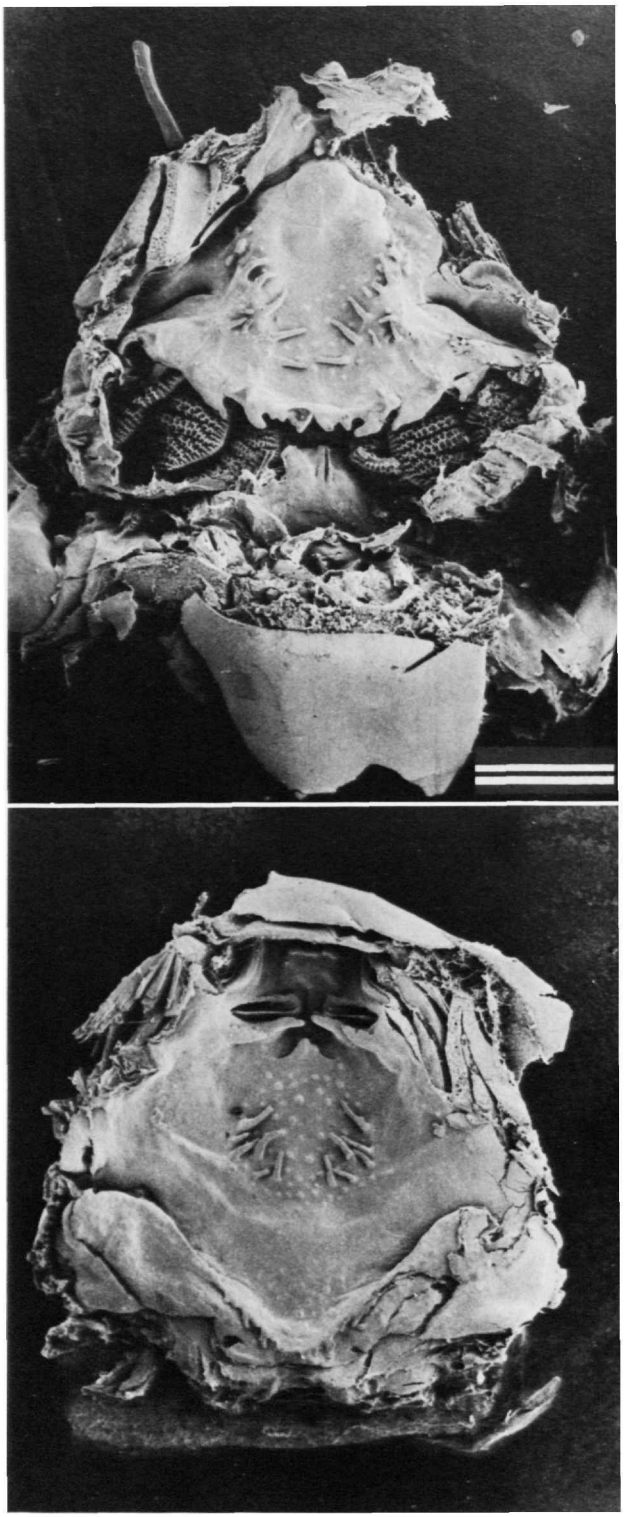


FIGURE 23.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Leptodactylus wagneri;* scale line = 1 mm.

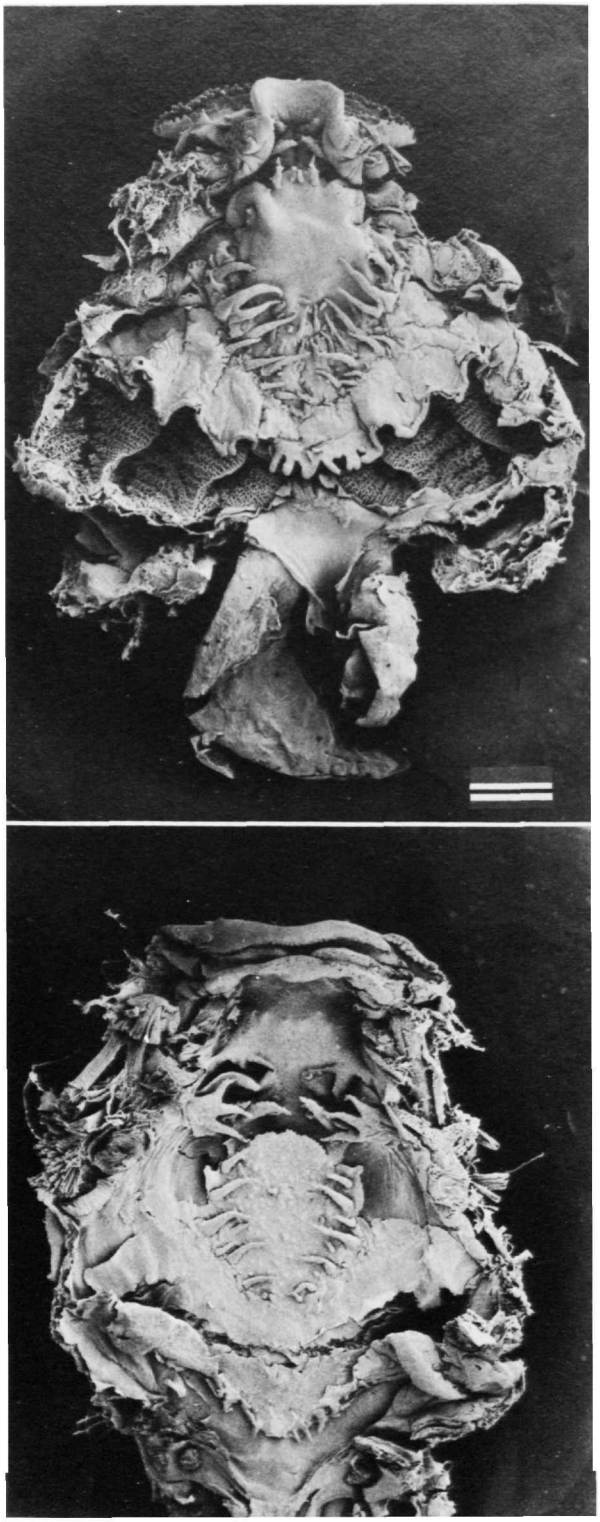


FIGURE 24.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Macrogenioglottus alipioi;* scale line = 1 mm.

interhyoideus and orbitohyoideus musculature. Lungs average length, longest about equal length of buccal floor, sacculate, other lung shorter but more sacculate.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth ovoid-triangular, about as long as wide. Four infralabial papillae, 1 pair anteromedial, 1 pair posterolateral, not touching on midline, all small, conical, with serrate and rugose anterior surfaces (Figure 52*c*). Four lingual papillae in slightly bowed forward transverse line; lingual papillae of average size, lateral larger, with surface rugosities. BFA egg-shaped; 15–25 papillae on each side; very small, conical, anterior BFA papillae extending to base of tongue anlage; 2 larger papillae on each side medial to buccal pockets arising from common base; all BFA papillae simple, thin, lacking bifurcations or extensive surface sculpturing; 4 medium-sized papillae in one transverse row, 6 papillae in a second row running across the BFA about 2/3 distance posteriorly; assorted pustulations and small papillae scattered about the posterior half of BFA. Three or four very small, prepocket papillae on each side. Another half dozen papillae just posteromedial to buccal pockets near BFA and as a cluster continuous with posterior BFA papillae. Buccal pockets long, 50% wider than long; primarily transversely oriented; perforated (?). Free velar surface of average length; conspicuous spicular support; very wavy free margin, broad peaks over free edge of each filter plate plus additional, small, irregular peak medially, medial to peak over 4th filter plate; distinct but irregular peaks bounding median notch; median notch broad, of average depth; secretory pits small, dense, conspicuous, associated with all marginal projections and in narrow zone along posterior margin of free velar edge.

Pharyngeal Cavity: Branchial baskets slightly wider than long, triangular; each branchial basket about 70% or more of remaining buccal floor area; deep, twice as wide as deep; 2nd filter cavity largest, 50% larger than 1st, 3–4 times 3rd; 1st filter cavity more longitudinally oriented than 2nd or 3rd. Second filter plate with straight dorsal edge; 3rd filter plate with slightly upward-bowing dorsal edge; 2nd filter plate 50% longer than tall, 3rd as long as tall; 2nd filter plate tipped medially at 45°, ventral portion of 3rd filter plate horizontal, dorsal portion of free edge curving upward overlapping lateral half of 3rd filter cavity by about 45°; cb 1 with 11 filter rows; cb 2 with 13; cb 3 with 10, cb 4 with 8. Filter mesh dense; filter rows wide with quaternary and higher order folding common. Filter rows of relatively even size, fully abutting. Filter canals 50% or less width of rows; 100% canopied except where exposed in dissection. Branchial food traps with secretory ridges. Glottis 50% covered by ventral velum; relatively small; lips average thickness; laryngeal disk not evident. Esophageal funnel narrow; esophagus of small diameter.

DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth triangular, about as wide as long; nares 25% distance from front of mouth to esophagus; median ridge 40% distance from front of mouth to esophagus. Prenarial arena with largely transverse but irregular row of 8 large pustulations. Nares large; internarial distance about 30% length of naris; nares largely transversely oriented; anterior narial wall thin, not tall, with tall, posteriorly directed, conical, prenarial papilla with some surface rugosities arising from midportion; posterior narial wall large with gently curved margin pointing downward, but no distinct narial-valve projection. Postnarial arena defined by 6 papillae on each side with largely transverse orientation although smaller more medial papillae turning anteriorly; largest papillae in middle of row; larger papillae with rugose anterior surfaces; transverse row of 4 unequal-sized conical papillae in posterior portion of postnarial arena. Median ridge large; semicircular free edge with many tiny serrations; anterior surface largely smooth with only 1 or 2 pustulations. Lateral-ridge papillae laterally compressed, flap-like structures, each with 3 conical projections, each projection with surface rugosities/pustulations; each lateral-ridge papilla about 1/2 size of median ridge. BRA egg-shaped; 10 papillae on each side; smallest papillae most caudal; pustulations scattered within BRA, a few extending anteriorly onto posterior surface of median ridge; all BRA papillae thin, pointed, not bifurcate. Few small papillae on far lateral midportion of buccal roof. Glandular zone very distinct; medium small secretory pits, barely continuous on midline; maximum length 1/8 length of buccal floor. Dorsal velum interrupted on midline; of average size; medial third on each side with papillate fringe, turning medially into esophagus.

Pharyngeal Cavity: Two distinct pressure cushions, lateral one (partially destroyed in dissection) apparently smaller, more medial cushion an elongate oval running anteromedial to posterolateral. Ciliary groove destroyed in dissection.

Megaelosia goeldii (Baumann)

FIGURE 25

MATERIAL.—USNM 241293, 241297 (two specimens dissected, stage 25, SVL 21.8 mm; stage 37, SVL 54.7 mm). Collected from a stream near Teresópolis, Rio de Janeiro, Brazil, 25 December 1977. Stage 25 specimen illustrated.

REFERENCE.—Lutz (1931) described and illustrated the external morphology.

GENERAL REMARKS.—Description based on stage 37 specimen, stage 25 specimen differences indicated in parentheses. Luxuriant gill filaments. Lungs slightly smaller than average, about equal to length of buccal floor (75%); not inflated.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth oval, but very broad, slightly wider than long, buccal floor overall strongly concave. Three pairs infralabial papillae in approximately transverse row; most medial pair small with unbifurcated rugose apices; 2nd pair lateral and slightly anterior, also of simple shape; largest pair posterolateral with hand-like palps bearing 6 long, rough fingers. (Two pairs of infralabial papillae; one huge anterior and lateral pair of hand-like structures with about 7 long, attenuate, interdigitating fingers; second pair simpler, smaller, each with a bifurcation, apices

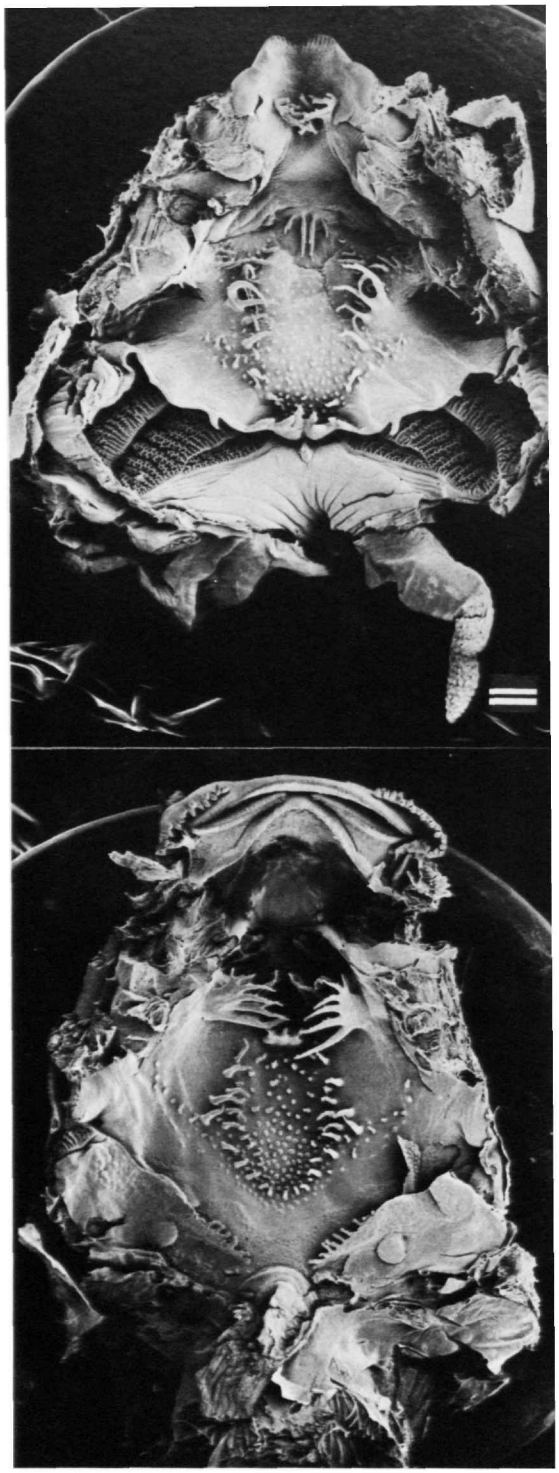


FIGURE 25.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Megaelosia goeldii;* scale line = 1 mm.

of posterior and more medial "fingers" touching on midline; all papillae with knobby anterior surfaces; see Figure 52*d*.) Long bare area between infralabial papillae and tongue anlage; 2 pair simple, pointed lingual papillae in transverse row, medial pair larger, but unequal in size. BFA an elongate oval, defined by 20–25 papillae on each side; largest papillae medial to buccal pockets; only largest BFA papillae bifurcate, all others thin cones with pointed apices but rugose anterior margins. Four to six (6–10) small assorted pustulations in prepocket region. About 4 small papillae within posterior portion of BFA, 10–12 irregularly scattered additional small papillae and pustulations immediately lateral to posterior 1/3 of BFA. Buccal pockets long, almost as long as wide; transversely oriented; perforated (not perforated). Free velar surface long with long, distinct, spicular support; area on one side 1/6–1/8 that of remainder of buccal floor; middle 1/2 of posterior margin of ventral velum directed dorsally rather than posteriorly; most medial portion of velum recurved such that free margin pointing toward front of mouth; posterior velar margin with distinct peak over 2nd filter plate and 3rd filter cavity; 6 long marginal papillae of subequal size in midportion, 1 marginally serrated; median notch present, but 1 of 5 (7) subequal notches in this region; secretory pits distinct, large, limited to marginal peaks and ventral surface of velum.

Pharyngeal Cavity: Branchial baskets transversely oval, slightly wider than long, of average size, each one equal in area to 1/4 (1/2) area of buccal floor; shallow, 6 times wider than deep. Filter cavities transversely oriented anteriorly, obliquely oriented posteriorly; filter cavities small due to dorsoventral depression; dorsal margins of 2nd and 3rd filter plates slightly concave, 2nd filter plate twice as long as tall, 3rd filter plate as long as tall; medially and posteriorly filter plates oriented almost horizontally such that top of 3rd filter plate touching bottom of 4th filter plate posteriorly, however, 3rd filter plate overlapping 4th filter plate anteriorly; cb 1 with 12 (10) filter rows, cb 2 with 15 (11), cb 3 with 11 (12), cb 4 with 11 (6). Filter mesh moderately dense with quaternary filter folds on some ridges. Filter rows wide, not abutting neighboring rows. Filter canals about equal to width of filter rows; 75%–90% canopied. Branchial food traps average size, relatively shallow; distinctly visible, evenly spaced, large, conspicuous secretory ridges. Glottis fully exposed (50% exposed), small, open (closed but probe patent); lips very distinct but narrow; glottis oriented forward on a large laryngeal disc projecting upward and over midportion of ventral velum (not over ventral velum). Esophageal funnel with wide profile.

DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth approximately triangular, length and width subequal; nares about 20% distance from front of mouth to esophagus; median ridge about 40% distance from front of mouth to esophagus. Prenarial arena smooth (arch of pustulations), surface bowed downward; one very small prenarial papilla far posterior adjacent to anteromedial corner of anterior narial wall. Nares small (large);

internarial distance very short; nares obliquely oriented; anterior narial wall tall, thickened particularly posterolaterally (height equal to internarial distance); anterior wall partially supported by cartilage posterolaterally; anterior wall with 2 or 3 attenuate, bifurcate papillae projecting posteromedially over posterior narial valve; posterior narial wall a simple thin flap with weak narial-valve projection. Postnarial arena an elongate isosceles triangle with median ridge as its base and apex between nares; postnarial papillae in multiple, evenly spaced rows in a triangular patch with about 20 (12–20) papillae on each side; largest postnarial papillae most medial, curved, pointing medially or posteromedially with rough, anterior, serrated edges; postnarial papillae decrease in size anterolaterally; single papilla on midline within postnarial arena. Median ridge square with projections from its two free corners and medial projection on ventral edge; all projections with rough anterior surfaces. Lateral-ridge papillae in form of very large longitudinally oriented ridge with 6 or 7 palmate (moose antler-like) projections, several of which with secondary bifurcations and rugosities (Figure 61*c*). BRA elongate "U" defined by about 15–20 papillae on each side; all BRA papillae thin, larger ones with terminal bifurcations and rugosities. Assorted small papillae in anterior portion of buccal roof grading posteriorly into smaller, more densely packed papules, other pustulations and papules extend laterally slightly anteriorly from posterior 1/3 of BRA; 6–10 papillae on each side within this area. Glandular zone narrow with irregular (wavy) anterior margin but distinctly visible with small (large), relatively dense (average density), secretory pits; glandular zone barely continuous across midline. Dorsal velum very distinct flap with secretory pits on full ventral surface; lateral 2/3 of free margin smooth, medial 1/3 papillate; turning strongly posteriad; dorsal velum discontinuous on midline.

Pharyngeal Cavity: Two very faint pressure cushions; lateral one more obliquely oriented, second rounded. Ciliary groove shallow, narrow (wider).

Odontophrynus americanus (Duméril and Bibron)

FIGURE 26

MATERIAL.—USNM 253687 (one specimen dissected, stage 37, SVL 22.9 mm). Collected from a reservoir at Hotel El Tirol, 19.5 km by road NNE Encarnación, Itapuá, Paraguay, 14 November 1976, by Mercedes S. Foster.

REFERENCE.—Cei (1980) provides a description and figure of the tadpole.

GENERAL REMARKS.—The full morphological description for this genus is based on *O. occidentalis* (following account). Differences only between *O. americanus* and *O. occidentalis* are noted. Lungs about equal buccal floor length; inflated. In general, papillae smaller and less numerous than in *O. occidentalis*.

VENTRAL ASPECT.—*Buccal Cavity:* Medial pair of infralabial papillae shorter than lateral pair. Buccal pockets perfo-

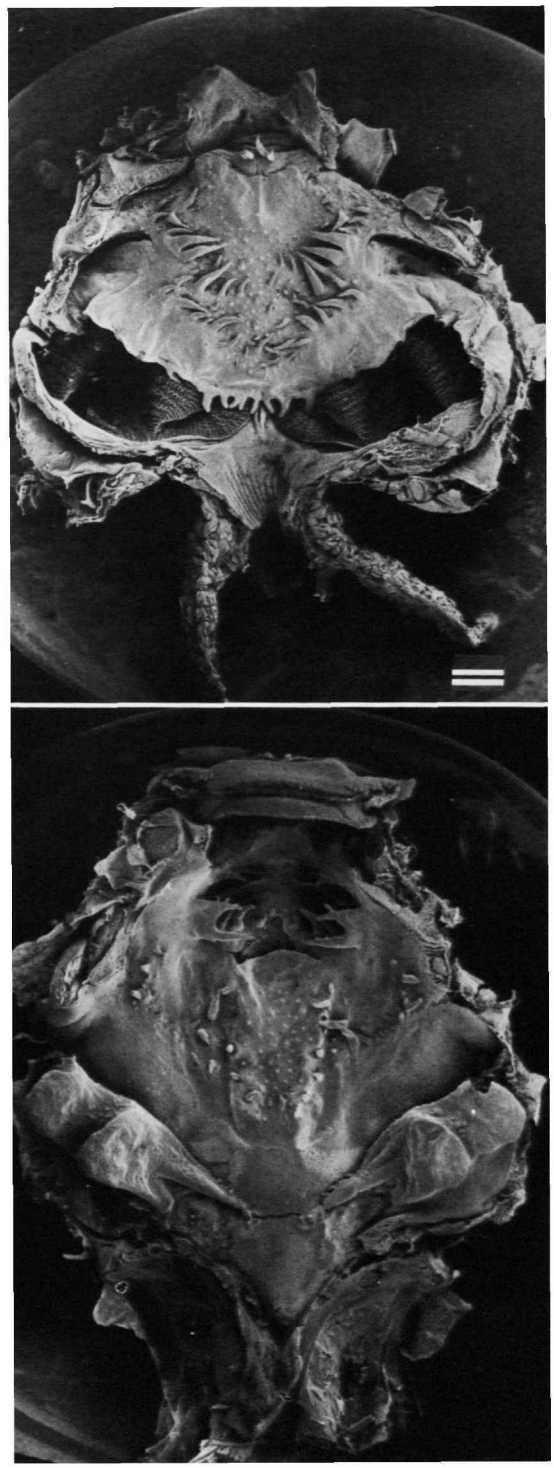


FIGURE 26.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Odontophrynus americanus;* scale line = 1 mm.

rated. Lateral peaks of free velar margin less distinct than in *O. occidentalis* with 6 papillae across midsection. Ceratobranchial 1 with 10 filter rows, cb 2 with 10, cb 3 with 10, cb 4 with 11.

Pharyngeal Cavity: Branchial food traps large, secretory rows even. Glottis 100% visible.

DORSAL ASPECT.—*Buccal Cavity:* Prenarial arena with poorly defined transverse ridge with pustulate apex. Anterior narial wall not as thickened as in *O. occidentalis;* posteriorly directed, conical, prenarial papillae arising from midportion of anterior wall. Median ridge broad, semicircular flap (Figure 61*d*).

Pharyngeal Cavity: Medial pressure cushion slightly larger than lateral. Ciliary groove broad and shallow.

Odontophrynus occidentalis (Berg)

FIGURE 27

MATERIAL.—No number (one specimen dissected, stage 36, SVL 18.5 mm). Collected from Sosneado, Río Salado Valley, SW Mendoza Province, Argentina, 6 March 1977.

REFERENCE.—Cei (1980:308–310, fig. 125) described and illustrated the external morphology and indicated that the larvae occur in clear streams or springs in semi-arid sandy areas.

GENERAL REMARKS.—Lungs well developed, running length of body, subequal to floor of mouth; inflated. Gill filaments typical.

VENTRAL ASPECT.—*Buccal Cavity:* Buccal floor triangular, approximately as wide as long. Four infralabial papillae in transverse line; medial 2 tall and attenuate; lateral ones cup-shaped with anterior surface pustulate. Four tall, attenuate, lingual papillae in transverse row. U-shaped BFA with 20–30 BFA papillae per side; BFA papillae pointed, sickle-shaped, unbifurcated, pointing medially or anteriorly. Five to ten prepocket papillae. Fifteen to twenty thin, medium to large, anteriorly directed papillae in posterior 1/2 of BFA; four times as many pustulations scattered among the papillae. Buccal pockets shallow, elongate, 50% wider than long; transversely oriented; perforated (?). Long, free, velar margin with conspicuous spicular support; semicircular, free, velar edge with distinct papillae above each filter cavity and a transverse row of 5 irregular blunt papillae in the midsection above the glottis; small, shallow, median notch; secretory pits visible in dorsal view, but largely limited to papillae on free velar margin.

Pharyngeal Cavity: Branchial baskets 75% wider than long; each branchial basket about 60%–70% remaining buccal floor area; relatively deep; 1st and 2nd filter cavities subequal, 3rd filter cavity 30% of other two. Straight dorsal margin on 2nd filter plate and upward curving margin on the 3rd filter plate; dorsal edge of 3rd filter plate folded over lateral edge of 3rd filter cavity; cb 1 with 9 filter rows, cb 2 with 12, cb 3 with 11, cb 4 with 9. Filter mesh dense; many tertiary filter

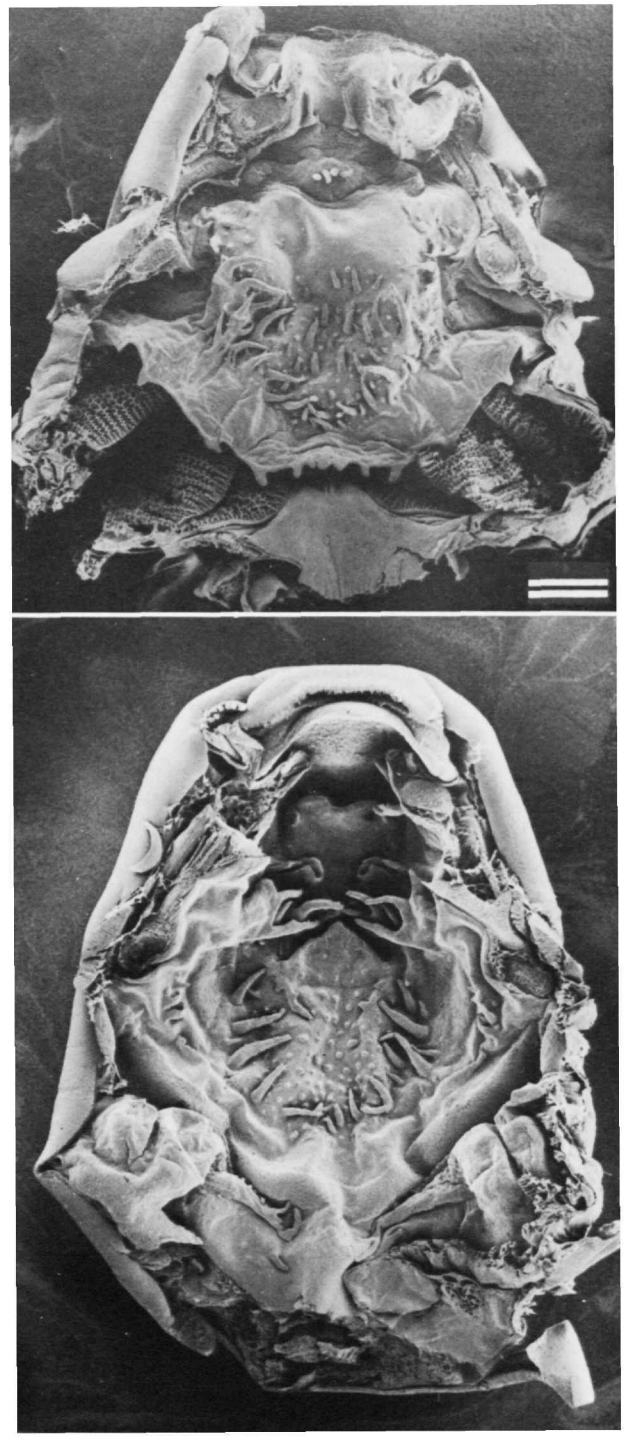


FIGURE 27.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Odontophrynus occidentalis;* scale line = 1 mm.

folds; filter rows relatively uniform; of average width; rows not abutting, slightly separated. Filter canals narrower than rows; filter canals 80% canopied. Conspicuous secretory ridges on branchial food traps. Glottis 50% visible; narrow lips. Esophageal funnel narrow; esophagus of average diameter.

DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth diamond-shaped, length equal to width; nares about 25% distance from front of mouth to esophagus; median ridge about 50% distance from front of mouth to esophagus. Prenarial arena with ridged plate projecting forward and downward from center of the prenarial arena; free edge broad and doubly convex. Nares average size; internarial distance about 50% width of naris; anterior narial wall thick and pustulate with lateral,V-shaped projection; posterior narial wall tall and medially elongate, yielding an anteriorly directed flap. Three postnarial papillae in oblique line parallel to nares and 1/2 way from nares to median ridge on each side; 2nd postnarial papilla largest, all with jagged anterior margins. Median ridge large, simple, triangular flap. Lateral-ridge papillae a rectangular flap with 2 large, medially directed, finger-like projections and secondary papillae on anterior free edge, in line with the postnarial papillae. Two small papillae immediately anterior to median ridge. BRA oval with 8–15 papillae on each side, 4 small papillae lateral to BRA in tight cluster; heavy pustulation in middle of BRA. Distinct glandular zone with relatively smooth anterior margin. Dorsal velum not long; interrupted on the midline; few small but distinct papillae on medial termination.

Pharyngeal Cavity: Two distinct pressure cushions on each side; medial 50% larger than lateral. Ciliary groove destroyed in dissection.

Paratelmatobius lutzii Lutz and Carvalho

FIGURE 28

MATERIAL.—USNM 209371 (one specimen dissected, stage 27, SVL 9.8 mm). Collected from a roadside rivulet at Brejo da Lapa, Rio de Janeiro, Brazil, 18 January 1976.

REFERENCE.—Heyer (1976) described and figured a tadpole that is presumed to be the larva of *P. lutzii*.

GENERAL REMARKS.—Buccal roof cracked in SEM preparation. Lungs very narrow, about 80% length of buccal floor; not inflated. Moderate amount of filamentous gills.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth almost inverted T-shaped, about as long as wide. Single infralabial papilla on each side consisting of short, laterally compressed palp with knobby margins; hemispheric swelling in far lateral and posterior edge of infralabial region with keratinized apical peak. Eleven lingual papillae arranged in large anteriorly directed arch; of unequal size, largest most anterior and medial, pointing anteriorly; papillar arch very wide, as wide as lower beak (Figure 53*c*). BFA shape a truncated oval, open anteriorly, pointed posteriorly; bounded by about 50 papillae on each side,

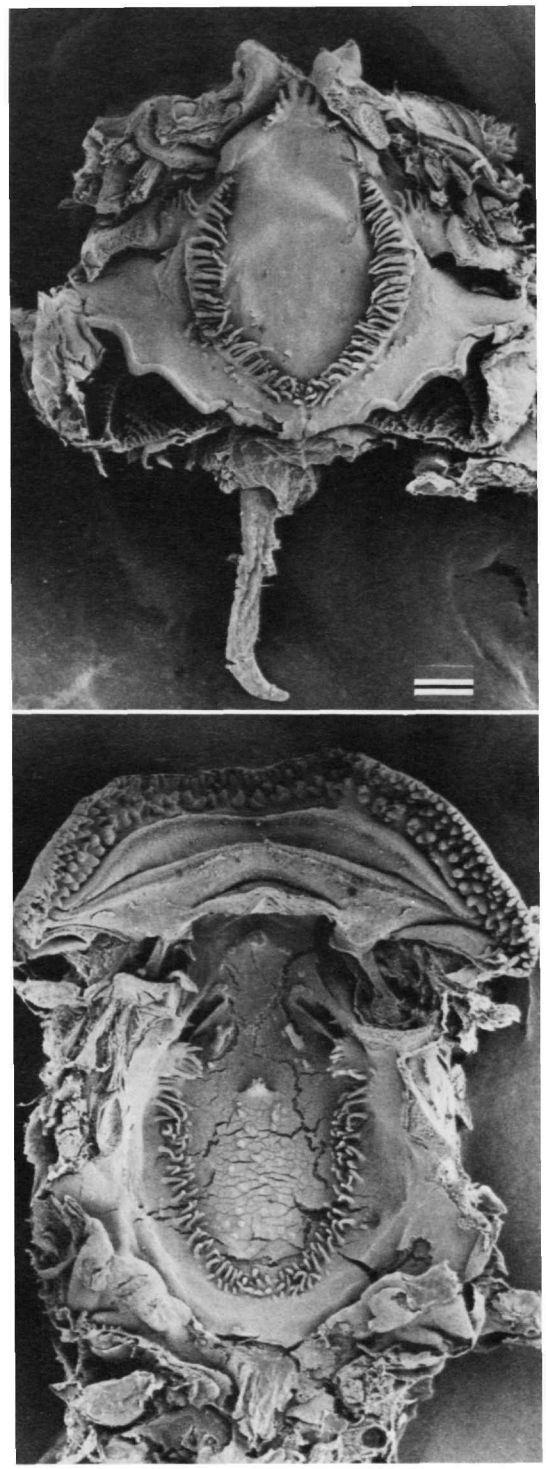


FIGURE 28.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Paratelmatobius lutzii;* scale line = 400 μm.

unusual in their uniformity in size and origin from such a narrow band; all BFA papillae medially directed, thin, pointed, some with tops a bit turned or twisted, otherwise straight; most anterior and posterior BFA papillae noticeably smaller than others; no pustulations or papillae within BFA. Anteriorly directed papillate fringe of 6–10 prepocket papillae on each side, running in a cluster almost perpendicular to anterior BFA papillae. A row of tiny anterolateral to posteromedially arranged papillae on each side running parallel to row of papillae defining posterior 1/3 of BFA, each row consisting of about 6–10 stubby papillae. Buccal pockets small; 4 times as wide as long; oriented at about 25° from transverse plane; perforated. Free velar surface relatively short, particularly medially; no obvious spicular support; posterior margin transverse rather than curved; large but blunt cusp over edge of 2nd filter plate, weaker cusp over edge of 3rd filter plate; median notch shallow and tiny, not bounded by distinctive papillae; uniform zone of secretory tissue in band along entire posterior edge of ventral velum with small secretory pits of uniformly high density on and between peaks.

Pharyngeal Cavity: Branchial baskets 10% wider than long; right-triangular in shape with anterolateral to posteromedial hypotenuse; each branchial basket about 50% remaining area of buccal floor; branchial baskets shallow, 4 times as long as deep. Second filter plate free edge arched downward slightly, 3rd filter plate lying on side such that the normally free dorsal margin of the 3rd plate abutting instead with the ventral margin of a very abbreviated 4th filter plate, resulting in a single, common, medial, filter cavity rather than separate 2nd and 3rd cavities; 2nd filter plate 3 times as long as tall, 3rd twice as long as tall; 2nd filter plate tipped at about 45°, 3rd tipped up at about 45°, meeting base of very short 4th filter plate; cb 1 with 10 or 11 filter rows, cb 2 with 12, cb 3 with 9, cb 4 with 5. Filter mesh low density; secondary but few tertiary folds. Filter rows thin, not abutting. Filter canals equal to twice width of filter rows; 20%–80% canopied. Branchial food traps shallow; secretory ridges shallow and evenly spaced. Glottis open; 80% covered by ventral velum; bounded by narrow lips; round but not distinct laryngeal disk. Esophageal funnel narrow.

Dorsal Aspect.—*Buccal Cavity:* Roof of mouth unusually broad anteriorly, just longer than wide; nares about 30% distance from front of mouth to esophagus; median ridge about 50% distance from front of mouth to esophagus. Prenarial arena very long and large with large, single, blunt, knobby, median papilla and few pustulations on each side extending in arc posterolaterally from median papilla. Nares large; internarial distance about 50% length of naris; 45° orientation from transverse plane; anterior narial wall with distinct anteromedial swelling and distinct, conical, posteromedially directed, prenarial papilla arising from lateral 1/3 of wall bounded by pustulations on both sides; posterior narial wall lacking projections. Postnarial arena broad and defined by 3 papillae on each side; papillae arranged in oblique row from anteromedial to posterolateral; anterior and posterior postnarial papillae very small, simple, conical; middle postnarial papilla 5–10 times size of other 2 with irregular, jagged, anterior surfaces and apex; small pustulations but no papillae within postnarial arena.

Median ridge narrow, tall, triangular; of average size; papillate apex, pustulate lateral margins. Lateral-ridge papillae far lateral; laterally compressed flaps supporting up to 10 relatively small, thin, finger-like papillae, most with pointed tips, few with terminal bifurcations. BRA U-shaped; about 50 papillae on each side; BRA papillae rather uniform size, larger anteriorly, less dense posteriorly; papillae simple, thin, pointed, lacking rugosities or bifurcations; BRA papillate rows relatively straight anteriorly running to base of lateral-ridge papillae. One or two papillae scattered within central portion of BRA along with several dozen pustulations; fine pustulate fringe in longitudinal row in most lateral portion of buccal roof. Glandular zone a narrow band, just discontinuous on midline, with very small secretory pits. Dorsal velum with fairly smooth anterior margin; broadly interrupted medially; most medial portion slightly papillate.

Pharyngeal Cavity: Two pressure cushions, lateral one smaller, longitudinally oriented, medial one 3 times as large, transversely oriented. Ciliary groove relatively narrow and deep.

Physalaemus petersi (Espada)

Figure 29

Material.—USNM 247549 (one specimen dissected, stage 37, SVL 14.1 mm). Collected from a stream and swamp at Zona Reservada de Tambopata, Madre de Dios, Peru, 19 August 1983 by S.L. Jewett, H. Ortega, and R.P. Vari. Roof of mouth destroyed during SEM preparation.

Reference.—Duellman (1978) described the larva.

General Remarks.—The full morphological description for this genus is based on *P. pustulosus* (following account). Only those features that differ from *P. pustulosus* are described. Lungs large; larger twice size of smaller; larger 20% longer than buccal floor; inflated.

Ventral Aspect.—*Buccal Cavity:* Four asymmetrical lingual papillae, 3 clustered on midline, 1 separated; not as tall as in *P. pustulosus*. One or two very small prepocket papillae. Buccal pockets perforated. Secretory tissue band broader than in *P. pustulosus*.

Pharyngeal Cavity: Branchial baskets shallower than in *P. pustulosus*. Free edge of 3rd filter plate taller and oriented more vertically, as in most other tadpoles, such that 2nd and 3rd filter cavities distinct; cb 1 with 11 filter rows, cb 2 with 10, cb 3 with 10, cb 4 with 7. Filter mesh denser than in *P. pustulosus*, quaternary folds common. Filter rows wide, largely abutting; filter canals 80%–100% canopied. Glottis 50% exposed.

Dorsal Aspect.—*Buccal Cavity:* Prenarial arena ridge

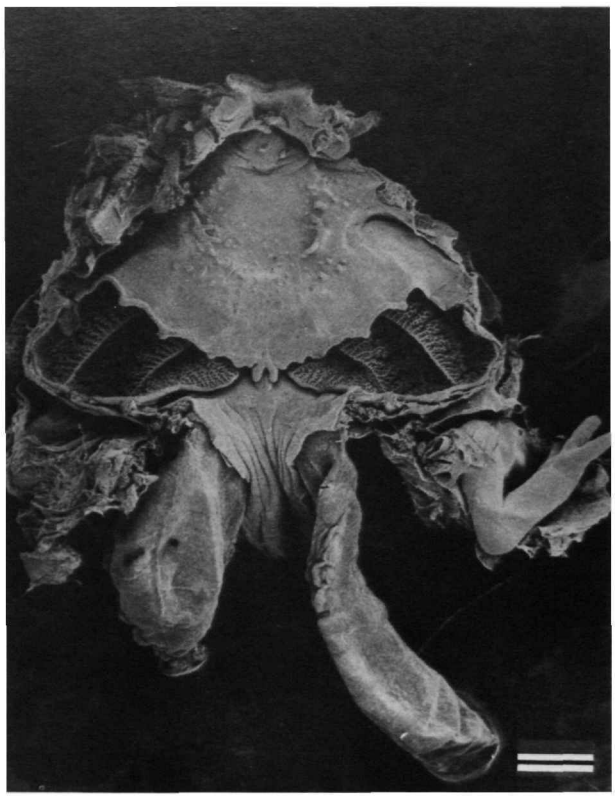


FIGURE 29.—SEM micrograph of floor of oral cavity of *Physalaemus petersi;* scale line = 1 mm.

lacking median notch, structurally simpler than in *P. pustulosus*. Nares smaller and slightly farther apart than in *P. pustulosus*. Thickened bicuspid ridge extending from anterolateral portion of anterior narial wall with serrated margin. Prenarial arena wider with papillae not as large as in *P. pustulosus;* anterior prenarial papillae about twice size of posterior prenarial papillae. Lateral-ridge papilla slightly larger than median ridge. BRA more oval than in *P. pustulosus*.

Physalaemus pustulosus (Cope)

FIGURE 30

MATERIAL.—No number (one specimen dissected, stage 37, SVL 9.5 mm). Collected from Playa Blanca, Costa Rica, 5 March 1970, by R.J. Wassersug.

REFERENCE.—Breder (1946) described and figured the external morphology.

GENERAL REMARKS.—The tadpole lives in small ephemeral pools of water. Lungs of a second specimen, stage 29, curled, long, and septate, just less than length of buccal floor; uninflated. Typical filamentous gills.

VENTRAL ASPECT.—*Buccal Cavity:* Buccal floor approximately 20% wider than long. Four infralabial papillae, 1 pair small and anteromedial; other pair large and posterolateral; larger pair extending dorsally and abutting anterior to the tongue; both pairs with pustulate, jagged margins. Four equal-sized, very tall and thin, lingual papillae, with pustulate tips; arranged in a square pattern. BFA wide, defined by nearly parallel lateral rows of papillae; approximately 6 BFA papillae on each side; papillae with short, truncated tips, a few bifurcated. No prepocket papillae. Four papillae scattered about the posterior portion of BFA; approximately 20 pustulations on the central buccal floor. Buccal pockets shallow; obliquely

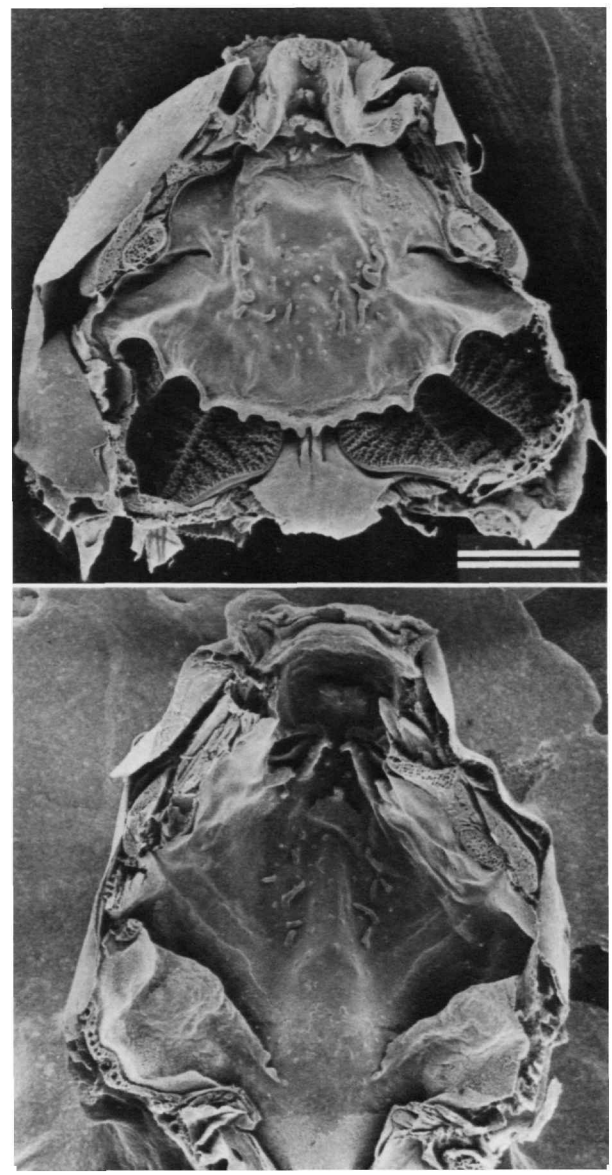


FIGURE 30.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Physalaemus pustulosus;* scale line = 1 mm.

oriented at about 30° from transverse plane; unperforated. Free velar surface gently scalloped; long with distinct spicular support; small, distinct, median notch with a short blunt papilla on each side; distinct band of secretory tissue along whole free velar margin.

Pharyngeal Cavity: Branchial baskets wide, 30% wider than long; each branchial basket 60%–70% of remaining buccal floor area; 50% longer than deep. Most medial filter plate more horizontal than vertical and abutting with top of 3rd filter plate such that only a single, large, common, 2nd and 3rd filter cavity defined. Free margins of 2nd and 3rd filter plates relatively straight; cb 1 with 8 filter rows, cb 2 with 12, cb 3 with 11, cb 4 with 7. Filter mesh fairly dense with conspicuous tertiary folds; filter cavities at least 80% canopied. Branchial food traps of moderate size with conspicuous, long, uniform, secretory ridges. Glottis open; fully exposed below and between medial papillae of ventral velum; glottal lips tall; large, elevated laryngeal disc. Esophageal funnel narrow.

Dorsal Aspect.—*Buccal Cavity:* Roof of mouth triangular; slightly wider than long. Nares about 25% distance from front of mouth to esophagus; median ridge about 40% distance from front of mouth to esophagus. Anteriorly directed, crescentic ridge with median notch in middle of prenarial arena; anterior margin pustulate, posterior base with a single median papilla. Nares average size; internarial distance short, less than 50% long axis of naris; anterior narial wall thick and pustulate; thickened bicuspid ridge extending from anterolateral portion of anterior narial wall; tall posterior narial wall, elongated medially. Postnarial arena a narrow triangle with 2 very tall papillae, each with smooth posterior margin and pustulate anterior margin, arranged in oblique line on each side with lateral-ridge papillae. Triangular, asymmetrical, median ridge, 1/2 height of prenarial papillae. Lateral-ridge papillae short, anteriorly concave palps with rugose margins, slightly smaller than median ridge. BRA shaped like elongated rectangle with 6 papillae on each side; papillae small with jagged tips. Approximately 16–20 pustulations randomly distributed within BRA. Conspicuous glandular zone with uniformly dense secretory pits; anterior margin of zone V-shaped but wavy anterolaterally and irregular medially. Dorsal velum long laterally, broadly interrupted on the midline.

Pharyngeal Cavity: Two pressure cushions per side; both oval; largest medial. Ciliary groove very distinct; very broad and shallow.

Pleurodema borellii (Peracca)

Figure 31

Material.—KU 160729 (two specimens dissected, both stage 37, SVLs 12.6, 14.2 mm). Collected from 18 km SSE Tafi del Valle, 1800 m, Tucumán, Argentina.

Reference.—Cei (1980) described the larva.

General Remarks.—Description based on first specimen. Lungs well developed, about equal length of buccal floor.

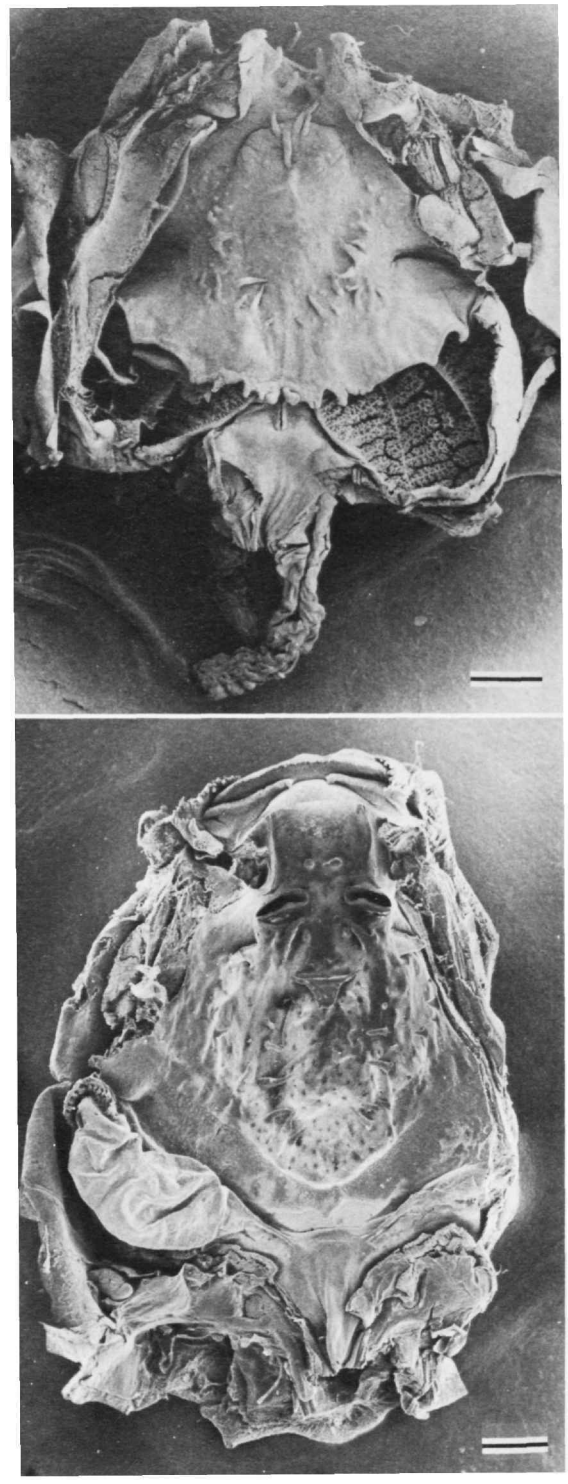


Figure 31.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Pleurodema borellii;* scale lines equal 1 mm.

Filamentous gills short, not extensive.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth triangular, length about equal width. Four infralabial papillae in a transverse row, directed anteriorly; subequal, slightly curved, conical, medium small, with rugose surfaces (second specimen Figure 54, top). Four lingual papillae in a transverse row; attenuate; medial pair 50% larger than lateral pair. BFA U-shaped; 10–15 BFA papillae on each side, small, simple, attenuate cones, most curving anteromedially. No prepocket papillae. About 12 pustulations on posterior 1/2 of buccal floor; about 6 anterior to buccal pockets. Buccal pockets small; twice as wide as long; transversely oriented; perforated. Free velar surface relatively long with delicate spicular support; posterior margin irregularly sculptured with simple gradual peaks over free edge of 2nd filter plate and cluster of irregular peaks running across middle 1/3 of free velar edge; median notch small, bounded by distinct round papilla on each side; secretory pits present but largely limited to peaks on free velar margin.

Pharyngeal Cavity: Branchial baskets as long as wide, roundish; branchial baskets large, each about 70% remaining buccal floor area, almost as deep as wide. Bottom of 4th filter plate abutting directly with top of 3rd filter plate, resulting in common 3rd filter cavity; first filter plate very shallow such that 1st filter cavity barely separated from 2nd and 3rd filter cavity. First filter plate almost vertical, 2nd filter plate tipped 45°; 3rd filter plate with single anterolateral face, sloping about 45°; 4th filter plate almost vertical. First filter plate almost as tall as long, 2nd and 3rd filter plates 4 times as long as tall, 4th filter plate as long as tall; cb 1 with 10 filter rows, cb 2 with 10, cb 3 with 10, cb 4 with 7. Filter mesh dense with tertiary and higher folds; filter rows of relatively uniform width; filter rows slightly separated; filter canals as wide as filter rows, 80% canopied. Two branchial food traps on each side with well-developed, secretory ridges descending to anterior medial portion of 2nd filter plate. Glottis open; small; 75% exposed; thin but distinct lips; indistinct laryngeal disk. Esophageal funnel very narrow.

DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth triangular; nares about 25% distance from front of mouth to esophagus; median ridge about 40% distance from front of mouth to esophagus. Prenarial arena smooth except for 2 small blunt papillae in transverse row in middle of arena. Nares of average size; internarial distance about 60% length of naris; orientation 15° from transverse plane; anterior narial wall simple, lacking projections; posterior wall with weak, triangular, narial-valve projection. Postnarial arena bounded on each side by 3 papillae in an anteromedial to posterolateral row; 1st and 3rd papillae very small, blunt; middle larger and more attenuate with slightly roughened anterior surfaces. Median ridge an elongate trapezoid of average size with a few pustulations on lateral margins. Lateral-ridge papillae laterally compressed small triangular flaps, about equal in area to median ridge. BRA poorly defined by 7 papillae on each side; BRA papillae all simple, attenuate, conical. Two pustulations in transverse row at anterior end of postnarial arena; random pustulations within posterior end of postnarial arena; 2 or 3 lateral-roof papillae isolated on buccal roof. Glandular zone very long with V-shaped, smooth, anterior margin, narrowing anteriorly; 1/6 length of buccal floor; smooth, distinct, anterior margin; secretory pits particularly conspicuous anteriorly and laterally. Dorsal velum of average length, barely continuous across midline with smooth free edge.

Pharyngeal Cavity: Single, large, round pressure cushion on each side. Ciliary groove broad and shallow.

Pleurodema brachyops (Cope)

FIGURE 32

MATERIAL.—KU 129101 (one specimen dissected, stage 37, SVL 13.8 mm). Collected from Cumaná, Sucre, Venezuela.

REFERENCE.—Duellman and Veloso (1977) provide external characteristics of the larva.

GENERAL REMARKS.—Lungs present, of average size. Gill filaments present, of average development.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth 20% wider than long. All infralabial papillae with rugose surfaces; lateral pair pointing more dorsally than in *P. borellii.* In addition to pustulations, 4 or 5 papillae within BRA. Area above median notch irregular; median notch asymmetrical and small.

Pharyngeal Cavity: Branchial baskets 25% wider than long; each branchial basket 80% area of remaining buccal floor area, 50% wider than deep. Second and 4th filter plates larger and taller than in *P. borellii;* 4th filter plate almost horizontal (Figure 56*c*). Second filter plate twice as long as tall, 3rd 3 times as long as tall; cb 1 with 11 filter rows, cb 2 with 10, cb 3 with 11, cb 4 with 7. Glottis 50% exposed. Esophageal funnel broader than in *P. borellii.*

DORSAL ASPECT.—*Buccal Cavity:* Prenarial arena with 2 lunate shelves in middle of arena. Anterior narial wall with some rugosity. A small median papilla just in front of median ridge in postnarial arena. Median ridge wider, triangular. Lateral-ridge papillae more irregular in shape. Less than 6 BRA papillae on each side. Secretory pits smaller and secretory zone of more uniform length than in *P. borellii.* Dorsal velum discontinuous across midline.

Pleurodema bufonina Bell

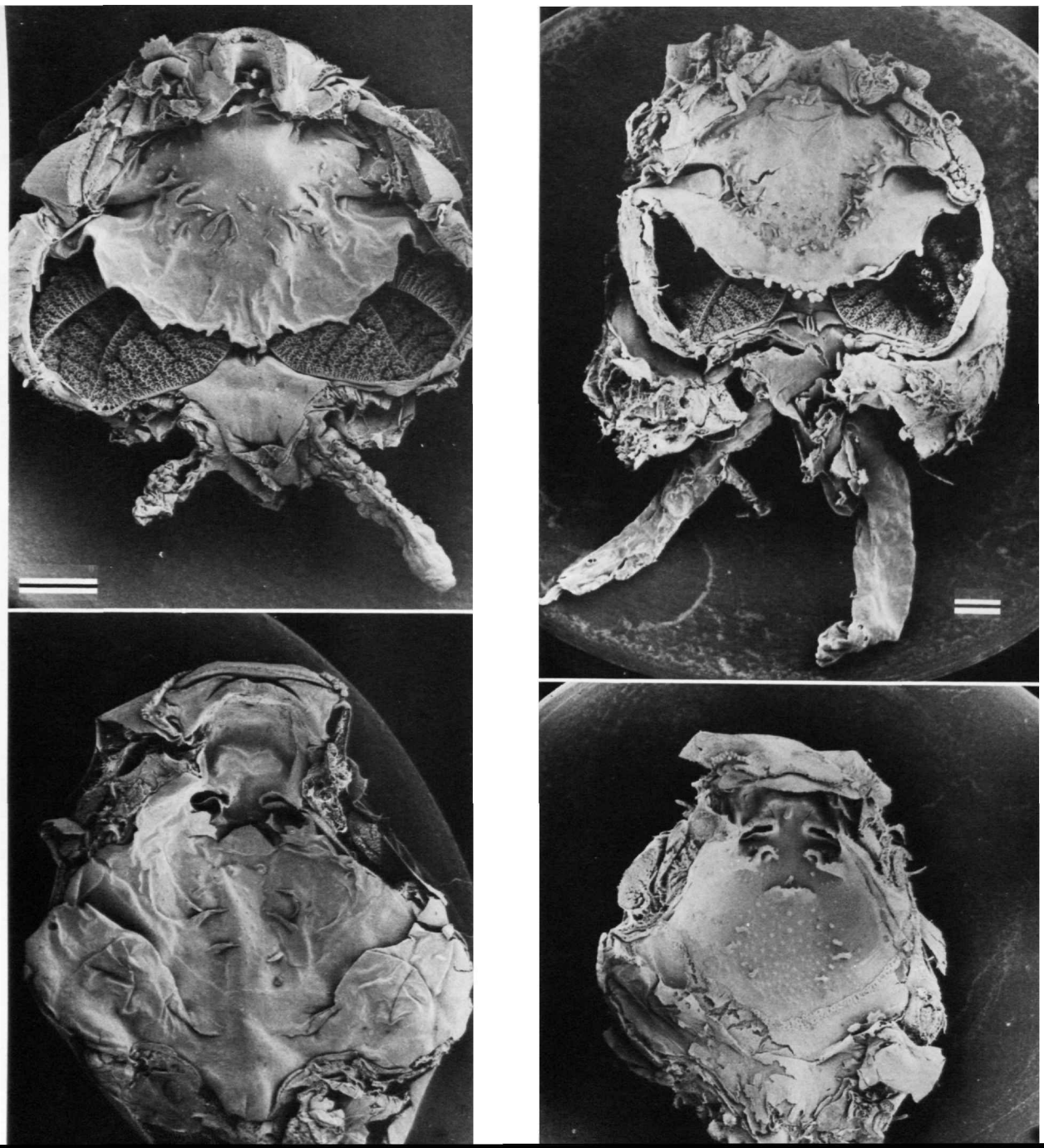
FIGURE 33

MATERIAL.—KU 160772 (two specimens dissected, stages 37, 38, SVLs 16.6, 19.0 mm; first specimen illustrated). Collected from Confluencia Traful, 750 m, Neuquén, Argentina.

REFERENCE.—Cei (1980) described and figured the larva.

GENERAL REMARKS.—Lungs larger than in *P. borellii.*

VENTRAL ASPECT.—*Buccal Cavity:* BFA wider than in *P. borellii;* 20 BFA papillae on each side, in a row turning laterally



in prepocket area (approximately 6 prepocket papillae on each side). About 30 pustulations on posterior 1/2 of BFA; 6–10 pustulations anterior to buccal pockets. Velar marginal cusps more distinct than in *P. borellii,* 3 distinct cusps on each side, one over each of 2nd, 3rd, and 4th filter plates, additional cusp near median notch in addition to peaks surrounding median notch. Secretory pits on very margin of velum between and on cusps.

Pharyngeal Cavity: Second filter plate a bit taller than in *P. borellii;* cb 1 with 10 filter plates, cb 2 with 12, cb 3 with 10, cb 4 with 8. Glottis 50%–100% exposed.

Dorsal Aspect.—*Buccal Cavity:* Lunate ridges in prenarial arena with pustulate margins, not as distinct as in *P. brachyops;* single median papilla just behind ridges. Anterior narial wall similar to but more rugose than in *P. brachyops.* First papilla in postnarial arena larger than in *P. borellii,* 2nd papilla curving backwards; additional median cylindrical papilla in posterior portion of postnarial arena. Median ridge with broad base tapering to truncated peak. BRA defined by less than 6 papillae on each side. Thirty to forty pustulations scattered throughout postnarial arena. Glandular zone of uniform length with extremely conspicuous margin with very large secretory pits. Dorsal velum discontinuous across midline.

Pleurodema cinerea Cope

Figure 34

Material.—KU 164009 (3 specimens dissected, stages 31, 32, 33, SVLs 21.0, 20.6, 23.9 mm respectively; stage 32 specimen illustrated). Collected from 4 km W Santa Rosa, 4010 m, Puno, Peru.

Reference.—Cei (1980) described and illustrated the larva.

General Remarks.—Because of the distinctiveness of this species from the previous species of *Pleurodema* dissected, a complete description is given. Lungs large, 25% longer than buccal floor; sacculate. Luxuriant external gill filaments. Rostrum curves ventrally more than is evident in illustration of the roof of the mouth.

Ventral Aspect.—*Buccal Cavity:* Floor of mouth triangular; about as long as wide. Four infralabial papillae in a transverse row; medial pair simple, attenuate; lateral pair about 4–5 times larger than medial pair, anteroposteriorly flattened, projecting dorsally, with very serrate margins and rugose anterior surfaces. Two lingual papillae, attenuate, with or without slightly roughened surfaces. BFA ovoid; 30–40 BFA papillae per side; BFA papillae attenuate, sickle-shaped; largest bifurcate or trifurcate, rest simple. Six to ten prepocket papillae per side; all relatively simple, conical. About 10 papillae in middle and posterior region of BFA; additional oblique row of papillae on each side beginning anterolaterally to buccal pockets running posteromedially and merging with papillae forming back of BFA; scattered pustulations amongst all

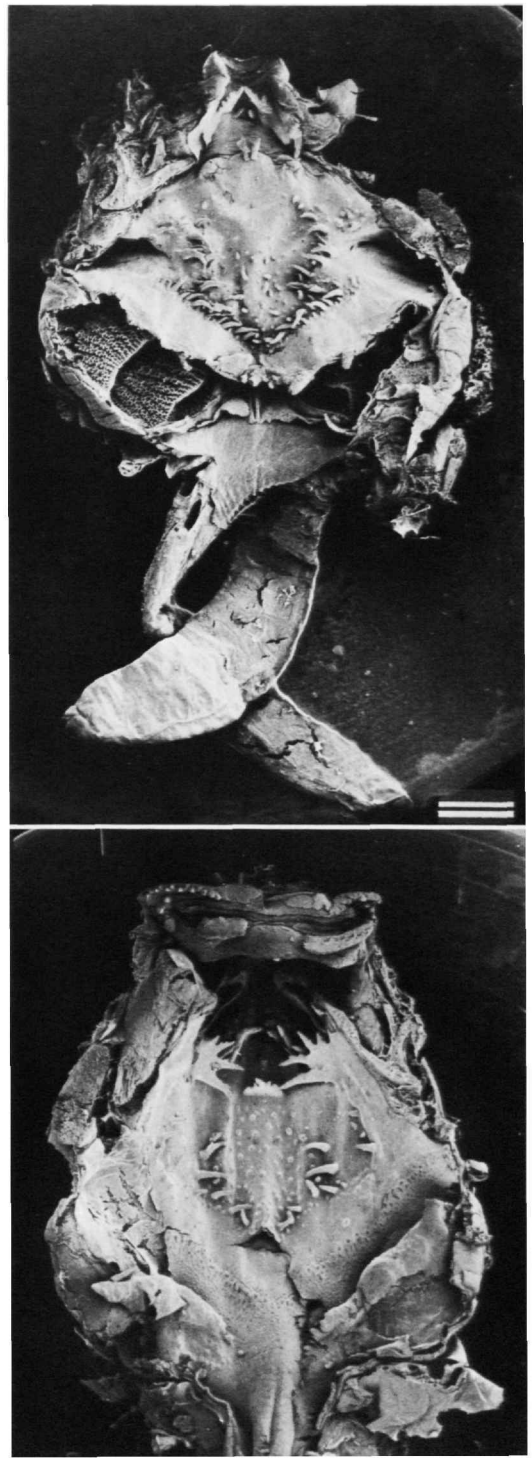


Figure 34.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Pleurodema cinerea;* scale line = 1 mm.

papillae, densest in posterior 1/2 of BFA. Buccal pockets of average size, but larger than in other *Pleurodema;* 25% wider than long; as deep as long; oriented about 15° from transverse plane; perforated. Free velar surface of average length, entire extent about 60% rest of buccal floor; distinct spicular support; posterior margin sculptured, with more distinctive peaks than in other *Pleurodema* dissected; 3 distinct peaks over filter cavities, largest over medial margin of 4th filter plate; peaks over 3rd and 4th filter plates directed medially; narrow, small, median notch surrounded by fairly large globose papillae; secretory pits large and conspicuous, particularly on margin of free velar surface.

Pharyngeal Cavity: Branchial baskets about as wide as long, rounded; each branchial basket about 60% remaining buccal floor area; 2/3 as deep as long; 1st and 2nd filter cavities subequal, 3rd 50% smaller (Figure 56*d*). Dorsal edge of 2nd filter plate relatively straight; edge of 3rd filter plate curving upward greatly, covering 3/4 of 3rd filter cavity; 1st filter plate 20% longer than tall, 2nd, 3rd, and 4th filter plates as long as tall; 1st and 4th filter plates vertical, 2nd tipped at 45°, 3rd tipped at 30° from horizontal with top running horizontally over 3rd filter cavity; cb 1 with 10 filter rows, cb 2 with 11, cb 3 with 8, cb 4 with 7. Filter mesh of average density; tertiary folds abundant; filter rows of variable width; filter rows largely not abutting; filter canals of equal width to rows or 20% wider, 0%–80% exposed. Three branchial food traps; secretory ridges present. Glottis 50% or more exposed; large, open, with thin, relatively small lips on an indistinct laryngeal disk. Esophageal funnel relatively broad; esophagus of average diameter.

Dorsal Aspect.—*Buccal Cavity:* Roof of mouth pentagonal, 20% longer than wide; nares 25%–30% distance from front of mouth to esophagus; median ridge 45% distance from front of mouth to esophagus. Prenarial arena long, but surface smooth. Nares large; internarial distance 50% length of naris; nares obliquely oriented at 45°; anterior narial wall with rugosities on most anterior portion; a small papilla arising from midportion of anterior wall; posterior narial wall a thin flap lacking a narial-valve projection. Postnarial arena defined by 5 papillae on each side running in an oblique row parallel to nares; next to last papilla in series largest, with knobby apex; smallest papilla most anterior, other papillae ascendingly larger except last, last 50% length of penultimate; postnarial papillae simple; single, small, median papilla in posterior postnarial arena.

Median ridge small, jagged, lunate flap with terminal papilla. Lateral-ridge papillae laterally compressed, hand-like structures with 4–6 attenuate pointed fingers with jagged margins, 3–4 times size of median ridge. BRA diamond-shaped, almost as wide as long; 8–12 BRA papillae per side, all simple, attenuate. Four small, lateral-roof papillae in row running from anteromedial to posterolateral on each side; pustulations scattered between postnarial arena and nares; other pustulations between posterior limit of papillae on lateral-roof region and BRA and within BRA proper. Glandular zone distinct; defined by large, conspicuous, secretory pits, anterior secretory pits primarily oriented in longitudinal row. Dorsal velum widely interrupted on midline; tiny papillae/pustulations at medial end providing delicate sculpture to medial edge on each side.

Pharyngeal Cavity: At least 2 pressure cushions, otherwise region destroyed in all specimens. Ciliary groove broad and shallow.

Pleurodema nebulosa (Burmeister)

Figure 35

Material.—No number (2 specimens dissected, stage 35 and 37, SVL 11.2 and 14.5 mm respectively, former specimen illustrated). Collected from 20 km W Encan, San Juan, Argentina, 10 February 1977, by J.M. Cei.

Reference.—Cei (1980:380, fig. 164) described and illustrated the external morphology and reported that the larva occurs in clayish water of lagoons and temporary summer pools in xerophilous scrub arid zones.

General Remarks.—Because of distinctiveness of this species from the other species of *Pleurodema* dissected, a complete description is given. Lungs well developed, medium-sized, less than 20% length of head. Gill filaments average size.

Ventral Aspect.—*Buccal Cavity:* Floor of mouth triangular, relatively wide posteriorly; length to width ratio 1:1. Two pair simple, unbifurcated infralabial papillae in transverse row; 1 pair adjacent to midline, other near angle of jaw; lateral pair larger. Four tall, thin, lingual papillae in slightly forward-arching, transverse row; subequal. BFA almost square; approximately 25–40 BFA papillae in a patch of even density across the midline, all strongly curved medially or posteriorly and unbifurcated. Six to eight large prepocket papillae, posteriorly directed. Buccal pockets conspicuous, deep; nearly transversely oriented; perforated; 50% wider than long. Lateral, free, posterior edge of ventral velum recurved such that the more lateral portions convex anteriorly and medial 1/2 of ventral velum concave anteriorly; slight spicular support; free velar surface relatively short; margin unsculptured except for small flap over glottis, narrow median notch in flap in specimen not photographed; no conspicuous secretory pits.

Pharyngeal Cavity: Branchial baskets 1 1/2 times as wide as long; each branchial basket equal to rest of buccal floor area; baskets moderately deep. Second and 3rd filter plates oriented about 30° from transverse plane, tipped about 45°; third filter plate short without filter ruffles on posteromedial surface; dorsal edge of 3rd filter plate concave superiorly, vertical, its dorsal edge meeting base of 4th filter plate such that the 3rd filter cavity poorly defined and more or less continuous with the 2nd filter cavity; cb 1 with 8–13 filter rows, cb 2 with 11, cb 3 with 9 or 10, cb 4 with 8–10. Filter mesh of average to low density; many tertiary filter folds; filter rows narrow; filter rows abutting completely or almost abutting; filter canals

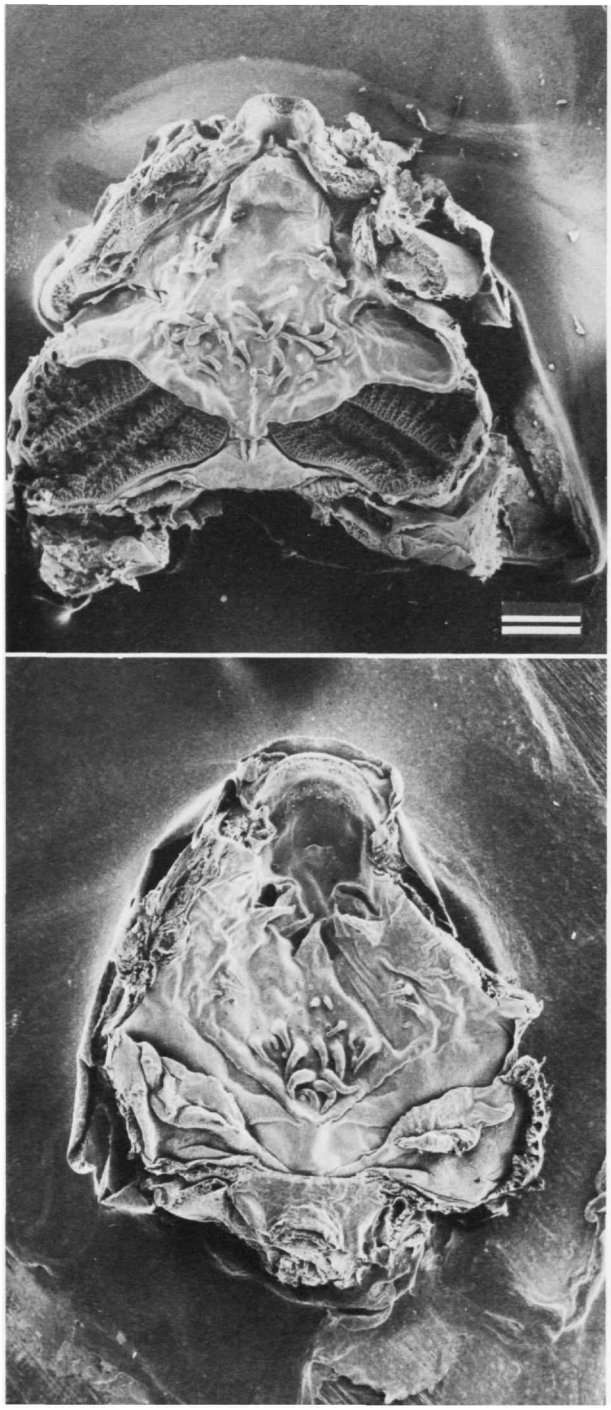


FIGURE 35.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Pleurodema nebulosa;* scale line = 1 mm.

narrow, 80%–100% canopied. Lacking well-defined branchial food traps; no secretory ridges (Figure 60*a,b*). Glottis 1/2 exposed; glottal lips tall; laryngeal disc indistinct. Wide esophageal funnel.

DORSAL ASPECT.—*Buccal Cavity:* Shape of roof of mouth triangular; nares 30% distance from front of mouth to esophagus, median ridge 45% distance from front of mouth to esophagus. Prenarial arena shallow, with one large central pustulation. Nares large; anterior narial wall thin, shallow, without pustulations; posterior narial wall simple flap. Postnarial arena with two simple blunt papillae near midline; two larger tall papillae posterolateral to these. Median ridge simple, tall, triangular flap. Lateral-ridge papillae far lateral, as tall as median ridge, with faint pustulations on anterior margin. BRA diamond-shaped cluster of 18–20 papillae, largest in medial posterior portion of BRA; all BRA papillae curved posteriorly; no secondary ornamentation. Four to six tall, thin, medially directed, lateral-roof papillae on each side. Very distinct, large uniform glandular zone; anterior margin distinct; bounded by a weak V-shaped ridge; approximately 1/7 length of roof of mouth. Dorsal velum not long; faint on midline; no marginal papillae.

Pharyngeal Cavity: Two transversely oriented pressure cushions per side; tall, elongate, oval; posteromedial cushions smaller than anterolateral ones. Ciliary groove wide laterally and narrowing toward the midline.

Proceratophrys appendiculata (Günther)

FIGURE 36

MATERIAL.—USNM 241334 (one specimen dissected, stage 38, SVL 14.1 mm). Collected from a small stream near Teresópolis, Rio de Janeiro, Brazil, 29 November 1978.

REFERENCE.—Peixoto and Cruz (1980) described and figured the external morphology and provided habitat data for this species.

GENERAL REMARKS.—Beak slightly compressed laterally. Lung buds extremely small, length <1/4 maximum width of mouth; uninflated. Long gill filaments.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth triangular, broad anteriorly, slightly wider than long. Two pair of infralabial papillae; anteromedial pair stout with jagged anterior margin, extending forward to posterior edge of keratinized beak; 2nd pair posterolateral with complexly branching apices, touching each other on midline (Figure 53*d*). Four very tall lingual papillae, each divided near base into 2 or 3 terminal branches, terminal branches further divided, creating a dense collection of attenuate, jagged papillae above the tongue anlage. W-shaped BFA; 45–60 BFA papillae on each side; BFA papillae medium tall, very attenuate, sharply pointed; largest BFA papillae directly medial to buccal pockets originating from common transversely oriented ridge; very few papillae with terminal bifurcations or marginal serrations. Eight

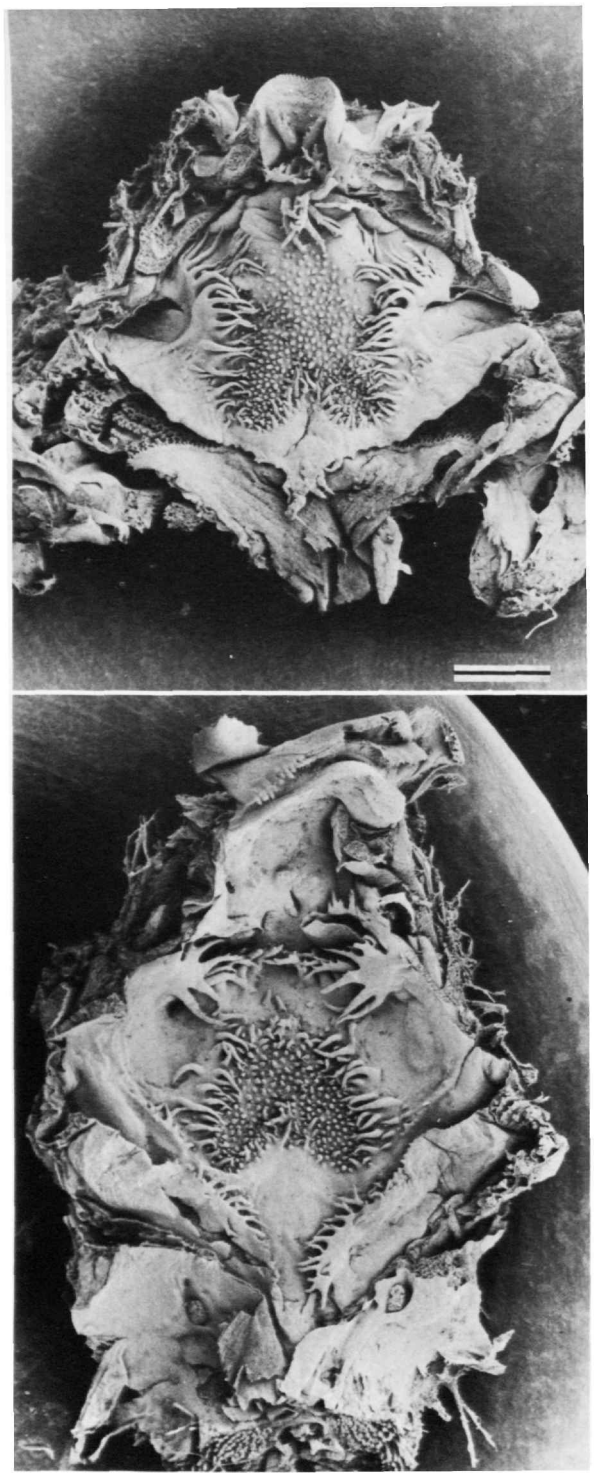


FIGURE 36.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Proceratophrys appendiculata;* scale line = 1 mm.

to twelve tall, attenuate, prepocket papillae on each side, largest arising from common base running into base of BFA papillae. Buccal pockets very wide, shallow; horizontally oriented; perforated. Free velar surface of average length, total area on each side <1/10 area of buccal floor; spicular support conspicuous; posterior margin gently curved with only slight irregularities except medially; medial 1/10 of velar margin with long, irregularly shaped, posteriorly directed apron completely covering glottis; median notch absent; secretory pits small, largely confined to very narrow band along posterior margin of ventral velum.

Pharyngeal Cavity: Branchial baskets small, triangular, 50% wider than long; total area 1/3–1/4 area of rest of buccal floor; baskets shallow, 4–5 times wider than deep. First filter cavity small, shallow, obliquely oriented; 3rd filter plate virtually horizontal with its dorsal margin meeting rather than overlapping ventral margin of 4th filter plate (such that a single filter cavity formed rather than a separate 2nd and 3rd filter cavity, as seen in most other tadpoles); 1st filter plate very strongly curved medially, overlapping 80% of 2nd filter plate; dorsal edge of 2nd filter plate with slightly concave dorsal margin; 2nd filter plate 6 times as long as tall; 3rd filter plate horizontal (lacking height); 2nd, 3rd, and 4th filter plates abutting rather than overlapping; cb 1 with 8 filter rows on one side, 6 on other, cb 2 with 8, 7, cb 3 with 5, 8, cb 4 with 4. Filter mesh of moderately low density; tertiary folds common. Filter rows of average width, but widely spaced, such that filter canals as broad as rows and the canals only 50%–75% canopied. Branchial food traps shallow; average to medium small in size; secretory ridges present, average-sized, uniform. Glottis extremely small, fully occluded; lips most conspicuous anteriorly; laryngeal disc broad but poorly defined anteriorly. Esophageal funnel extremely broad; esophagus of average diameter.

DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth diamond-shaped, slightly longer than wide; nares about 30% distance from front of mouth to esophagus; median ridge about 45% distance from front of mouth to esophagus. Prenarial arena very long, strongly curved, smooth except for a medial, small, transversely oriented flap with a jagged ventral margin and 2 tiny papillae lateral to it, approximately halfway between edge of prenarial arena and midline. Nares very large, obliquely oriented; internarial distance about 60% length of naris; anterior narial wall thin, shallow, but supporting a comb-like array of long anteriorly directed papillae; 3 tall and several minor prenarial papillae on each side; posterior narial wall tall very thin flap; narial-valve projection very small. Five postnarial arena papillae on one side, 6 on other, arranged in oblique rows parallel to nares; all tall with pustulate anterior margins. Median ridge very small trapezoidal flap with pointed pustulations on anterior surface and free ventral edge. Lateral-ridge papillae elaborate flaps oriented lengthwise with free margin covered with attenuate finger-like papillae oriented medially; marginal papillae on the lateral-ridge "papillae"

serrated on anterior surface; 2 asymmetrical papillae in postnarial arena. BRA an inverted heart-shape; BRA bounded by approximately 30–35 papillae on each side; all attenuate, pointed papillae, only 1 bifurcate; largest papillae most lateral. Even field of pustulations within BRA; oblique row of papillae/pustulations running from posterolateral corner of BRA anterolaterally. Lateral-roof papillae absent. Glandular zone poorly defined, with a few isolated secretory pits behind most caudal portion of BRA, no secretory pits on midline, largest pits lateral to midline, zone discontinuous. Dorsal velum very long; absent on midline; medial portion of margin extensively papillate, with papillae of the attenuate, pointed, occasionally bifurcate form seen elsewhere on buccal roof and floor; medial portion of dorsal velum curving gradually backward towards esophagus.

Pharyngeal Cavity: Very weakly defined pressure cushion, single on each side. Ciliary groove shallow and very wide.

Proceratophrys boiei (Wied)

FIGURE 37

MATERIAL.—USNM 241336 (one specimen dissected, stage 35, SVL 14.0 mm). Collected from a small stream near Teresópolis, Rio de Janeiro, Brazil, 18 January 1978.

REFERENCE.—Izecksohn, Cruz, and Peixoto (1979) described and illustrated the external morphology and provided habitat data for this species.

GENERAL REMARKS.—Beak more U-shaped than in *P. appendiculata,* not as laterally compressed. Lung buds larger, lung length from glottis to posterior tip equal to approximately $^2/_3$ maximum width of mouth; uninflated. Gill filaments present.

VENTRAL ASPECT.—*Buccal Cavity:* Posterolateral pair of infralabial papillae smaller, not touching on midline. Four lingual papillae, all bifurcate or trifurcate near base, but not complexly branching. BFA oval with transverse band of papillae in posterior region of BFA; 25 papillae on each side; ridge supporting largest BFA papillae obliquely oriented. Fewer prepocket papillae than in *P. appendiculata.* Posterior margin of ventral velum with small cusps over 2nd, 3rd, and 4th filter plates and a slightly jagged margin across midregion, lacking posteriorly directed apron over glottis.

Pharyngeal Cavity: Branchial baskets triangular; as long as wide; total area 50% of rest of buccal floor. Three distinct filter cavities; 3rd filter plate overlapping part of 4th filter plate rather than abutting with ventral margin of 4th plate; dorsal margin of 3rd filter plate convex upward; 2nd filter plate 3 times as long as tall; 3rd filter plate imbricated, not horizontal; approximately as tall as long; cb 1 with 7 filter rows, cb 2 with 12 relatively narrow rows, cb 3 with 10 relatively wide rows, cb 4 with 6. Filter mesh denser than in *P. appendiculata.* Filter rows wide; filter canals 25% narrower than filter rows; canals 80% canopied. Branchial food traps of average depth; secretory ridges present. Glottis average size, fully occluded; 50%–75%

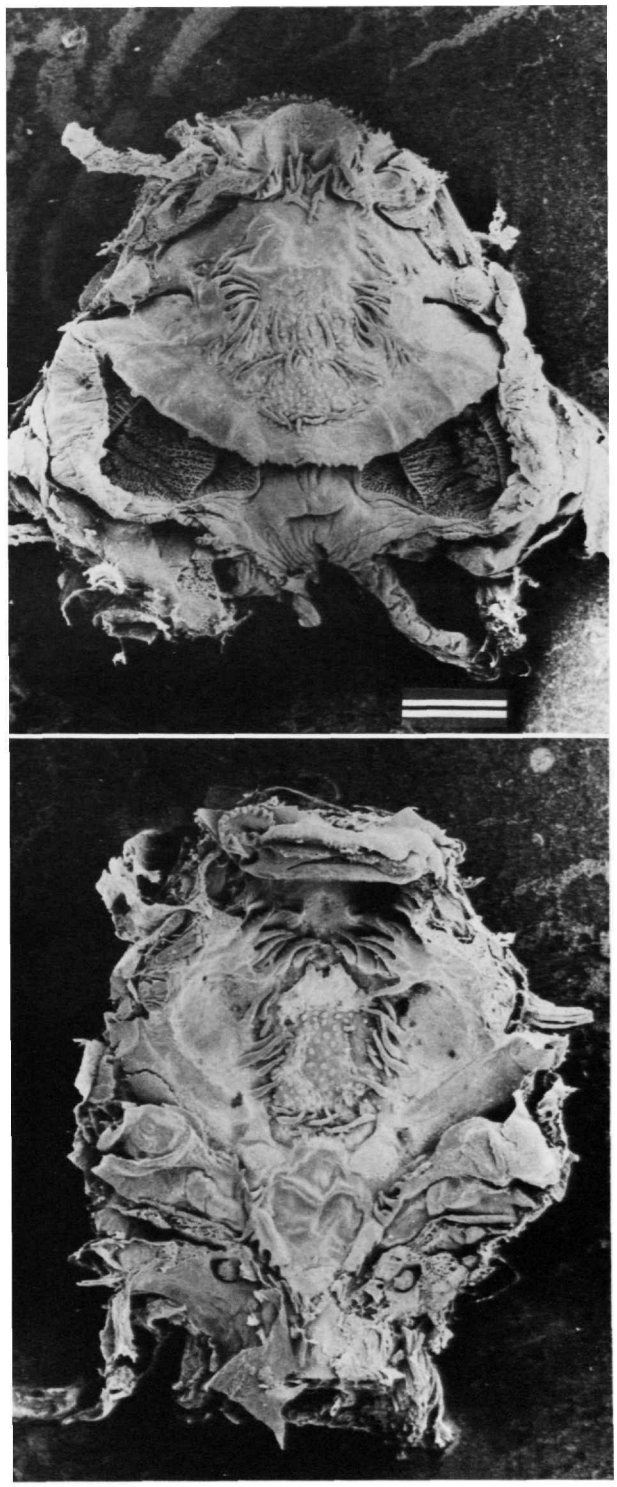


FIGURE 37.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Proceratophrys boiei;* scale line = 1 mm.

covered by ventral velum. Esophageal funnel not as broad.

DORSAL ASPECT.—*Buccal Cavity:* Prenarial arena long, not as strongly curved ventrally; smooth except with simple medial papilla and single pustulation posterolateral on each side. Anterior narial wall rugose, but lacking large papillae. Median ridge much larger. Several pustulations and a small, medially notched flap present within postnarial arena. BRA simple, U-shaped; BRA bounded by approximately 15 papillae on each side; papillae not bifurcate. Additional papillae/pustulations absent on buccal roof. Glandular zone well defined by large secretory pits of moderately low density; secretory zone broadly interrupted on midline. Dorsal velum not quite as long; absent on midline; marginal papillation not quite as extensive.

Pharyngeal Cavity: Weakly defined pressure cushions; asymmetrical, 2 on one side, 1 on other.

Pseudopaludicola species

FIGURE 38

MATERIAL.—USNM 218232 (two specimens dissected, stages 36, 37; SVL 7.8, 10.3 mm, respectively; first specimen figured). Collected in extremely shallow, slowly running water in a boggy, grassy area near Chapeu de Sol, Minas Gerais, Brazil, 31 January 1980.

REFERENCE.—The *Pseudopaludicola* from this region cannot be identified to species with certainty. The larvae generally share features of other *Pseudopaludicola* (such as described and illustrated in Cei, 1980:412, fig. 175), namely: spiracle sinistral; anus median; mouthparts directed more ventrally than anteriorly; oral disc laterally indented, single row of marginal papillae interrupted anteriorly; denticle formula 2(2)/2(1); overall habitus somewhat fusiform in having low dorsal and ventral tail fins.

GENERAL REMARKS.—Description applicable to both specimens dissected unless noted otherwise. Lung buds small, thin, and just slightly longer than 1/4 maximum width of mouth; not inflated. Filamentous gills present.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth shape approximately equilateral triangle. Single blunt infralabial papilla on each side and small cluster of papules anterior to it (Figure 54). Three lingual papillae, 1 on midline with long groove from base to apex suggesting fusion of 2 papillae; other 2 papillae lateral and slightly posterior; posterolateral pair laterally compressed, taller, curved medially, surfaces knobby. BFA shape an inverted "U" in one specimen, more oval in 2nd; BFA defined by 10–12 papillae on each side in 1 specimen, 8–10 papillae in 2nd (smaller) specimen; all BFA papillae thin, long, simple, pointed. Single, very small, prepocket papilla on each side anteromedial to buccal pockets; additional small papilla on each side farther anterior to medial edge of buccal pocket, neighboring BFA papillae; field of small pustulations scattered about posterior floor of BFA. Buccal pockets of average width; shallow; transversely

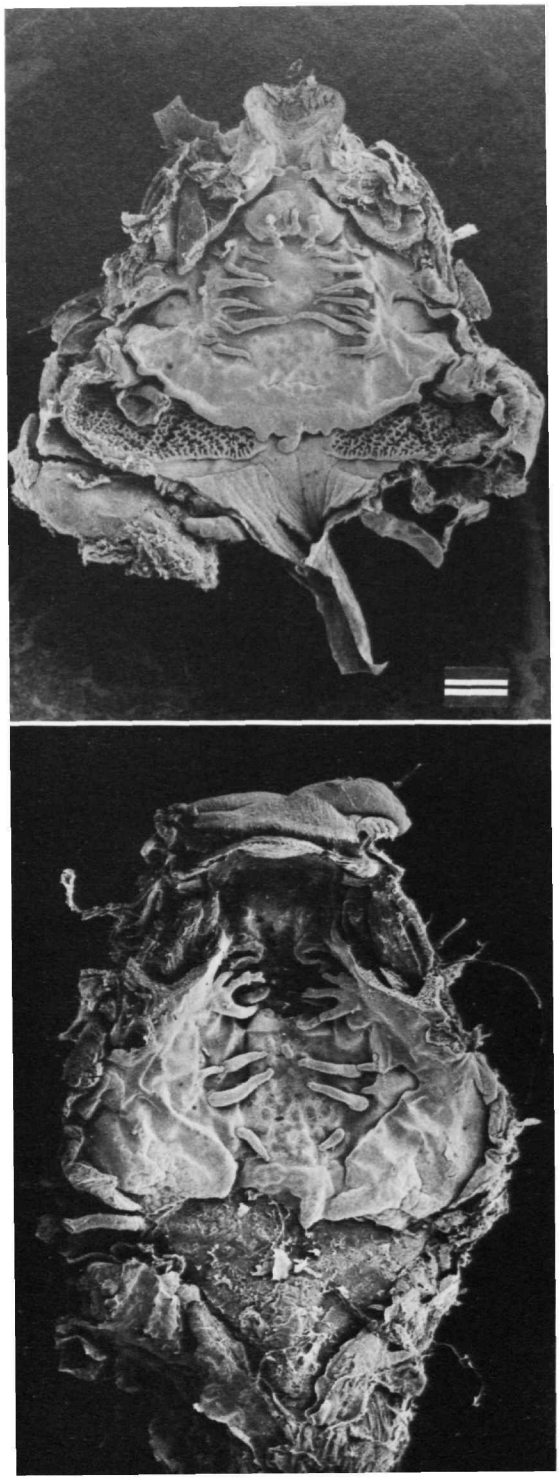


FIGURE 38.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Pseudopaludicola* species; scale line = 400 μm.

oriented; perforated (?). Free velar surface of average length with distinct spicular support; posterior margin of ventral velum irregular in shape particularly near midline with very distinct secretory pits that form a thickened rim on dorsal side of ventral velum particularly on medial 2/3; velum irregular on midline such that a distinct median notch not defined.

Pharyngeal Cavity: Branchial baskets smaller than average; triangular in dorsal view, 20% wider than long; each branchial basket about 1/3 area of remaining buccal floor area; each basket about 5–6 times wider than deep. Single filter cavity on each side; obliquely oriented; filter plates extremely shallow, abutting each other; cb 1 with 7 filter rows, cb 2 with 7, cb 3 with 8, cb 4 with 6. Filter mesh moderately to slightly less than average density; however, rows abutting, fully canopying filter canals; tertiary folds present, higher order folds rare; filter rows about as wide as filter canals. Branchial food traps shallow but long, of average overall area; secretory ridges straight, visible under light microscope. Glottis fully covered by posterior edge of ventral velum in larger specimen, 50% covered in smaller specimen; glottis average to small size; occluded; lips faint; laryngeal disk small. Esophageal funnel very broad, esophagus of average to large diameter.

Dorsal Aspect.—*Buccal Cavity:* Roof of mouth truncated, diamond-shape; nares 15%–20% distance from front of mouth to esophagus; median ridge about 40% distance from front of mouth to esophagus. Prenarial arena smooth except for 2 faint knobs about 2/3 way back and directly anterior to medial end of nares. Nares of average size; internarial distance about 2/3 length of naris; nares more transversely than obliquely oriented, curving medially; narial walls very shallow, medial portion rugose; nares 3 times wider than height of anterior wall; prenarial papillae absent; posterior narial wall smooth, lacking narial-valve projection, except for an asymmetrical papilla or knob in middle of narial valve on one side. Postnarial arena transversely oval, bounded laterally by 1 or 2 postnarial papillae on each side; postnarial papillae between nares and median ridge in larger specimen, more posterior in smaller specimen; postnarial arena papillae average size, slightly rugose. Median ridge trapezoidal, slightly concave free edge in larger specimen, straighter in smaller specimen; free edge of median ridge with marginal sculpturing. Lateral-ridge papillae large longitudinal flaps extending as far forward as lateral edge of nares, each with 3 jagged, finger-like projections, extending medially over postnarial papillae, 1 papilla with secondary bifurcation. BRA defined by 4–6 papillae on each side in rows converging slightly posteriorly; BRA papillae attenuate, simple, with slightly irregular apices. Assorted pustulations in postnarial arena and BRA, otherwise buccal roof lacking pustulations/papillae. Irregular and continuous glandular zone defined by large, distinct, secretory pits of moderate density. Dorsal velum average length, medial 2/3 papillate, slightly interrupted on midline.

Pharyngeal Cavity: Single, very poorly defined pressure cushion. Ciliary groove very shallow, narrow.

Rhinoderma darwinii Duméril and Bibron

Figure 39

Material.—KU 161531 (one specimen dissected, stage 38 [based on hind limbs], SVL 6.6 mm). Collected from Parque Nacional Nahuelbuta (Cabrerías), 1030 m, Malleco, Chile.

Reference.—Cei (1962) described and figured the larva.

General Remarks.—Lungs about length of buccal floor; flat, sacculate, not inflated. Gill filaments present, short.

Ventral Aspect.—*Buccal Cavity:* Floor of mouth oval; 1/3 wider than long. Infralabial papillae effectively absent; arch of mouth filled with large precociously developed tongue. Three or four irregular bumps on tongue perhaps homologous to larval lingual papillae. BFA a wide U-shape; 20–30 subequal, simple, cylindrical BFA papillae on each side in a very narrow band. No prepocket papillae. No other papillae on buccal floor; 20–30 small pustulations in posterior 1/2 of BFA. Buccal pockets wide, 3 times as wide as long; 30° orientation from transverse plane; perforated. Free velar surface relatively short; posterior margin semicircular, an overall gentle curve, with very irregular cluster of 12 marginal papillae spread along middle 1/2 of ventral velum not in line with underlying filter plates or cavities; no visible spicular support; no visible secretory pits.

Pharyngeal Cavity: Branchial baskets 50%–60% wider than long, triangular with a long transversely oriented base; each branchial basket less than 50% remaining buccal area, branchial baskets extremely shallow; 1st and 2nd filter cavities subequal, 3rd 50% smaller. Dorsal edge of 2nd filter plate straight, dorsal edge of 3rd filter plate very slightly curved dorsally; 1st filter plate 3 times as long as tall, 2nd 4 times as long as tall, 3rd twice as long as tall; 2nd, 3rd, and 4th filter plates tipped about 45°; cb 1 with 5 filter rows, cb 2 with 7, cb 3 with 8, cb 4 with 4 or 5. Low-density filter mesh; filter rows sparse or degenerate; weakly developed secondary filter folds; filter rows wispy; filter canals about twice filter row width, fully exposed. Branchial food traps with secretory tissue present, but not organized into ridges (determined from two serially sectioned specimens: FMNH 3684, stages 36 and 37, SVLs 5.1 and 6.1 mm). Glottis relatively large; 100% exposed; open; with thick lips; on an indistinct laryngeal disk. Esophageal funnel very broad; esophagus of large diameter.

Dorsal Aspect.—*Buccal Cavity:* Shape of roof of mouth an elongate diamond, broad in front; length about same as width; nares about 10% distance from front of mouth to esophagus; median ridge about 20% distance from front of mouth to esophagus. Prenarial arena bare. Nares small; widely separated, internarial distance about length of naris; nares obliquely oriented at 45°; anterior narial wall thickened medially and ill-defined laterally; posterior narial wall a simple flap lacking narial-valve projection. One pustulation on one

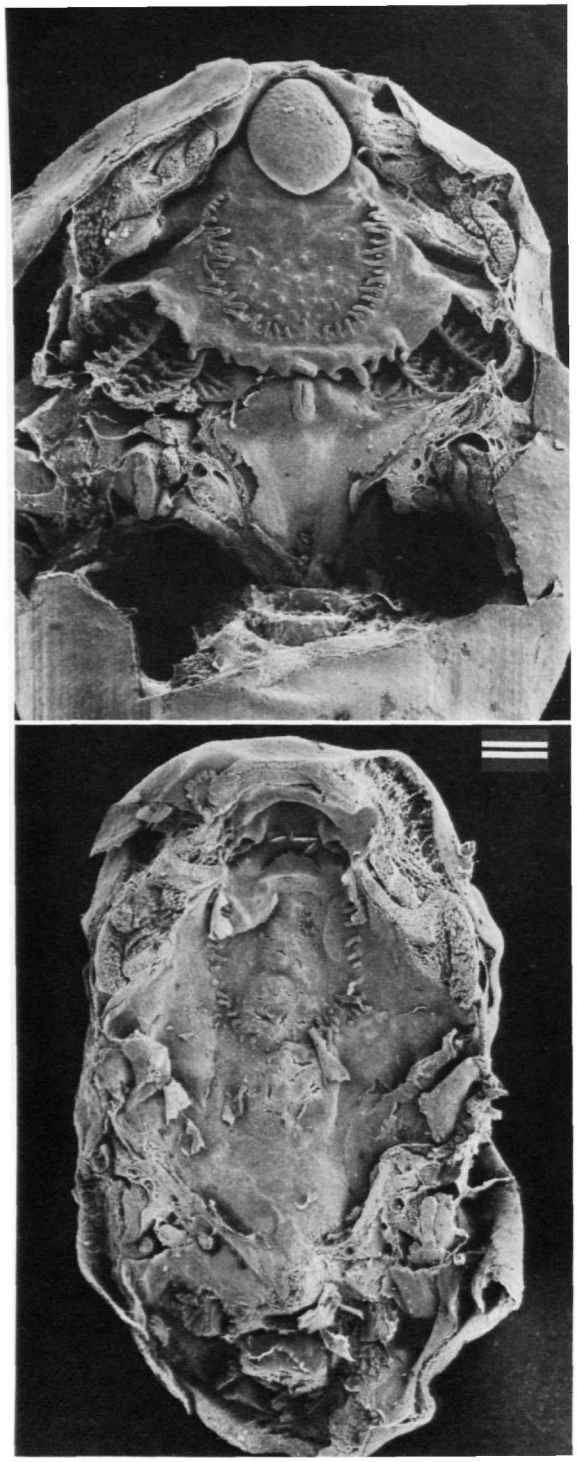


FIGURE 39.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Rhinoderma darwinii;* scale line = 400 μm.

side and two on other asymmetrically positioned behind nares, otherwise no postnarial arena papillae or pustulations. Median ridge a simple half moon with slightly jagged margins. Lateral-ridge papillae absent. BRA U-shaped with array of papillae similar to those on floor of mouth but more widely spaced, papillae beginning almost as far forward as median ridge, 15–20 per side; relatively uniform, simple. No other pustulations/papillae on buccal roof. Dorsal portion of buccal roof lacking well-defined field of secretory pits, i.e., no glandular zone (based on sectioned specimens). Dorsal velum relatively short; widely separated on midline.

Pharyngeal Cavity: Pressure cushion region destroyed in dissection. Very broad and shallow ciliary groove.

Telmatobius jelskii (Peters)

FIGURE 40

MATERIAL.—KU 181850 (one specimen dissected, stage 37, SVL 38.7 mm). Collected from Tarma, 3100 m, Junín, Peru.

REFERENCE.—Vellard (1951) described and figured the tadpole.

GENERAL REMARKS.—Filamentous algae in gill filters. Lungs large, 50% longer than buccal floor length; uninflated. Luxuriant gill filaments.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth triangular, slightly wider than long. Bicuspid keratinized spur at corner of jaw, medially directed. Two pairs of infralabial papillae in transverse rows; lateral pair much larger and with roughened texture, not bifurcate; more medial pair very small, round. Lingual papillae asymmetrical; 2 main papillae small and simple, third irregular, attached to base of one main papilla. V-shaped BFA; 18–24 BFA papillae on each side, larger papillae with slightly serrate anterior edges; largest papillae medial to buccal pockets and medially directed, largest papillae sickle-shaped and rising from anterolateral to posteromedial ridge-like base, papillae simple, without bifurcations. Large cluster of small, simple, conical, prepocket papillae, 8 on one side, 9 on other. About a dozen papillae and 2 dozen pustulations randomly distributed on posterior half of BFA. Buccal pockets average size; 3 times as wide as long; transversely oriented; perforated. Free velar surface relatively long; conspicuous spicular support; several distinct marginal peaks; lateral-most peak above free edge of 2nd filter plate and pointing posteriorly on each side; next peak over edge of 3rd filter plate and recurved, pointing medially; third peak just over anterolateral edge of esophagus, pointing medially; most posterior portion of free velar surface with small, distinct, medial notch bounded by rounded papillae and irregular sculpturing immediately lateral to medial notch and lateral to 3rd peak; large secretory pits on margin, conspicuous under light microscope.

Pharyngeal Cavity: Branchial baskets irregularly ovoid, 50% wider than long, each about 1/3 remaining buccal area;

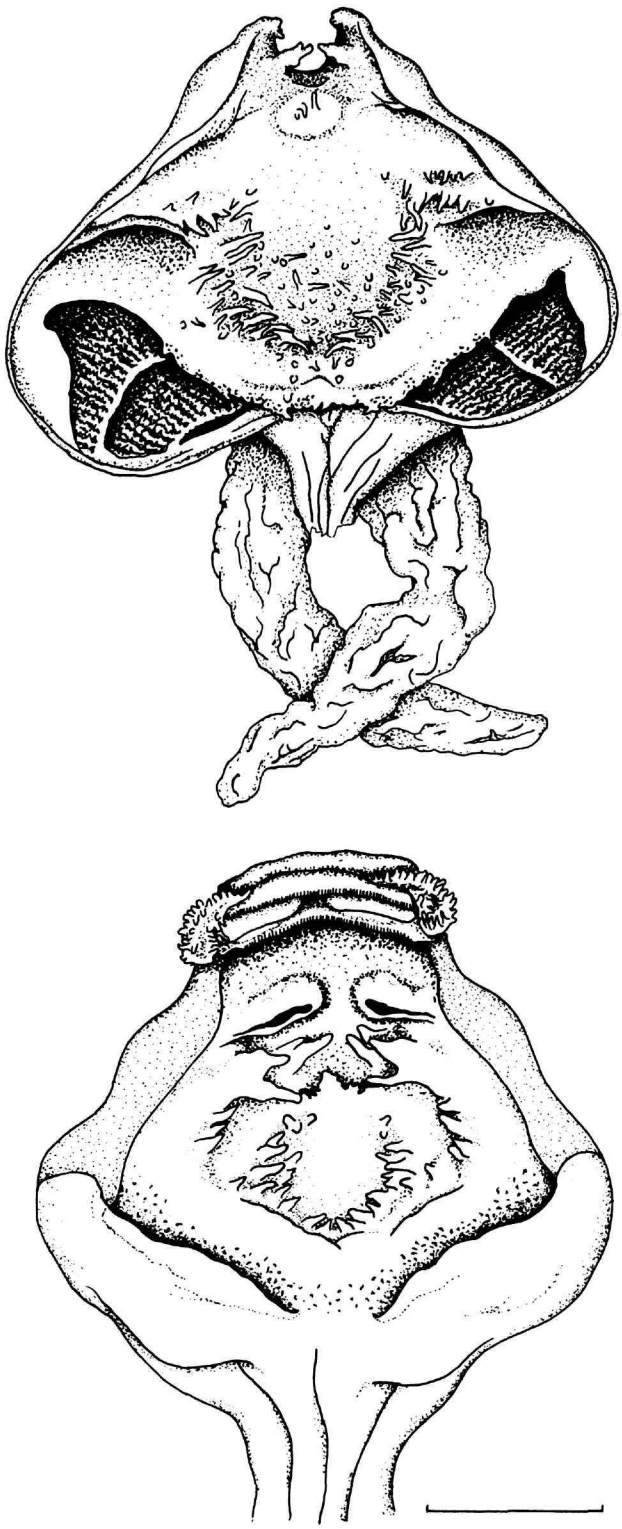


FIGURE 40.—Camera lucida drawings of floor (above) and roof (below) of oral cavity of *Telmatobius jelskii;* scale bar = 5 mm.

baskets relatively shallow. Lateral filter cavity largest, 2nd and 3rd filter plates strongly tipped medially such that 3rd filter cavity largely obscured from view; 2nd filter plate with relatively straight edge, 3rd filter plate with strongly bowed dorsal edge; 2nd filter plate about 2 times as long as high, 3rd filter plate about as tall as long; cb 1 with 12 filter rows, cb 2 with 12, cb 3 with 9, cb 4 with 6. Filter mesh of average density; tertiary or higher order folding. Filter rows wide, rows abutting dorsally but separate ventrally; filter canals of average width, 70%–80% canopied. Branchial food traps large; secretory tissue organized into greatly interrupted ridges with a predominantly transverse orientation rather than uninterrupted ridges seen in most leptodactylid larvae. Glottis occluded, oriented vertically and mostly covered by medial portion of ventral velum; lips shallow; laryngeal disk an irregularly shaped, longitudinally oriented oval. Esophageal funnel relatively broad.

DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth triangular, about as long as wide; nares about 1/4 distance from front of mouth to esophagus; median ridge about 40% distance from front of mouth to esophagus. Prenarial arena smooth, lacking distinct topographic features. Nares large, obliquely oriented; internarial distance small, about 1/3 distance of long axis of naris; medial portion of anterior narial wall expanded to an irregular knobby structure; no prenarial papillae; no narial-valve projection. Postnarial arena triangular, defined by 6 or 7 papillae in oblique rows on each side; papillae simple, conical; postnarial papillae reduced to pustulations anteriorly, enlarged posteriorly, with penultimate papilla largest; rows of pustulations running parallel between the postnarial papillae and posterior wall of nares. Median ridge tricuspid with large central cusp; no serrations or secondary papillae on ventral margin or on anterior surface. Lateral-ridge papillae large, compressed structures with 3 cusps of which the anterior smallest, most posterior largest and most attenuate with jagged anterior margin; lateral-ridge papillae collectively 1 1/2 times size of median ridge. BRA U-shaped; defined by 10 papillae on 1 side, 8 on other and 10 pustulations on each side; all simple, some with 1 or 2 pustulations on anterior edge. About 6 papillae randomly distributed within postnarial arena, several dozen pustulations in BRA; 3 simple, slightly curved papillae on one side, 4 on other, posterolateral to lateral-ridge papillae. Distinct glandular zone with diffuse anterior margin; large secretory pits. Large dorsal velum broadly interrupted medially.

Pharyngeal Cavity: Two very poorly defined pressure cushions on each side. Ciliary groove shallow.

Telmatobius marmoratus (Duméril and Bibron)

FIGURE 41

MATERIAL.—KU 164021 (one specimen dissected, stage 37, SVL 35.5 mm). Collected from 34 km E Tincopalca (Laguna), 4130 m, Puno, Peru.

REFERENCE.—Cei (1980) described and figured the tadpole.

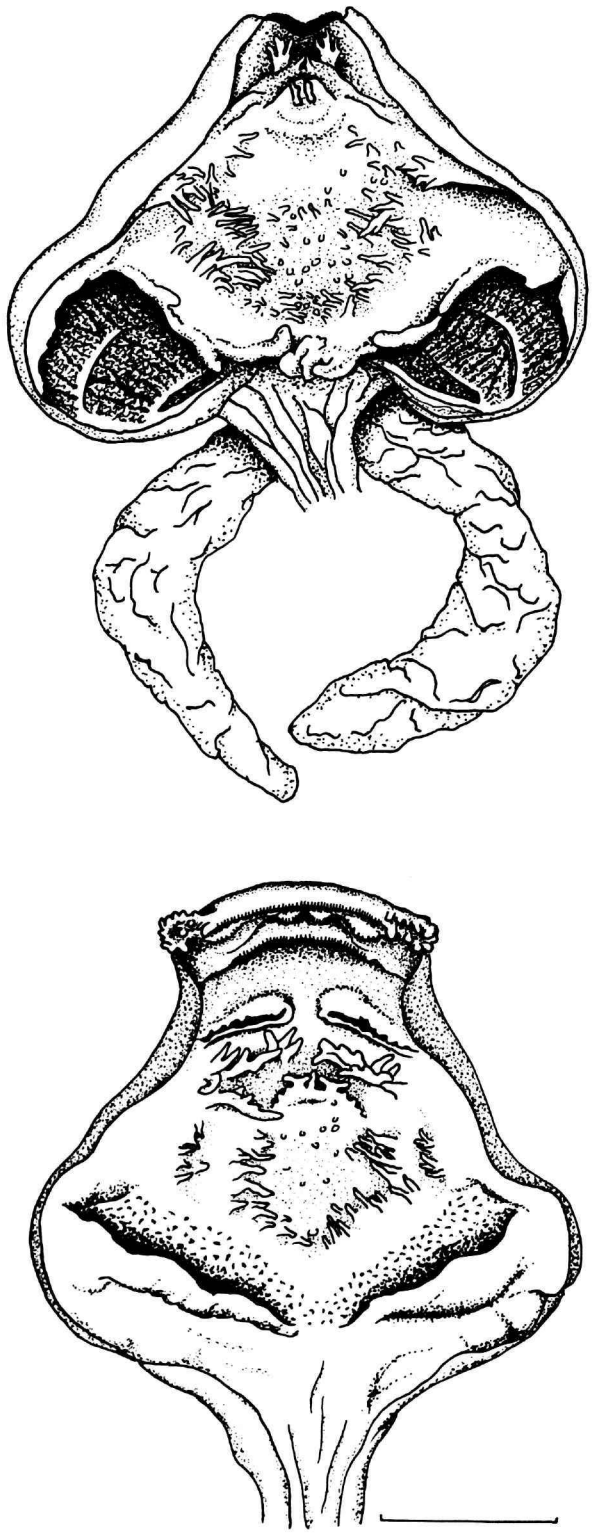


FIGURE 41.—Camera lucida drawings of floor (above) and roof (below) of oral cavity of *Telmatobius marmoratus;* scale bars = 5 mm.

GENERAL REMARKS.—Only those features which differ from *T. jelskii* are described. Lungs 40% longer than buccal floor length.

VENTRAL ASPECT.—*Buccal Cavity:* Lateral pair of infralabial papillae more hand-like than in *T. jelskii,* with multipapillate margins; medial pair of infralabial papillae taller and more attenuate. Two lingual papillae with slightly pustulate anterior margins. Diamond-shaped BFA; about 30 BFA papillae per side, posterior margins of arena with broad zone of more than 100 papillae in or around BFA; largest BFA papillae directly lateral to buccal pockets, multibranched; most others attenuate and sickle-shaped with jagged concave edges. Prepocket papillae taller, thinner, with more rugose margins than in *T. jelskii.* Papillae and pustulations within BFA extending anteriorly halfway to level between buccal pockets and lingual papillae. Margin of ventral velum thicker and marginal projections more rounded than in *T. jelskii.* Medial notch of free velar surface larger than in *T. jelskii.*

Pharyngeal Cavity: Branchial baskets slightly deeper than in *T. jelskii.* Third filter cavity 50% obscured from view; 2nd filter plate dorsal margin arched downward slightly more than in *T. jelskii,* 3rd not arched upward as much as in *T. jelskii;* cb 1 with 12 filter rows, cb 2 with 11, cb 3 with 11, cb 4 with 9. Filter rows more separate, tending not to abut. Secretory ridges more continuous than in *T. jelskii.* Glottis closed.

DORSAL ASPECT.—*Buccal Cavity:* Medial portion of anterior narial wall not as expanded as in *T. jelskii.* Postnarial arena papillae larger, more curved than in *T. jelskii,* with rougher anterior edges; rows of pustulations and papillae running parallel between the postnarial papillae and posterior wall of nares. Median ridge with very irregular, papillate-free margin with pustulations on anterior surface. Lateral-ridge papillae large, elkhorn-like (lost in dissection on one side), with at least 6 arms, some with further bifurcations. BRA defined by about 20 papillae on each side and an equal number of pustulations; largest lateral BRA papillae bifurcated. Six papillae in lateral groove group on each side, simple. Distinct glandular zone, anterior margin better defined than in *T. jelskii.* Dorsal velum smaller than in *T. jelskii,* medial portion of free edge sculptured.

Pharyngeal Cavity: Pressure cushions small, subequal, more distinct than in *T. jelskii.*

AUSTRALIAN LEPTODACTYLOIDS

Crinia tasmaniensis (Günther)

FIGURE 42

MATERIAL.— UMMZ 154858 (one specimen dissected, stage 31, SVL 8.5 mm). No locality data.

REFERENCE.—Watson and Martin (1973) described the external morphology.

GENERAL REMARKS.—Lungs very small, diameter about 0.03 mm; asymmetrical; length of longest lung about 0.16 mm. Well-developed gill filaments.

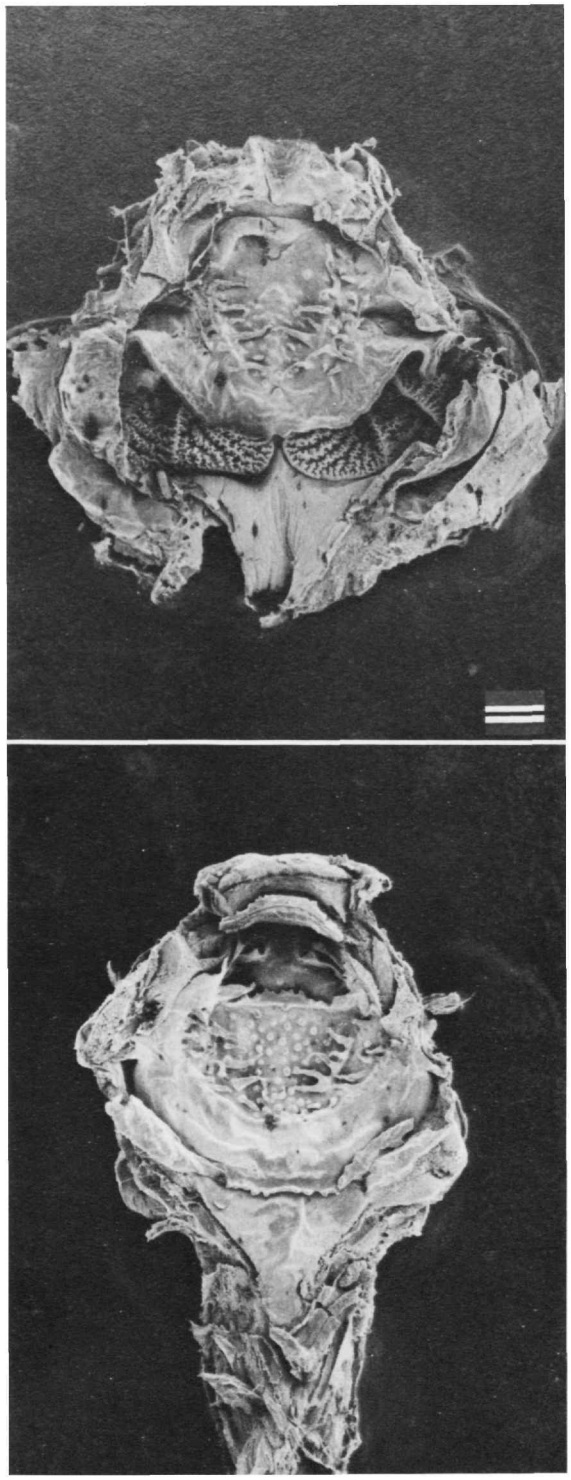


FIGURE 42.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Crinia tasmaniensis;* scale line = 400 μm.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth 20% wider than long. Infralabial papillae a single, small, anteroposteriorly compressed, square flap on each side with irregular edges. Two symmetrical lingual papillae. BFA V-shaped; 12 BFA papillae on each side; BFA papillae simple, relatively thin, some slightly knobby, none bifurcate. Two or three small prepocket papillae per side. Large field of pustulations covering posterior 2/3 of buccal floor. Buccal pockets average-sized; 3 times as wide as long; transversely oriented; not perforated. Free velar surface of average length; area on each side about 20%–25% area of rest of buccal floor; spicular support faint, not extensive; posterior margin somewhat truncate in overall shape, with thickened rim of secretory tissue; tissue of uniform thickness along free edge with scattered secretory cells, but no distinct pits; free edge lacking marginal papillae except for small median notch surrounded by single, short, blunt papilla on either side (Figure 55).

Pharyngeal Cavity: Branchial baskets 50% wider than long, obliquely oval; baskets relatively large, each about 1/2 remaining area of buccal floor; baskets about 75% as deep as wide. First filter plate vertical, 2nd tipped at 45°, 3rd with short vertical ridge with lateral edge oriented horizontally; filter rows on medial edge of 3rd filter plate extremely short, abutting filter rows of 4th filter plate; 4th filter plate horizontally oriented (Figure 55), single common 2nd and 3rd filter cavity resulting from primarily horizontal orientation of 3rd and 4th filter plates; cb 1 with 8 filter rows, cb 2 with 9, cb 3 with 6 or 7, cb 4 with 6. Filter mesh of slightly lower density than average; many 2° and some tertiary folds; no higher order folding. Filter rows relatively narrow, non-abutting; many filter canals as wide as, or wider than, filter rows, up to 50% exposed. Branchial food traps relatively deep; large; second and 3rd food traps merged; distinct secretory ridges near lateral limits of food traps in lattice-like pattern, otherwise in parallel ridges (Figure 57*b*). Glottis not visible from above, occluded (Figure 55); laryngeal disk absent. Esophageal funnel very broad, relatively large esophageal bore.

DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth oval, almost round, length about equal width; nares about 20% distance from front of mouth to esophagus; median ridge about 40% distance from front of mouth to esophagus. Weak, anteriorly directed ridge in prenarial arena. Nares large; internarial distance about 1/2 length of naris; nares transverse medially, but laterally curving backward at a 45° angle; anterior narial wall tall, of average thickness with single, large, blunt papilla near medial margin; posterior narial wall with a thin but tall valve, with a relatively large, triangular, narial-valve projection. Single, medial, postnarial papilla in middle of postnarial arena, rest of arena featureless. Median ridge very wide with crescentic, irregular, serrate-free, anteroventral edge, approximately 50% wider than tall; single medial papilla arising from middle of posterior surface. Lateral-ridge papilla arising directly lateral to median ridge from edge of faint ridge-like line continuous with median ridge proper; lateral-ridge papillae tall palps, each with single anteriorly curved

finger and straight posterior edge (destroyed in dissection on one side). BRA semicircular; 8 or 9 BRA papillae, all relatively simple, conical or with tapered tips, thin. Lateral-roof papillae forming continuous arc just lateral to BRA papillae, 9 or 10 on each side; entire BRA filled with 40–50 large, distinct pustulations. Glandular zone present; secretory cells, but no distinct pits, not organized into distinct band; indistinct zone about 10% length of buccal floor with irregular anterior wavy margin; not continuous across midline. Dorsal velum 15% length of buccal floor; very distinct across the midline forming a continuous elevated ridge with a crenulate margin.

Pharyngeal Cavity: Single, poorly defined, elongate, oblique pressure cushion on each side. Ciliary groove very broad and shallow, not continuous with esophagus.

Heleioporus species

FIGURE 43

MATERIAL.—No number (one specimen dissected, stage 29, SVL 8.2 mm). Collected from Perth, Western Australia, by D.S. Liem.

REFERENCE.—Watson and Martin (1973) described the external morphology of *H. australiacus*, which is similar to the tadpole dissected.

GENERAL REMARKS.—Lungs present, relatively large, destroyed in dissection.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth as wide as long, triangular. Two infralabial papillae on each side in a transverse row; subequal in size; tall palps with smooth posterior and medial edges but very knobby apices and anterior surfaces; all 4 directed anteromedially; additional transverse row of tiny papillae right at base of lower beak in line with apices of infralabial papillae. Two tall, distinct, lingual papillae. BFA V-shaped; 12 or 13 BFA papillae of quite irregular size, overall medium to small; those medial to buccal pockets arising from common obliquely oriented base; largest 2 papillae on each side terminally bifurcate. Irregular cluster of 4 knobby prepocket papillae on each side. Just posteromedial to buccal pockets, 2 papillae on one side, 4 on other running in oblique row merging with BFA papillae; 2 very small papillae in a field of about 20 small pustulations in posterior 1/2 of BFA. Buccal pockets very long, almost as long as wide; average depth; transversely oriented; perforated. Free velar surface of average length, about 10% length of buccal floor; spicules present; posterior margin symmetrical and wavy with a distinct crest overlying each filter cavity on each side; wide and rounded peaks with a very broad crest defining a median notch; thickened rim of secretory tissue along entire edge with distinct secretory pits.

Pharyngeal Cavity: Branchial baskets average size, oblique ovals, each about 1/3 remaining area of buccal floor; 50% wider than deep; 1st and 2nd filter cavities approximately equal size, 3rd slightly smaller; filter cavities oriented 45° from midline. Dorsal edge of 2nd filter plate relatively straight, 3rd

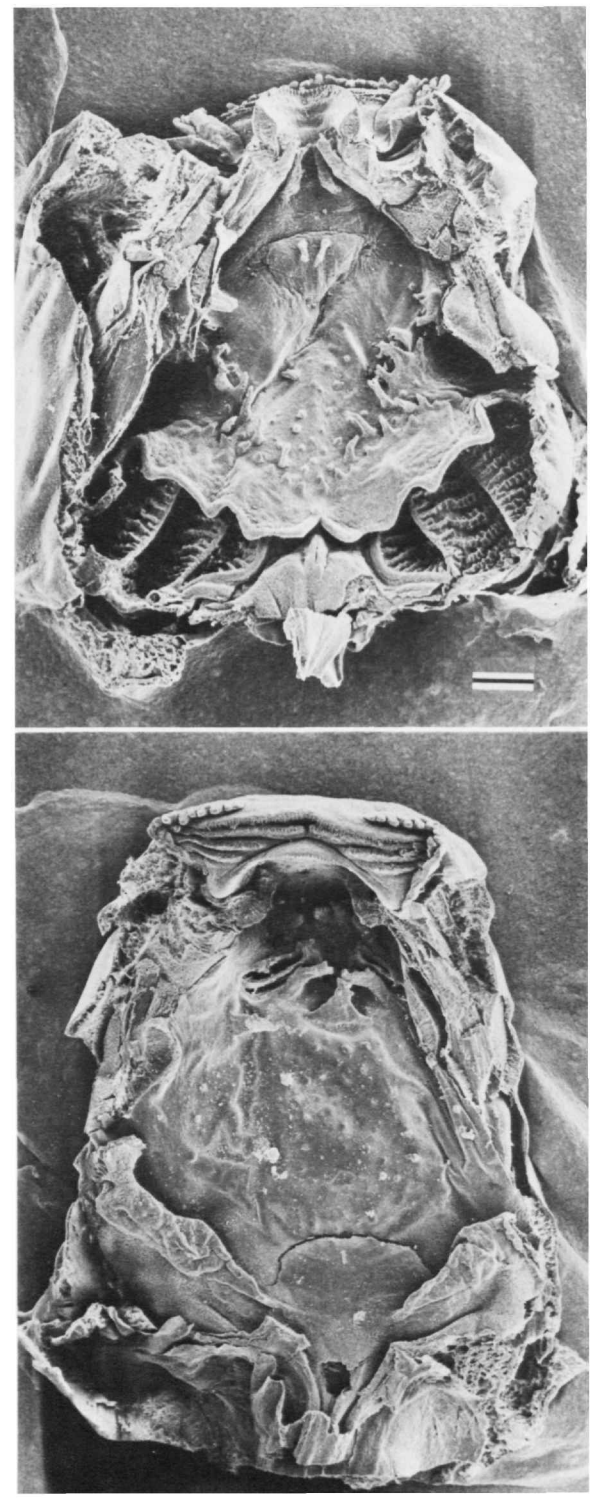


FIGURE 43.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Heleioporus* species; scale line = 400 μm.

dorsal edge curving slightly upward; filter plates tall, about as tall as long; plates tipped at 45° such that 2nd and 3rd filter plates covering about 25% medial filter cavity; cb 1 with 6 filter rows, cb 2 with 7 or 8, cb 3 with 7, cb 4 with 6. Filter mesh of average to low density; no filter rows abutting; filter canals as wide or wider than most of rows, 50% canopied; tertiary filter folds common, no higher order folds; filter rows of average width. Branchial food traps with irregular but distinct secretory ridges. Glottis 100% visible from above; of average size; open; glottal lips tall, distinct; laryngeal disk not well defined. Esophageal funnel narrow, of average bore.

DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth diamond-shaped, elongate; nares 20%–25% distance from front of mouth to esophagus; median ridge 30% distance from front of mouth to esophagus. Transversely oriented knobby ridge in prenarial arena. Nares of average size, internarial distance about 50% length of naris; nares obliquely oriented; anterior narial wall with distinct rugosities at medial edge as well as distinct prenarial papilla 2/3 distance posterolaterally; posterior narial wall with small but distinctly triangular papilla at medial terminus. Single postnarial papilla on each side, very large, sickle-shaped; medially directed apex with rugose anterior edge, almost as tall as length of naris; no other papillae near nares. Median ridge a tall triangular flap with a truncated jagged apex; median ridge equal in height to length of postnarial papillae. Single lateral-ridge papilla on each side posterolateral to median ridge (destroyed in dissection on one side), smaller than single postnarial papilla by nearly 40%; lateral-ridge papilla a rectangular longitudinally oriented flap with slightly sculptured apex on one side. No BRA papillae; a dozen or so pustules scattered around buccal roof. Faint glandular zone present, secretory pits at very low density, glandular zone about 10% length of buccal floor, with smooth, anterior, arched margin. Dorsal velum short, broadly interrupted on midline with gently wavy free edge; no marginal papillation.

Pharyngeal Cavity: Two small, ill-defined, oval, obliquely oriented pressure cushions of subequal size on each side. Ciliary groove distinct and broad.

Limnodynastes tasmaniensis Günther

FIGURE 44

MATERIAL.—No number (one specimen dissected, stage 37, SVL 20.7 mm). Collected from "Oakdale," near Sutton, New South Wales, Australia.

REFERENCE.—Watson and Martin (1973) described the larva.

GENERAL REMARKS.—Lungs smaller than average, unequal in size, length of longest about equal to length of floor of mouth; not inflated. Short but dense gill filaments.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth triangular, 20% wider than long. Four widely separated infralabial papillae in a transverse row; all elongate, anteroposteriorly compressed with pointed apices and a variety of surface

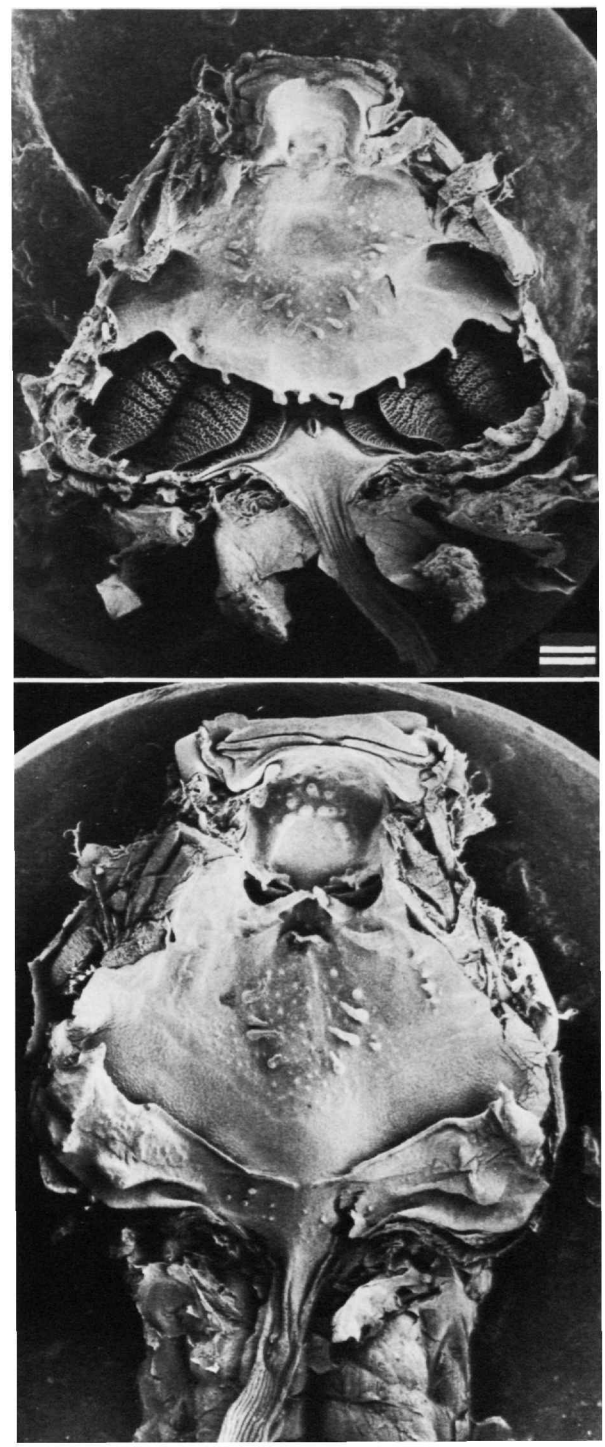


FIGURE 44.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Limnodynastes tasmaniensis;* scale line = 1 mm.

sculpturing, lacking bifurcations; in addition, small pustulations far forward in a transverse row. Two simple, thin, cone-shaped lingual papillae. BFA egg-shaped; about 10 BFA papillae on each side; BFA papillae thin, conical, non-bifurcate with very few surface rugosities; several with a curved apex. Two small prepocket papillae per side. Six to twelve small pustulations anterior to buccal pockets; 4 unequal-sized papillae in a tranvserse row running anterior and lateral to posterior and medial, beginning posteromedial to buccal pockets; about 12 tiny pustulations scattered about the posterior 1/2 of BFA. Buccal pockets average size; about 4 times as wide as long, relatively shallow; more transversely oriented than obliquely; not perforated. Free velar surface of average length; area of each side about 1/6–1/8 area of rest of buccal floor; conspicuous, thin, spicular support; posterior margin forming gentle hemicircle with relatively small, distinct peaks above 2nd, 3rd, 4th filter plates on each side and a single medium-sized papilla bounding the median notch on each side; median notch deep; secretory pits dense on margins of papillae and in a thin band along the remaining free edge of the ventral velum.

Pharyngeal Cavity: Branchial baskets 50% wider than long, triangular; area of each branchial basket about 80% area of remainder of buccal floor area; branchial baskets twice as wide as deep; first and 2nd filter cavities subequal, 3rd 30% smaller; filter cavities longitudinally oriented, especially 1st and 2nd, with 3rd oriented at 45° to sagittal plane. Dorsal edge of 2nd filter plate arching up and coiled slightly so edge pointing inferiorly and medially, top of 3rd filter plate curved upward sharply; 1st filter plate about twice as long as tall, 2nd about 50% longer than tall, 3rd and 4th as long as tall; filter plates moderately imbricated, 2nd filter plate covering about 25% of 2nd filter cavity, 3rd filter plate covering about 80% of 3rd filter cavity, 2nd and 3rd filter plates tipped at 45° except for curving dorsal edges; cb 1 with 11 filter rows, cb 2 with 12, cb 3 with 11, cb 4 with 7. High-density filter mesh; quaternary folds on most rows; filter rows relatively uniform and of average width; filter rows not abutting except ventrally; filter rows 25% wider than filter canals, canals 90% canopied. Branchial food traps large with secretory ridges conspicuous under light microscope, secretory ridges large and of uniform dimensions. Glottis 100% visible from above, small, occluded, with sharp, thin lips; faint laryngeal disk. Esophageal funnel narrow, esophagus of average to narrow diameter.

DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth triangular, a bit wider than long; nares 25% distance from front of mouth to esophagus; median ridge 40% distance from front of mouth to esophagus. Prenarial arena with an anteriorly convexed arch supporting a row of about 10 short squat papillae/pustulations; arch extending to base of anterior narial wall; in addition, 5–10 pustulations scattered anterior to arch in prenarial arena. Nares large; internarial distance about 2/3 length of naris; nares oriented obliquely with lateral corner slightly anterior to medial corner; anterior narial wall forming a strong triangular flap with a posteroventrally directed, pointed apex and a small, anteriorly directed, tab-like process on the medial edge of the anterior wall; posterior narial wall a simple thin flap of uniform height except for a tiny, faint, narial-valve projection near median end of valve. Postnarial arena defined by single large papilla arising approximately midway between the lateral edge of naris and lateral edge of median ridge on each side; postnarial papilla directed anteromedially with apices of each almost touching; postnarial papillae simple columns with some rugosity on anterior surfaces. Median ridge a small semicircular flap with some faint rugosities on the anterior surface otherwise lacking sculpturing. Lateral-ridge papillae arising from buccal roof immediately lateral to median ridge; simple, sickle-shaped structures, similar in shape to, but 50% smaller than, postnarial papillae. BRA V-shaped; 3 simple, conical BRA papillae on one side, 4 on other. Longitudinal line of small papillae laterally on buccal roof made up of 4 papillae on one side, 2 on other, plus a couple of pustulations; 1 or 2 very small papillae just posterior to lateral portion of BRA; many small pustulations scattered within BRA, smallest and most densely packed in posterior portion of BRA. Glandular zone of uniform length, about 1/8 length of rest of buccal roof; glandular zone made up of large, relatively dense secretory pits, continuous across the midline with a distinct anterior border. Dorsal velum of average length; just interrupted on midline; lacking marginal papillation; 2–4 small papillae posterior to dorsal velum just to side of midline.

Pharyngeal Cavity: Two pressure cushions on each side; lateral larger, longitudinally oriented, oval; medial smaller and more spherical. Ciliary groove of average width, shallow.

Megistolotis lignarius Tyler, Martin, and Davies

FIGURE 45

MATERIAL.—KU 180057 (one specimen dissected, stage 29, SVL 12.9 mm). Collected from 4 km N Lake Argyle Village, Western Australia, Australia.

REFERENCE.—Tyler et al. (1979) described and illustrated the larva.

GENERAL REMARKS.—Specimen in poor condition and did not prepare well for SEM; not all features discernible in figure. Lungs well developed, about equal in length to buccal floor; inflated. Gill filaments present.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth round, about as long as wide. Two pairs of infralabial papillae, dorsoanterior pair small, cup-like, with anterior ragged edges; second pair slightly more ventral and medial, slightly smaller. Two lingual papillae; tall and thin with slightly roughened surfaces. BFA broadly U-shaped; 15–20 BFA papillae, all relatively small, tall, conical, subequal, a few sickle-shaped; BFA papillae a bit rugose, none bifurcate. Three prepocket papillae per side, similar in size to BFA papillae. About 20 papillae scattered in posterior 1/2 of BFA; small row of 4 or 5 papillae running anterolateral to posteromedial in region

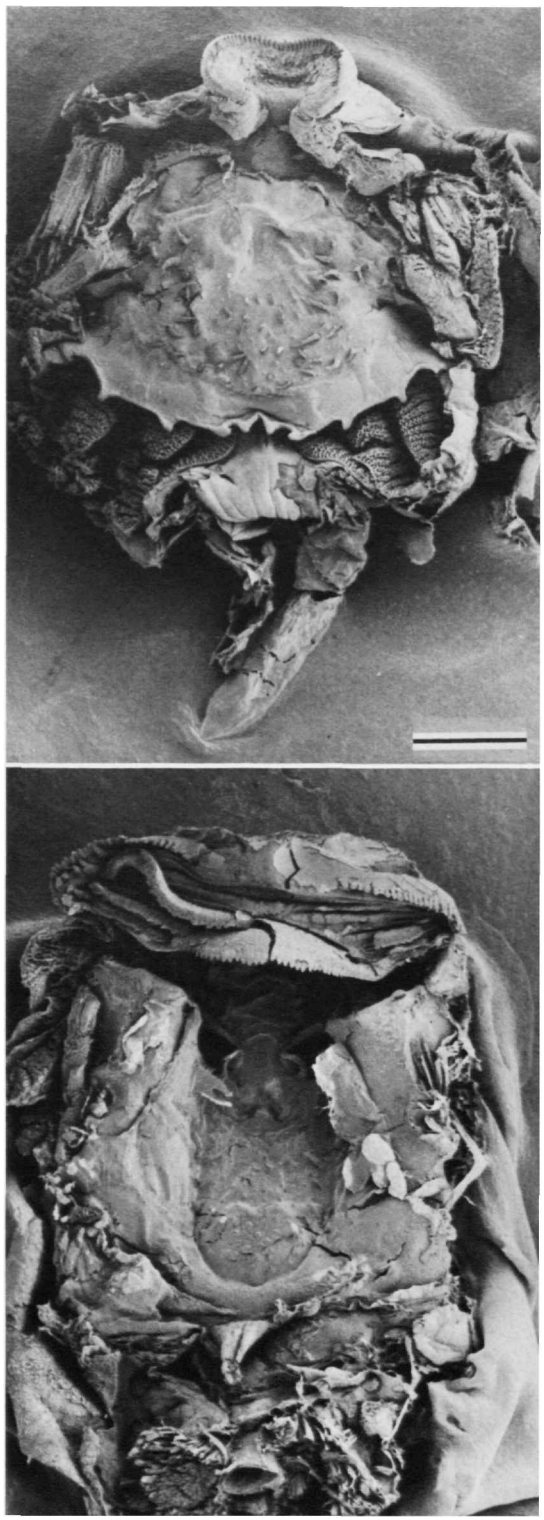


FIGURE 45.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Megistolotis lignarius;* scale line = 1 mm.

posteromedial to buccal pockets. Buccal pockets small; 3 times as wide as long; oblique; perforation uncertain. Free velar surface 15%–20% length of buccal floor; spicules conspicuous and broad; posterior velar margin of average length, a smooth arch with distinct marginal papillae directly dorsal to 2nd, 3rd, and 4th filter plates on each side; peaks above 4th filter plate pointing medially; median notch deep, surrounded by single papilla of average size on each side; posterior margin with thin but continuous band of small secretory pits.

Pharyngeal Cavity: Branchial baskets of average size, as wide as tall, triangular, longitudinally oriented, 40% rest of buccal floor area, very deep; filter cavities subequal in size. Second, 3rd, and 4th filter plates with free dorsal margin bowing upward; filter plates 20% longer than tall; ventrally, plates vertical, but dorsal edge tilting over medial portion of filter cavity; dorsal edge arched but tipped medially; cb 1 with about 8 filter rows, cb 2 with about 11, cb 3 with 10, cb 4 with 10. Filter mesh moderately dense; many quaternary folds; ventrally filter rows wide, most rows complete; at least 1/4 filter rows contacting neighbors; filter canals slightly narrower than filter rows, 80% or more canopied. Branchial food traps with well-formed, uniform secretory ridges (Figure 58*c,d*). Glottis small, fully exposed in median notch; laryngeal disk not visible, laryngeal lips medium to small in size. Esophageal funnel narrow.

DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth triangular, about as long as wide; nares 20% distance from front of mouth to esophagus; median ridge 50% distance from front of mouth to esophagus. Prenarial arena long and large with faint, ridge-like, anteriorly directed arch with weakly pustulate, free ventral edge. Nares of average size, fully open, internarial distance about 80% width of naris; nares obliquely oriented anterolaterally to posteromedially; anterior narial wall with weak triangular flap as a prenarial papilla; posterior narial wall very thin, no narial-valve projection. Four postnarial papillae per side, largest on each side immediately posterior to medial 1/3 of nares; attenuate, curved medially; immediately posterolateral to large papillae, a small attenuate papilla on each side, much farther posteriorly, directly anterior to lateral edge of median ridge, two similarly small but simpler papillae; about 6 additional pustulations scattered in postnarial arena. Median ridge a small trapezoidal structure with a jagged apex. Lateral-ridge papillae lobster claw-shaped, arising from a longitudinally oriented ridge; each lateral-ridge papilla nearly twice size of median ridge proper; each lateral-ridge papilla laterally compressed, bifurcate, with jagged apices and jagged, anterior, free edge. BRA an elongate rectangle, poorly defined by 5 simple, thin, conical papillae on each side. Cluster of 3 small, lateral-roof papillae on each side; about 50 small pustulations scattered within BRA proper. Glandular zone of large, conspicuous, secretory pits forming continuous band across midline; zone with relatively smooth anterior edge. Dorsal velum of average length, not continuous on midline, barely interrupted, smooth.

Pharyngeal Cavity: Two pressure cushions per side, of

subequal size, lateral pair more elongate and oval, medial more spherical. Ciliary groove narrow.

Mixophyes balbus Straughan

FIGURE 46

MATERIAL.—UMMZ 154850 (two specimens dissected, stage 25, SVLs 16.9, 17.1 mm). No locality data.

REFERENCE.—Watson and Martin (1973) described the external morphology.

GENERAL REMARKS.—Filamentous gills present. Lungs large, same length as buccal floor; not inflated. Information on second specimen provided in parentheses. First specimen figured.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth trapezoidal; length to width ratio 1:1.2. Four tall infralabial papillae; 2 medial, 2 lateral; all (not) touching at midline; non-bifurcated, but extremely pustulate. No lingual papillae. BFA open anteriorly, V-shaped posteriorly; 20–30 papillae on each side; BFA papillae all large, attenuate, conical, with pointed apices; no bifurcations. Few medium-sized prepocket papillae. Cluster of about 10 papillae on each side posteromedial to buccal pockets merging posteriorly and medially with BFA papillae; many small pustulations scattered randomly on buccal floor and 7 (10) anteriorly directed simple papillae scattered on mid- and posterior portion of BFA. Buccal pockets shallow, transversely oriented, wide; not perforated. Long, free, velar surface, equalling 1/2 length of buccal floor; spicular support evident on anterior portion of velum only; posterior ventral velar margin crenulate with 4 papillae per side, moderately tall peaks over filter cavities; conspicuous median notch; small secretory pits in uneven narrow band, especially on marginal papillae.

Pharyngeal Cavity: Branchial baskets 25% wider than long; 70% of buccal floor area; very deep. Dorsal edge of 2nd filter plate straight and horizontal; 3rd filter plate with tall V-shaped dorsal margin almost completely capping 3rd filter cavity; 2nd filter plate 50% longer than tall; 3rd filter plate 25% taller than long; cb 1 with 11 (9) filter rows, cb 2 with 12 (10), cb 3 with 10 (12), cb 4 with 8 (7). Filter mesh dense, particularly for a stream tadpole; most filter ruffles with tertiary folds; many rows wide and fully abutting neighbors, 100% canopying of filter canals. Branchial food traps large and deep; conspicuous, straight, secretory ridges. Glottis 30% exposed; narrow tall lips; laryngeal disc not obvious. Esophageal funnel narrow.

DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth narrow, 20% longer than wide (length about equal width); nares 30% of distance from upper beak to esophagus; median ridge 45% distance from front of mouth to esophagus. Long, narrow, prenarial arena with longitudinal midsagittal ridge; ridge with pustulate ventral margin; 2 (3) small papillae lateral to posterior end of ridge on an oblique line on each side with the largest papilla more medial; 2 additional pustulations in longitudinal

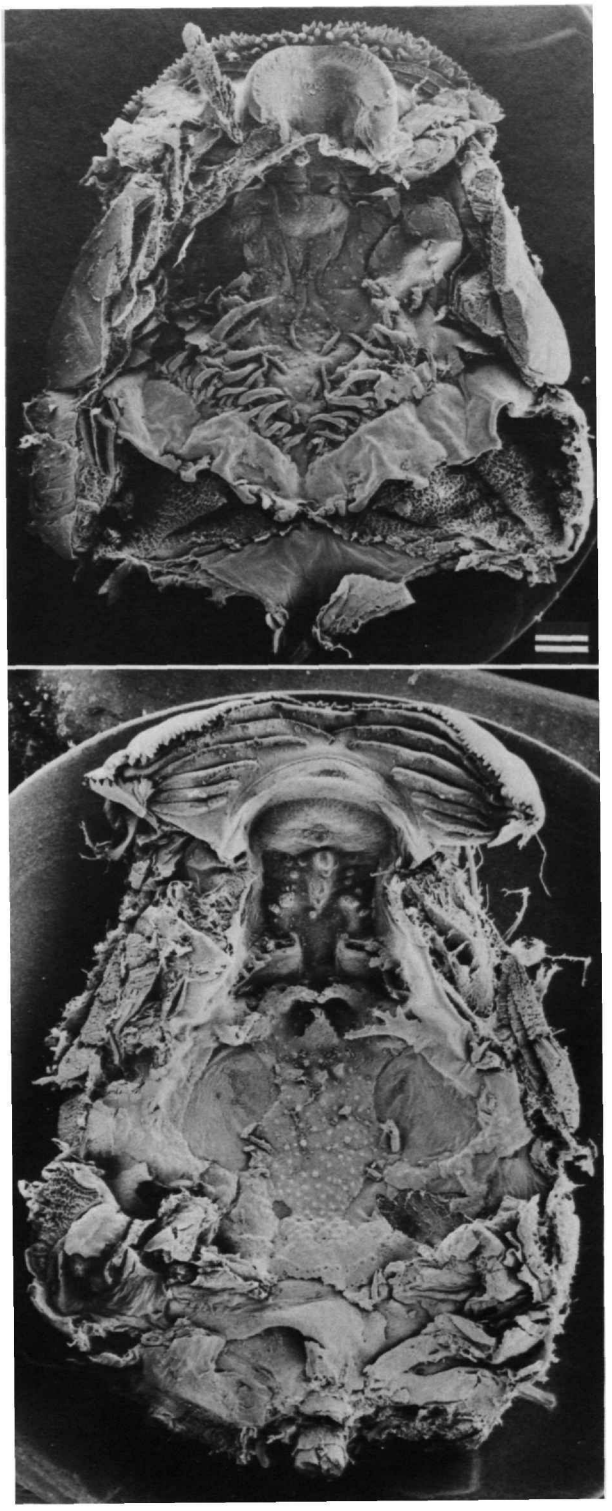


FIGURE 46.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Mixophyes balbus;* scale line = 1 mm.

row directly anterior to larger lateral papillae; approximately 5 or 6 pustulations and short papillae scattered about posterior 1/2 of the prenarial arena. Internal nares curving, orientation transverse medially and oblique laterally; internarial distance less than 50% narial width; small anterior narial papilla at medial margin of narial wall, but jagged papillate margin on whole anterior narial wall; posterior narial wall tall, thin, and smooth; very faint, broad, narial-valve projection. Two (four) papillae in the postnarial arena; small anteromedial pair; much larger posterolateral pair of equal height to postnarial wall, directed ventrally and medially such that apices touching (not touching) below the middle of the postnarial arena. Median ridge tall triangle with pustulate anterior surface and jagged free edge. Two lateral-ridge papillae on each side in line with postnarial papillae; larger and more lateral pair with multi-papillate margins. BRA poorly defined oval; 4 BRA papillae on each side laterally, an equal number anteriorly in BRA; all BRA papillae small and simple. Two tiny, lateral-roof papillae on far margins of the roof. Multitude of small pustulations in BRA, particularly dense posteriorly. Secretory pits large and distinct on glandular zone; not dense; relatively smooth anterior margin to zone. Dorsal velum long, absent on the midline with distinct papillae on medial margin.

Pharyngeal Cavity: Two pressure cushions on each side, most lateral one an oblique oval running anteromedial to posterolateral; medial cushion rounder and larger. Ciliary groove very broad.

Platyplectron ornatus (Gray)

FIGURE 47

MATERIAL.—FMNH 208955 (2 specimens dissected, stages 36, 37, SVLs 12.4, 12.0 mm respectively; stage 37 specimen illustrated.) Collected from Machan's Beach, Cairns, North Queensland, Australia on 25 February 1979, by W. Hosmer.

REFERENCE.—Watson and Martin (1973) provide external characteristics for the larvae of *Limnodynastes*, including representatives of the genus *Platyplectron*. Current work (Maxson, pers. comm.) may indicate that *Platyplectron* is a synonym of *Limnodynastes*.

GENERAL REMARKS.—Lungs large, about equal in length to that of buccal floor; sacculate; inflated. Gill filaments short but dense.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth roughly triangular, length about equalling width. Four infralabial papillae in an approximately transverse row; all triangular in cross-section with rough anterior faces; average height; jagged margins (Figure 53*f*). Two lingual papillae; tips bifurcated; average size, thin. BFA egg-shaped; 20–30 BFA papillae per side; most BFA papillae with jagged margins; all larger BFA papillae with branching apices. About 6 prepocket papillae on each side; anteromedially directed; largest with notched apices. Additional cluster of 8–10 papillae posteriorly on buccal floor running anterolateral to posteromedial at which point merging

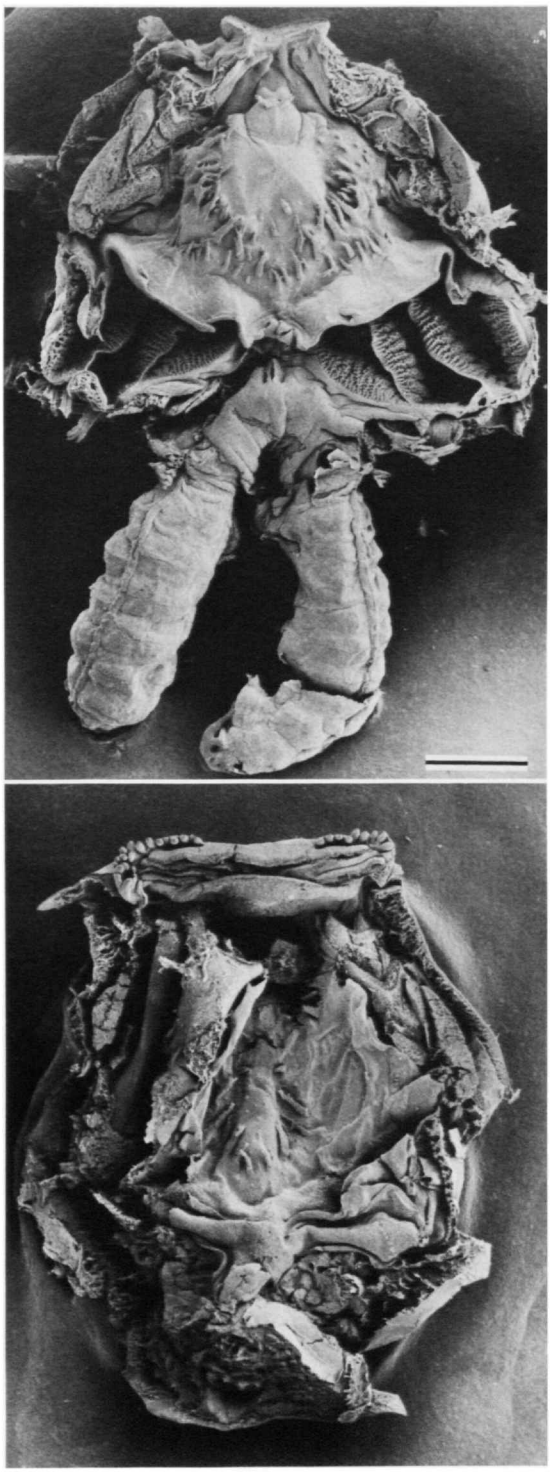


FIGURE 47.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Platyplectron ornatus;* scale line = 1 mm.

with posterior BFA papillae; 8–10 anteriorly directed attenuate papillae in posterior 1/3 of BFA, largest with bifurcate apices. Buccal pockets long and wide, 50% wider than long; obliquely oriented at 45° from transverse plane; perforated. Free velar surface of short to average length, less than 1/2 rest of buccal floor area; spicular support present; margin with 3 very distinct peaks above top edge of 2nd, 3rd, and 4th filter plates; small median notch surrounded by papillae; small dense secretory pits in thin band along edge of ventral velum.

Pharyngeal Cavity: Branchial baskets 20% wider than long, large, triangular; each branchial basket about 70% remaining area of buccal floor, as deep as long; all filter cavities subequal, oriented 45° from midline. Dorsal edge of 2nd filter plate curving upward slightly, dorsal edge of 3rd curving upward a bit more; 1st and 2nd filter plates about twice as long as tall, 3rd and 4th filter plates 30% longer than tall, filter plates vertically oriented; cb 1 with 11 filter rows, cb 2 with 10, cb 3 with 9, cb 4 with 7. Filter mesh dense; quaternary and higher order filter folds; rows wide, most abutting; filter canals 1/2 width or less of filter rows, 80%–100% canopied. Three distinct branchial food traps with well-organized secretory ridges in each, largely limited to ventral surface of ventral velum, not descending far into filter cavities. Glottis fully exposed; open; lips tapered; small laryngeal disk. Esophageal funnel of average profile; esophagus of average diameter.

Dorsal Aspect.—*Buccal Cavity:* Roof of mouth pentagonal; nares 20% distance from front of mouth to esophagus; median ridge 45%–50% distance from front of mouth to esophagus. Large, wide, anteroventrally directed arch descending from prenarial arena; 6 short subequal rugose papillae descending from arch. Nares of average size; internarial distance about length of naris; nares transversely oriented; variety of rugosities on entire length of anterior narial wall, none developed into a prenarial papilla; posterior narial wall a thin flap with a distinct narial-valve projection. Three or four postnarial papillae in a row just medial to medial end of nares, row curving backward and laterally, curving around so far that row continuous with posterior and lateral portion of anterior narial wall; most posteromedial papilla on each side large with club-like terminus touching its fellow medially; papillae grading to smaller size laterally. Median ridge a large triangular flap with fine serrations on apex and anterior surface. No lateral-ridge papillae. BRA egg-shaped; 5–10 BRA papillae per side, same morphology as BFA papillae. Three small, isolated, lateral-roof papillae on each side; 30–40 pustulations in BRA including some anterior to BRA on median ridge and lateral to it. Glandular zone long, about 1/4 length of buccal floor; with medium-sized secretory pits of uniform density; continuous across midline. Dorsal velum average length, widely divided; medial margin smooth and directed medially.

Pharyngeal Cavity: Pressure cushions distorted/destroyed in dissection. Ciliary groove narrow and shallow.

Pseudophryne bibronii Günther

Figure 48

Material.—UMMZ 154855 (two specimens dissected, description based on specimen stage 38, SVL 11.2 mm). No locality data.

Reference.—Watson and Martin (1973) described the external morphology.

General Remarks.—Lung buds small, asymmetrical; largest about 0.1 mm; not inflated.

Ventral Aspect.—*Buccal Cavity:* Floor of mouth a broad triangle, 10% wider than long. Single palp-like, medially directed, infralabial papilla located rather posteriorly on infralabial cartilage; irregular knobby anterior surface. No lingual papillae. BFA poorly defined; 3 or 4 thin, tall, pointed, medially directed BFA papillae on each side; BFA papillae not bifurcate. No prepocket papillae. Scattered field of pustulations in midportion of BFA; 2 or 3 small papillae clustered immediately anterior and medial to buccal pockets at base of the largest BFA papillae. Buccal pockets 3 times as wide as long; transversely oriented; perforation indeterminable. Free velar surface average-sized; spicular support slight, spicules short; velar surface laterally with straight, unsculptured, obliquely oriented edge, medially edge transversely oriented and with extensive irregular sculpturing; on middle portion 6 distinguishable peaks not aligned with filter plates or cavities below; large, asymmetrical, median notch; buff texture to free edge of velum (under light microscopy) with poorly defined secretory pits limited to posterior-most portion of ventral velum.

Pharyngeal Cavity: Branchial baskets slightly larger than average size, in dorsal view shaped like right triangle with hypotenuse on anteromedial side and posterior side 50% longer than lateral side; each basket about equal to 50% area of rest of buccal area; branchial baskets shallow, 4 times as wide as deep; most unusually, branchial baskets encroaching on midline, almost abutting under median notch of velum. Only 2 filter cavities; lateral cavity larger, 70% volume of basket; medial cavity a fusion of 2nd and 3rd filter cavities. Only 3rd filter plate with any depth, with straight dorsal edge; plate 4–5 times as long as tall; 4th filter plate very long and horizontally oriented; filter plates not imbricate; cb 1 with 8 filter rows, cb 2 with 7, cb 3 and 4 with 5 irregular rows. Filter mesh not very dense; few tertiary folds. Filter rows narrow and generally not abutting; filter canals subequal in size to filter rows and on average about 40% exposed in dorsal view. Branchial food traps with ill-defined, short and interweaving, secretory ridges. No glottis. Esophageal funnel region destroyed in dissection.

Dorsal Aspect.—*Buccal Cavity:* Roof of mouth same shape as floor, triangular; nares about 30% distance from front of mouth to esophagus; median ridge about 40% distance from front of mouth to esophagus. Prenarial arena devoid of topographic features. Nares large; internarial distance about equal to length of naris; 60° orientation from transverse plane;

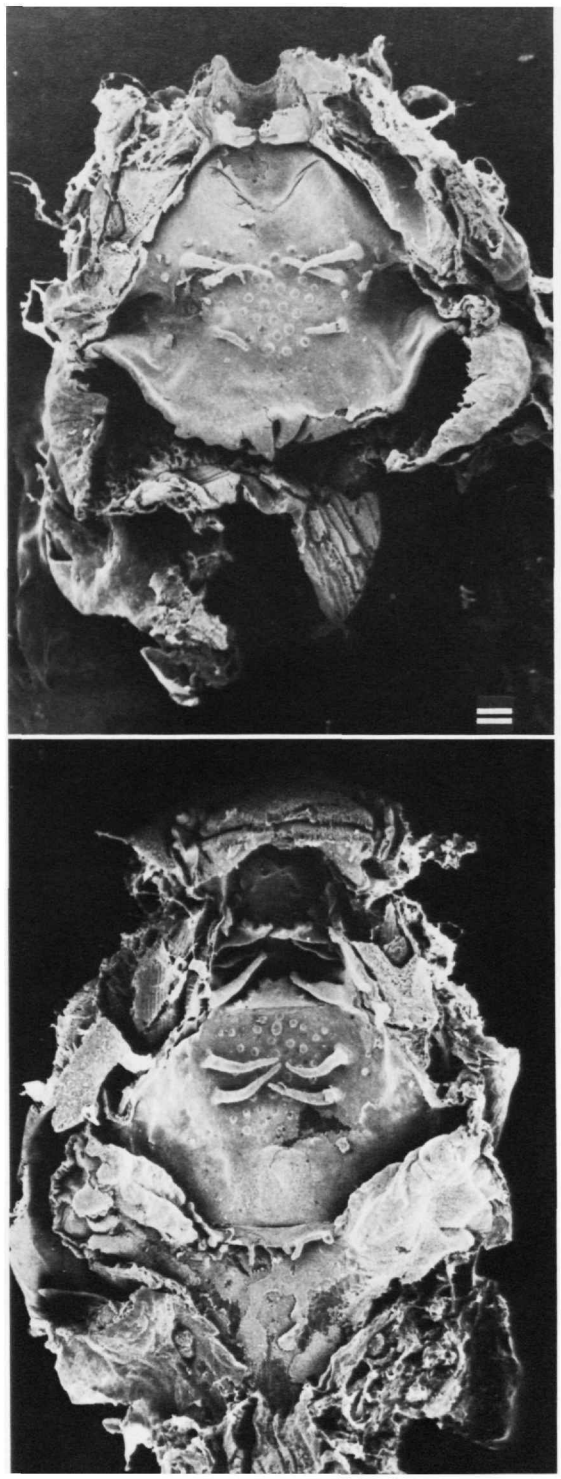


FIGURE 48.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Pseudophryne bibronii;* scale line = 2 mm.

very large, laterally compressed, medially directed projection covering anterior 1/3 of nares on anterior narial wall about 1/3 distance laterally; posterior wall with poorly defined, antero-medial, narial-valve projection. No postnarial papillae. Median ridge with broad, gently curved, free edge, no other sculpturing or detail. Lateral-ridge papillae simple, thin, conical, medially directed. BRA poorly defined, bounded by 2 papillae on each side; BRA papillae very tall, attenuate, simple, of subequal size, apices of largest pair crossing on midline, not bifurcate. Field of large pustules uniformly distributed throughout BRA up to base of median ridge. Glandular zone secretory pits present, small, and dense. Dorsal velum maximum length 20%–25% length of buccal floor; continuous on midline; extensively papillate on midline.

Pharyngeal Cavity: Single pillow-shaped pressure cushion on each side. Ciliary groove very broad.

Taudactylus diurnus Straughan and Lee

FIGURE 49

MATERIAL.—KU 180059 (one specimen dissected, stage 36, SVL 9.0 mm). Collected from Kilcoy Creek, Sunday Creek State Forest, Queensland, Australia.

REFERENCE.—Watson and Martin (1973) described and illustrated the larva.

GENERAL REMARKS.—Lungs small, collapsed; about 80% length of buccal floor, not obviously inflated.

VENTRAL ASPECT.—*Buccal Cavity:* Floor of mouth triangular-shaped, 25% wider than long. Two pair of infralabial papillae far posterior and medial; more medial and ventral pair 4 times size of more dorsal and lateral pair; more medial and ventral pair almost touching near midline; rotund; without major bifurcations/elaborations; some pustulations anteriorly on lower jaw. One pair of simple, small lingual papillae. BFA V-shaped; 7 or 8 BFA papillae per side, simple, attenuate, 2 on each side with bifurcate apices; BRA papillary row continuing into pustulate field of 8–10 pustulations anterior to BFA and lateral to tongue anlage. No prepocket papillae. Field of 15–20 pustules at the posterior extreme of the BFA just anterior to median notch. Buccal pockets primarily transversely oriented, about 5 times as wide as long; deep (unable to determine if perforated). Free velar surface of average length, about 1/7 length of buccal floor; with conspicuous spicular support; 3 marginal peaks over dorsal free edges of 2nd, 3rd, and 4th filter plates; an additional smaller posteriorly directed papilla immediately lateral to median notch on each side; small, sparse, secretory pits limited to free edge of ventral velum, rare except on peaks of free velar edge; deep median notch.

Pharyngeal Cavity: Branchial baskets approximately as long as wide, oval along an anterolateral to posteromedial axis; each branchial basket about 1/2 remainder of buccal floor, 1/2 as deep as wide; 2nd filter cavity largest, 50% bigger than 1st,

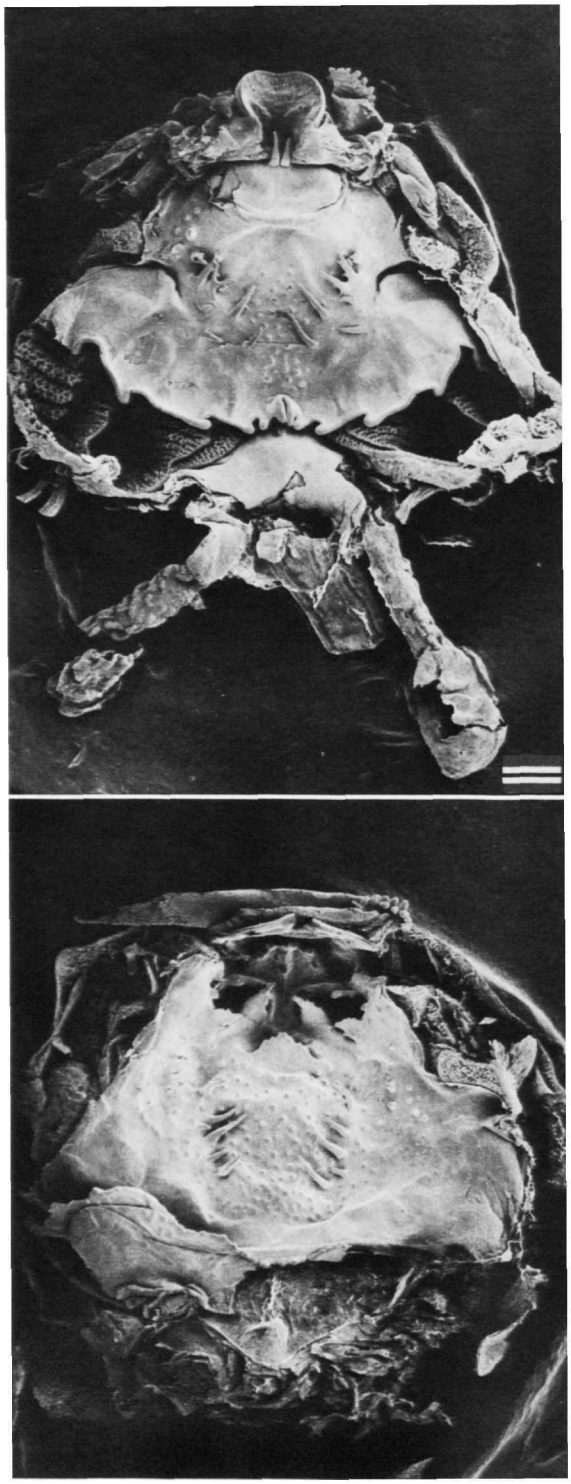


FIGURE 49.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Taudactylus diurnus;* scale line = 400 μm.

3rd 25% of 2nd, all obliquely oriented. Second filter plate with a relatively straight dorsal edge, 3rd rising to a single apex; 3rd filter plate almost as long as tall, 2nd filter plate overlapping 1st by 25%, 3rd filter plate overlapping 4th by 75%; filter plate orientation about 45° except for top of 3rd filter plate, top of 3rd plate curving over 4th filter cavity; cb 1 with 10 filter rows, cb 2 with 12 or 13, cb 3 with 12, cb 4 with 10. Filter mesh of high density; tertiary folds; filter rows relatively uniform and wide; filter canals 90%–100% canopied; filter rows 25% wider than canals. Branchial food traps with conspicuous secretory ridges, relatively uniform, very narrow, 1 or 2 cells wide. Glottis 20% visible from above; narrow but tall; no noticeable laryngeal disk. Esophageal funnel relatively broad.

DORSAL ASPECT.—*Buccal Cavity:* Roof of mouth relatively wide, 20% wider than long; nares about 20% distance from front of mouth to esophagus; median ridge about 40% distance from front of mouth to esophagus. Prenarial arena with anteriorly bowed arch descending from roof with 5 symmetrical points; medial point slightly bifurcate with single pustulation posterior to it. Nares large; internarial distance about 20% maximum length of naris; nares transversely oriented ovals; large vomeronasal pit at median edge of internal nares; anterior narial wall shallow except for single, distinct, tall papilla originating halfway between medial and lateral edge of naris; posterior narial wall shallow with large, triangular, narial-valve projection with jagged margins covering 1/4 area of naris on each side. Postnarial arena relatively smooth. Median ridge an average-sized triangular flap with a slightly jagged anterior surface. Single, small, lateral-ridge papilla on each side arising from common ridge-like base lateral and just posterior to narial-valve projections; lateral-ridge papillae triangular palps anterior and lateral to median ridge about 1/3 size of median ridge. BRA an elongate oval; single row of 6 papillae per side running relatively longitudinally; BRA papillae all tall, simple, attenuate. More than 15 small pustulations within BRA and 2 small fields of pustulations/papillae directly lateral to median ridge and lateral 1/2 of BRA. Glandular zone very poorly defined of small, indistinct, scattered, secretory pits, not continuous or very narrowly continuous across midline. Dorsal velum 25% length of buccal floor, barely continuous on midline with continuous pustulate margin.

Pharyngeal Cavity: At least one lateral large oval pressure cushion on each side. Ciliary groove very broad and shallow.

Discussion

There is as much or more variation of oral structures in leptodactyloids as in any other anuran taxa of comparable size and rank (e.g., Viertel, 1982; Wassersug, 1980). To interpret this variation the nature and degree of ontogenetic and intraspecific variation must be identified first. This is necessary, before the remaining interspecific variation can be correlated with either ecology, phylogeny, or both.

A framework for discussing and partitioning the variation observed is to summarize the data at the generic level. The generic synopses presented herein include three kinds of information. (1) Morphological features that either alone or in concert distinguish or characterize each genus, along with data presented in Table 1, provide an overview of the variation found within and among genera. (2) Based on morphology, predictions are presented on the basic microhabitat and feeding ecology of the larvae. Previous work (Wassersug, 1980; Wassersug and Heyer, 1983) has defined the following adaptive larval types: generalist pond larvae; stream larvae; fossorial larvae; subaerial larvae; obligate microphagous larvae; macrophagous, herbivorous larvae; and obligate, macrophagous, carnivorous larvae. Although we touch on character suites that define these types in the following summaries, we do not redefine the larval types here; rather, readers should refer to the two papers cited. (3) Lastly, larval ecologies, when known, are included in the synopses and compared with the microhabitat and dietary predictions.

Generic Synopses

The synopses presented are not definitive because most species of many genera have not been examined. Although the following provides a useful framework into which future work can be incorporated, we fully anticipate that several of these characterizations will have to be modified based on additional species data.

African Leptodactyloid

Heleophryne

The infralabial papillae are cup-like. There are two lingual papillae. The BFA papillae are organized into a continuous V-shaped ridge whereas BRA papillae are few and no ridge is present matching that found on the floor. The median ridge is reduced to a papilla. The nares are oriented longitudinally. The secretory tissue of the branchial food traps is not organized into ridges (Figure 57*a*).

Internally these larvae do not have the full set of oral characters that usually defines stream-living, neobatrachian tadpoles. Internal oral characters of *Heleophryne* that do suggest stream life are: (1) narrowing of the mouth anteriorly as a result of a short medial arm and long lateral arm of the ceratohyal, which Wassersug and Hoff (1979) indicated is adaptively designed for generating large buccal pump forces at the expense of buccal volume; (2) complex structures at the front of the oral cavity to obstruct the passage of large particles into the mouth; (3) a low density for the gill-filter mesh; and (4) shallow branchial baskets. Conspicuously missing from this suite is elaborate and complex buccal papillation or strong development of a median ridge (cf. stream leptodactylids such as *Hylodes* and *Crossodactylus* below). *Heleophryne* has the morphological pattern seen in *Ascaphus* and other tadpoles with suctorial oral disks extremely specialized for holding onto the substrate in fast-flowing water (e.g., *Amolops*, Inger, 1985).

A lack of secretory ridges in the branchial food traps indicates either a macrophagous diet or non-feeding in most neobatrachian tadpoles (Wassersug and Rosenberg, 1979), but it also characterizes the archaic frog families Ascaphidae, Discoglossidae, and Pelobatidae regardless of diet. Secretory ridges are present in the fast-flowing water larvae of *Amolops* (Wassersug, pers. obs.). *Heleophryne* larvae are most similar in oral morphology to tadpoles of *Ascaphus* (Wassersug and Rosenberg, 1979).

Hewitt (1922:64) described the habitat of *H. natalensis* as "a stream, strewn with boulders and interrupted by several falls and cascades..." and noted that the "tadpole attaches itself firmly to the rocks in the riverbed with the large circular oral sucker."

South American Leptodactyloids

Adenomera

The single species of *Adenomera* examined, *A. marmorata*, has a non-feeding tadpole. It has all papillae reduced, but still retains vestiges of 4 infralabial papillae (Figure 52*a*), a median ridge, and lateral-ridge papillae. The branchial baskets are extremely shallow and the gill filters are lost. The glottis is very large.

Adenomera marmorata is similar to many direct-developing and non-feeding, egg-brooding hylids (Wassersug and Duellman, 1984). It has not, however, lost all vestiges of larval features, such as seen in *Eleutherodactylus* and *Hemiphractus*. When dye was injected into the mouth of a stage 35 *A. marmorata* specimen, it came out the spiracle, indicating *A. marmorata* theoretically could have irrigated buccopharyngeal surfaces in life. This specimen had very short, stubby, reduced, gill filaments, whereas an *Eleutherodactylus coqui* at approximately the same stage of development had neither an open spiracle nor a suggestion of gill filaments. Not all larvae of *Adenomera* show the same degree of reduction of larval morphology; *Adenomera bokermanni* has a better-developed oral disk (see fig. 23 in Heyer, 1973:32), suggesting that the internal oral features of this species would have a more normal tadpole configuration.

Alsodes

Other than extreme imbrication of the third filter plate over the fourth filter plate and very large, deep, branchial baskets, the larval morphology is that of a generalized pond tadpole with relatively large lungs. The studied specimens of *A. monticola* presumably were collected from a lake. Diaz and Valencia (1985) reported that *Alsodes tumultuosus* larvae occur in pools with muddy bottoms and rocky crevices along a stream bank.

TABLE 1a.—Summary of character states for internal oral anatomy features of leptodactyloid larvae. Data for *Cycloramphus* and *Thoropa* previously published (Wassersug and Heyer, 1983); + = presence, – = absence; * = feature indistinguishable due to poor preservation or destroyed in dissection or SEM preparation.

Taxa	Total no. specimens examined	Total no. infralabial papillae	Total no. lingual papillae	No. BFA papillae (per side)	No. Prepocket papillae (per side)	Margin of ventral velum: Papillae above branchial baskets	Margin of ventral velum: Papillae medial to branchial baskets above laryngeal region
Heleophryne							
natalensis	1	8–12	2	9–10	0	+	–
Adenomera							
marmorata	1	4	2 (pustules)	0	0	+	–
Alsodes							
monticola	2	4	4	~25	8	+	+
species	1	4	4	~20	8–10	+	+
Atelognathus							
patagonicus	1	4	4	~20	>6	+	+
reverberii	1	4	4	~25	6+	+	+
Batrachyla							
taeniata	1	4	4	20–25	~6	+	+
Caudiverbera							
caudiverbera	1	4	4	10–15	0	+	+
Ceratophrys							
aurita	1	3	2	2–3	3–4	–	–
Crossodactylodes							
species	1	8–10	4	10	0	–	–
Crossodactylus							
gaudichaudii	1	4	4	30–40	5–6	+	+
schmidti	1	4	4	25–35	3–4	+	+
species	1	4	4	30–40	5–6	+	+
Cycloramphus							
izecksohni	2	2	4	9–10	0	+	+
stejnegeri	1	2	2	0	0	–	*
Eleutherodactylus							
species	1	0	0	0	0	–	–
Eupsophus							
roseus	1	4	4	20–30	8–12	+	+
Hylodes							
cf. asperus	1	4	2	25–30	4–5	+	+
Hylorina							
sylvatica	1	4	4	25–35	10–15	+	+
Lepidobatrachus							
laevis	1	2	4	0	0	–	–
Leptodactylus							
chaquensis	1	4	3	10–15	0	+	+
fuscus	1	3	4	10–15	1–2	+	+
gracilis	1	3	4	8–10	1–2	+	+
knudseni	1	5	3	10	2–3	+	+
mystacinus	1	3	4	7–8	0	+	+
pentadactylus	1	4	3	5–6	0	+	*
wagneri	2	3	0	10–15	0–3	+	+
Macrogenioglottus							
alipioi	1	4	4	15–25	3–4	+	+

TABLE 1a.—Continued.

Taxa	Total no. specimens examined	Total no. infralabial papillae	Total no. lingual papillae	No. BFA papillae (per side)	No. Prepocket papillae (per side)	Margin of ventral velum: Papillae above branchial baskets	Margin of ventral velum: Papillae medial to branchial baskets above laryngeal region
Megaelosia goeldii	2	4–6	4	20–25	4–10 (pustulations)	+	+
Odontophrynus americanus	1	4	4	20–30	5–10	+	+
Odontophrynus occidentalis	1	4	4	20–30	5–10	+	+
Paratelmatobius lutzii	1	2	11	~50	6–10	+	–
Physalaemus petersi	1	4	4	6	1–2	+	+
Physalaemus pustulosus	1	4	4	6	0	+	+
Pleurodema borellii	1	4	4	10–15	0	+	+
Pleurodema brachyops	1	4	4	10–15	0	+	+
Pleurodema bufonina	2	4	4	20	6	+	+
Pleurodema cinerea	3	4	2	30–40	6–10	+	+
Pleurodema nebulosa	2	4	4	25–40	6–8	–	+
Proceratophrys appendiculata	1	4	4	45–60	8–12	–	+
Pseudopaludicola boiei	1	4	4	25	6–10	+ (small)	+ (small)
Pseudopaludicola species	2	2	3	8–12	1	+ (weak)	+
Rhinoderma darwinii	1	0	3–4 (pustules)	20–30	0	+	+
Telmatobius jelskii	1	4	3	18–24	8–9	+	+
Telmatobius marmoratus	1	4	2	~30	8–9	+	+
Thoropa miliaris	2	2	4	6	4	–	+
Thoropa petropolitana	3	2	4	7–9	0	+	+
Crinia tasmaniensis	1	2	2	12	2–3	–	+
Heleioporus species	1	4	2	12–13	4	+	–
Limnodynastes tasmaniensis	1	4	2	10	2	+	+
Megistolotis lignarius	1	4	2	12–20	3	+	+
Mixophyes balbus	2	4	0	20–30	3–5	+	+
Platyplectron ornatus	2	4	2	20–30	~6	+	+
Pseudophryne bibronii	2	1	0	3	0	+	+
Taudactylus diurnus	1	4	2	7–8	0	+	+

TABLE 1b.—Summary of character states for internal oral anatomy features of leptodactyloid larvae. Data for *Cyclorampus* and *Thoropa* previously published (Wassersug and Heyer, 1983); + = presence, – = absence; * = feature indistinguishable due to poor preservation or destroyed in dissection or SEM preparation.

Taxa	Secretory pits	Branchial basket size and depth	Imbrication of 3rd filter plate	Orientation of 4th filter plate	No. of distinct filter cavities in dorsal view
Heleophryne					
natalensis	+	small, shallow	average	normal	3
Adenomera					
marmorata	–	very shallow	none	moderately inclined	1
Alsodes					
monticola	+	shallow	extreme	horizontal	3
species	+	shallow	extreme	horizontal	3
Atelognathus					
patagonicus	*	very deep	average	normal	3
reverberii	+(faint)	very deep	average	normal	3
Batrachyla					
taeniata	+	deep	below average	moderately inclined	2
Caudiverbera					
caudiverbera	+	large, deep	average	normal	3
Ceratophrys					
aurita	–	small, shallow	none	normal	3
Crossodactylodes					
species	+	deep	extreme	normal	2
Crossodactylus					
gaudichaudii	+	shallow	less than average	horizontal	2
schmidti	+	shallow	extreme	horizontal	2
species	+	shallow	less than average	horizontal	2
Cycloramphus	none under				
izecksohni	light microscope	extremely shallow	none	horizontal	1
stejnegeri	*	extremely shallow	*	*	1
Eleutherodactylus					
species	–	absent	NA	NA	0
Eupsophus					
roseus	+	moderately deep	average	average	3
Hylodes					
cf. *asperus*	+	shallow	above average	moderately inclined	2
Hylorina					
sylvatica	+	average	above average	normal	3
Lepidobatrachus					
laevis	–	average	none	NA	0
Leptodactylus					
chaquensis	+	deep	average	normal	3
fuscus	+	deep	average	normal	3
gracilis	+	deep	average	normal	3
knudseni	+	deep	average	normal	3
mystacinus	+	deep	average	normal	3
pentadactylus	+	deep	average	normal	3
wagneri	+	deep	average	normal	3
Macrogenioglottus					
alipioi	+	deep	average	normal	3

TABLE 1b.—Continued.

Taxa	Secretory pits	Branchial basket size and depth	Imbrication of 3rd filter plate	Orientation of 4th filter plate	No. of distinct filter cavities in dorsal view
Megaelosia					
goeldii	+	shallow	above average	normal	3
Odontophrynus					
americanus	+	deep	average	normal	3
occidentalis	+	deep	above average	normal	3
Paratelmatobius					
lutzii	+	shallow	less than average	moderately inclined	2
Physalaemus					
petersi	+	slightly shallow	average	moderately inclined	3
pustulosus	+	average	average	moderately inclined	2
Pleurodema					
borellii	+	deep	none	horizontal	2
brachyops	+	average	less than average	horizontal	2
bufonina	+	deep	less than average	horizontal	2
cinerea	+	average	average	normal	3
nebulosa	–	deep	less than average	moderately inclined	2
Proceratophrys					
appendiculata	+	shallow	less than average	horizontal	2
boiei	+	shallow	average	moderately inclined	3
Pseudopaludicola					
species	+	shallow	none	horizontal	1
Rhinoderma					
darwinii	–	extremely shallow	less than average	moderately inclined	3
Telmatobius					
jelskii	+	shallow	above average	normal	2
marmoratus	+	shallow	above average	normal	2
Thoropa					
miliaris	–	extremely shallow	less than average	horizontal	1
petropolitana	–	shallow	less than average	horizontal	1
Crinia					
tasmaniensis	–	shallow	less than average	horizontal	2
Heleioporus					
species	+	deep	average	normal	3
Limnodynastes					
tasmaniensis	+	deep	above average	normal	3
Megistolotis					
lignarius	+	deep	average	normal	3
Mixophyes					
balbus	+	very deep	above average	moderately inclined	2
Platyplectron					
ornatus	+	deep	average	normal	3
Pseudophryne					
bibronii	+	shallow	less than average	horizontal	2
Taudactylus					
diurnus	+	deep	above average	normal	3

TABLE 1c.—Summary of character states for internal oral anatomy features of leptodactyloid larvae. Data for *Cycloramphus* and *Thoropa* previously published (Wassersug and Heyer, 1983); + = presence, – = absence.

Taxa	No. filter rows per plate				Filter mesh density	Folding pattern of filter rows	Secretory ridges
	cbI	cbII	cbIII	cbIV			
Heleophryne							
natalensis	8	8	8	7	extremely low	few tertiary	–
Adenomera							
marmorata	–	5	5	4	no mesh	NA	–
Alsodes							
monticola	6	7	8	6	low	some quaternary	+
species	8	10	8	7	low	some quaternary	+
Atelognathus							
patagonicus	6+	11–12	10+	8+	moderate to dense	many quaternary	+
reverberii	10	12	10	8	moderate to dense	many quaternary+	+
Batrachyla							
taeniata	8	11	11	9	dense	few quaternary	+
Caudiverbera							
caudiverbera	12	12	12	11	dense	quaternary+	+
Ceratophrys							
aurita	3	5	3	3	no mesh	secondary	–
Crossodactylodes							
species	11+	14	9	8	slight	secondary	–
Crossodactylus							
gaudichaudii	9	10	8	5	moderate	tertiary	+
schmidti	10	10	9	6	moderate	tertiary	+
species	11	11	10	5	moderate	tertiary	+
Cycloramphus							
izecksohni	4	5–6	7–8	4	low	secondary	–
stejnegeri	1–3	4	4	3	low	primary	–
Eleutherodactylus							
species	0	0	0	0	no mesh	no filter folds	–
Eupsophus							
roseus	8	10	11	10	dense	tertiary	+
Hylodes							
cf. asperus	11	13	10	5	average	quaternary	+
Hylorina							
sylvatica	8	11	12	8	dense	quaternary	+
Lepidobatrachus							
laevis	9	8	7	6	no mesh	primary	–
Leptodactylus							
chaquensis	12	12	12	9	dense	tertiary	+
fuscus	10	11	10	7–8	dense	tertiary	+
gracilis	9–10	11	9–10	7	dense	quaternary	+
knudseni	11	12	12	7	dense	tertiary	+
mystacinus	10	10	10	8	dense	tertiary	+
pentadactylus	9	11	10	9	moderately dense	quaternary	+
wagneri	8	10	10	6	dense	tertiary	+
Macrogenioglottus							
alipioi	11	13	10	8	dense	quaternary	+

TABLE 1c.—Continued.

Taxa	No. filter rows per plate				Filter mesh density	Folding pattern of filter rows	Secretory ridges
	cbI	cbII	cbIII	cbIV			
Megaelosia							
goeldii	10–12	11–15	11–12	6–11	moderately dense	quaternary	+
Odontophrynus							
americanus	10	10	10	11	dense	tertiary	+
occidentalis	9	12	11	9	dense	tertiary	+
Paratelmatobius							
lutzii	10–11	12	9	5	low	tertiary	+
Physalaemus							
petersi	11	10	10	7	dense	quaternary	+
pustulosus	8	12	11	7	dense	tertiary	+
Pleurodema							
borellii	10	10	10	7	dense	some quaternary	+
brachyops	11	10	11	7	dense	some quaternary	+
bufonina	10	12	10	8	dense	some quaternary	+
cinerea	10	11	8	7	average	tertiary	+
nebulosa	8–13	11	9–10	8–10	average	tertiary	–
Proceratophrys							
appendiculata	6–8	7–8	5–8	4	less than average	tertiary	+
boiei	7	12	10	6	average	tertiary	+
Pseudopaludicola							
species	7	7	8	6	moderate	some quaternary	+
Rhinoderma							
darwinii	5	7	8	4–5	low	secondary	–
Telmatobius							
jelskii	12	12	9	6	average	some quaternary	+ (weak)
marmoratus	12	11	11	9	average	some quaternary	+ (weak)
Thoropa							
miliaris	<4	5	7	4	low	tertiary	–
petropolitana	4–5	6	6–7	4–5	average	tertiary	–
Crinia							
tasmaniensis	8	9	6–7	6	less than average	tertiary	+
Heleioporus							
species	6	7–8	7	6	less than average	tertiary	+
Limnodynastes							
tasmaniensis	11	12	11	7	dense	quaternary	+
Megistolotis							
lignarius	~8	~11	10	10	dense	quaternary	+
Mixophyes							
balbus	9–11	10–12	10–12	7–8	dense	tertiary	+
Platyplectron							
ornatus	11	10	9	7	dense	quaternary+	+
Pseudophryne							
bibronii	~8	7	5	5	low	tertiary	+
Taudactylus							
diurnus	10	12–13	12	10	dense	tertiary	+

TABLE 1d.—Summary of character states for internal oral anatomy features of leptodactyloid larvae. Data for *Cycloramphus* and *Thoropa* previously published (Wassersug and Heyer, 1983); * = feature indistinguishable due to poor preservation or destroyed in dissection or SEM preparation. Intermediate states of the median ridge are indicated by superscript + or –.

Taxa	No. postnarial papillae (per side)	Size of median ridge	Median ridge simple or complex	No. lateral ridge papillae (per side)	No. BRA papillae (per side)	Dorsal velum	
						Continuous across midline	Papillate medial edge
Heleophryne							
natalensis	0–1	very small (papilla)	simple	2 ridges	0	+	–
Adenomera							
marmorata	1	very small	simple	1	0	absent	
Alsodes							
monticola	2	small	complex	1	10	–	–
species	5	small	complex	1	15	–	–
Atelognathus							
patagonicus	2	very tall	complex	1	~10	–	–
reverberii	2	very tall	complex	1	~10	–	–
Batrachyla							
taeniata	3	moderately large	complex	1	6–8	–	+ (slight)
Caudiverbera							
caudiverbera	2–3	moderately broad	simple	1	4–5	–	–
Ceratophrys							
aurita	0–1	small	complex	0	0	–	–
Crossodactylodes							
species	2–3	shallow and wide	complex	2	4–5	–	–
Crossodactylus							
gaudichaudii	10–15	average	complex	4	30–40	–	+
schmidti	9–10	average	complex	4	20–30	–	+
species	10–15	average	complex	4	20–30	–	+
Cycloramphus							
izecksohni	1	small	complex	1	5–7	–	+ (tiny)
stejnegeri	0	essentially absent	simple	1	0	–	–
Eleutherodactylus							
species	0	absent	NA	0	0	–	–
Eupsophus							
roseus	3	average	complex	1	~10	–	–
Hylodes							
cf. asperus	8–11	small	simple	1	15–25	–	+
Hylorina							
sylvatica	2–3	*	*	*	15–20	–	+
Lepidobatrachus							
laevis	0	absent	NA	0	0	absent	
Leptodactylus							
chaquensis	1	average	complex	1	5–8	–	+
fuscus	2	average	complex	1	4–5	–	+
gracilis	1	average	complex	1	4–5	–	+
knudseni	1	average	complex	1	2–3	–	–
mystacinus	2	average	simple	1	4	–	–
pentadactylus	2	small	simple	1	1–2	–	*
wagneri	1	average	complex	1	6–8	–	+
Macrogenioglottus							
alipioi	6	large	simple	1	10	–	+

TABLE 1d.—Continued.

Taxa	No. postnarial papillae (per side)	Size of median ridge	Median ridge simple or complex	No. lateral ridge papillae (per side)	No. BRA papillae (per side)	Dorsal velum	
						Continuous across midline	Papillate medial edge
Megaelosia							
goeldii	2–3	average	complex	1	15	–	+
Odontophrynus							
americanus	3	large	simple	1	8–15	–	+
occidentalis	3	large	simple	1	8–15	–	+
Paratelmatobius							
lutzii	3	large	complex	1	~50	–	+
Physalaemus							
petersi	2	average	simple	1	6	–	–
pustulosus	2	average	simple	1	6	–	–
Pleurodema							
borellii	3	average	complex⁻	1	7	+	–
brachyops	3	average	complex⁻	1	4–5	–	–
bufonina	3	average	complex⁻	1	4–5	–	–
cinerea	5	small	complex	1	10–15	–	+ (tiny)
nebulosa	2	large	simple	1	18–20	+	–
Proceratophrys							
appendiculata	5–6	small	complex	1	30–35	–	+
boiei	5–6	average	complex	1	15	–	+
Pseudopaludicola							
species	1–2	average	complex	1	4–6	–	+
Rhinoderma							
darwinii	1	average	simple⁺	0	15–20	–	*
Telmatobius							
jelskii	6–7	average	simple⁺	1	8–10	–	–
marmoratus	6–7	average	simple⁺	1	8–10	–	–
Thoropa							
miliaris	1–2	small	complex	1	3–4	–	–
petropolitana	1–2	small	complex	1	5–9	–	–
Crinia							
tasmaniensis	1	large	complex	1	8–9	+	+
Heleioporus							
species	1	average	complex	1	0	–	–
Limnodynastes							
tasmaniensis	1	small	simple	1	3–4	–	–
Megistolotis							
lignarius	1	small	complex	1	5	–	–
Mixophyes							
balbus	2–4	average	complex	2	4	–	+
Platyplectron							
ornatus	3–4	large	simple⁺	0	5–10	–	–
Pseudophryne							
bibronii	0	average	simple	1	2	+	+
Taudactylus							
diurnus	0	average	complex	1	6	+	+ (weak)

Atelognathus

The only distinctive feature is a very tall median ridge that is taller than the lateral-ridge papillae. In all other features, the larvae are consistent with a pond larval morphology. Cei (1980:245) reports *A. reverberii* larvae from "shallow clay lagoons."

Batrachyla

The presence of only two filter cavities as a result of the top of the third filter plate meeting the bottom of the fourth filter plate distinguishes *Batrachyla*. The median ridge is relatively large and bifurcate and the ventral velum has blunt marginal papillae.

Other than having two, rather than three, filter cavities, the larval features are very standard for pond tadpoles. Cei and Capurro (1958) reported that eggs of *Batrachyla* are laid in terrestrial situations where development takes place for up to 40–45 days. The last four months of premetamorphic development occurred in swamps and marshes.

Caudiverbera

Except for its large size, all features identify the larva as a pond tadpole. Diaz and Valencia (1985:178) indicated that these "larvae prefer the bottom and borders of ponds and rivers; the large size of these larvae makes them sluggish and slow swimmers."

Ceratophrys

The infralabial papillae are large and flap-like. The buccal papillation is extremely reduced with a reduced median ridge. The ventral velar margin is thickened and non-papillate. The branchial baskets are extremely small and lack gill filters. The combination of three infralabial and two lingual papillae is unusual. The glottis is vertically oriented.

Extreme reductions of buccal papillae, mucus entrapment, and gill-filter systems are typical of carnivorous, macrophagous tadpoles. The diet for *C. aurita* has not been studied, but other *Ceratophrys* larvae are known to be carnivores and cannibalistic (e.g., Cei, 1980:221). Unlike obligatorily macrophagous carnivores (e.g., *Hymenochirus* or *Lepidobatrachus*), *Ceratophrys* retains a strong beak and can thus mechanically reduce large particles to smaller ones. In captivity they will eat commercial "frog brittle," liver, and dead conspecifics.

Crossodactylodes

There are a large number of infralabial papillae. The median ridge rises from a continuous semicircular base and runs between the lateral edges of the nares. Only two filter cavities exist, but the fourth filter plate is almost vertical. The filter-mesh density is relatively low.

The larval features suggest a tendency toward macrophagy; however, Peixoto (1983) considered these tadpoles to be detritivores. Compared to pond tadpoles of the same size, *Crossodactylodes* has a gill-filter mesh of low density. The reduction of the median ridge may relate to taking in relatively large food items. The presence of secretory ridges suggests that the larvae are capable of suspension feeding and are not particularly macrophagous or carnivorous.

Peixoto (1981) stated that the larvae occur in bromeliads; the relatively well-developed lungs correlate with this habitat.

Crossodactylus

The oral cavity overall is characterized by a large number of papillae of an attenuate nature, including large numbers of pustulations and papillae within the BFA and BRA. Long, finger-like processes are on the infralabial papillae (Figure 52*b*). The ventral velum has an asymmetrical fringe that covers the glottis (Figure 55). The fourth filter plate is very small and horizontally oriented. The filter density is low. The prenarial arena is long and has a longitudinal ridge. Multiple rows of papillae/pustulations parallel the nares in the postnarial arena. The lateral-ridge papillae are very large. A papillate fringe occurs on the medial half of the dorsal velum on each side (Figure 63*c*).

The extreme papillation and reduced filter density suggest that these larvae feed on a relatively coarse suspension. The shallowness of the branchial baskets, reduction to two filter cavities, horizontal orientation of the fourth filter plate, and elaboration of papillae at the front of the mouth, and other features listed above are characters found in benthic tadpoles that live in running water. The series of the three species examined shows a gradient with *gaudichaudii* having the largest and *schmidti* the smallest lungs. Based on this, we predict that *gaudichaudii* would be found in slower-flowing water than *schmidti*.

Crossodactylus larvae are reported from small- to moderate-sized streams. Comparative data for stream-flow rates and diets for *gaudichaudii* and *schmidti* are not available.

See *Hylodes* for comparisons with other genera.

Cycloramphus

Considerable morphological variation would be expected between feeding and non-feeding larvae in the same genus. All of the variation seen in *Cycloramphus* can be interpreted easily as a result of feeding structures used in *C. izecksohni* (Figure 50) being reduced or lost in *C. stejnegeri*. For example, *C. izecksohni* has two pustules and two papillae on the tongue (= 4 lingual papillae in Table 1), whereas *C. stejnegeri* has 2 pustules (= 2 lingual papillae in Table 1).

In terms of a progression towards loss of larval structures used in feeding, *stejnegeri* shares with *izecksohni* infralabial papillae of a palp-like nature; reduction of lingual papillae; secretory tissue not organized into conspicuous secretory pits on the free edge of the ventral velum or ridges on the secretory

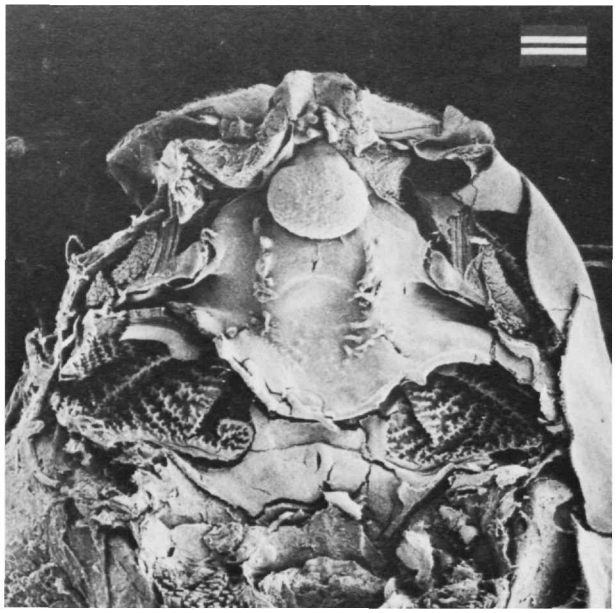


FIGURE 50.—SEM micrograph of floor of oral cavity of *Cycloramphus izecksohni;* scale line = 400 μm.

zone; gill filters reduced; only a single-filter cavity (more extreme in *stejnegeri*).

Additional features that characterize *C. izecksohni* as a representative of feeding *Cycloramphus* larvae are: mouth very narrow anteriorly, wider posteriorly; buccal pockets very large, without prepocket papillae; an elongate U-shaped BFA; an elongate narrow area in front of the nares; obliquely oriented nares.

We previously proposed (Wassersug and Heyer, 1983) that the feeding larvae of *Cycloramphus* and *Thoropa* represented a distinctive, subaerial, larval type. One hypothesized aspect of this larval type that requires correction, based on additional dissections, concerns the glottis of feeding *Cycloramphus* and *Thoropa* larvae, which is almost or fully exposed. Previously, Wassersug (1980) found that the exposed glottal condition correlated well with lung use. The lungs, however, are small in both *C. izecksohni* (about 50% length of buccal floor, not inflated) and *Thoropa petropolitana* (about 25% length of buccal floor, not inflated). The *C. izecksohni* larva also had a low-density field of gill filaments. Thus, these extremely elongated larvae, with a large surface area, are more likely relying on cutaneous rather than pulmonary respiration in the air. As recently noted by Feder and Burggren (1984), cutaneous respiration may be the predominant mode of respiration for anuran larvae under a variety of conditions.

Across our larger sample of leptodactylid tadpoles, the larva of *C. izecksohni* is still most similar to that of *Thoropa;* the resemblances are striking. In addition to differences between these larvae discussed previously (see especially Table 1 in

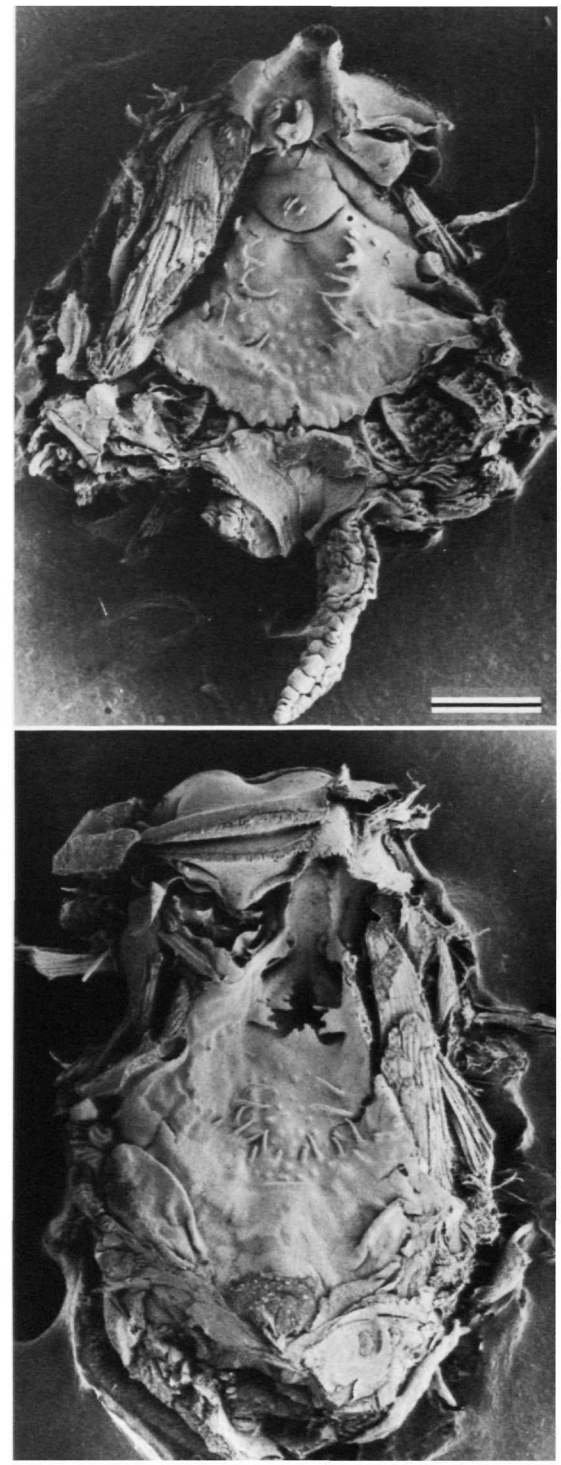


FIGURE 51.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Thoropa miliaris;* scale line = 1 mm.

Wassersug and Heyer, 1983:766), the BFA and BRA papillae are largely restricted to well-defined rows in *C. izecksohni;* in *Thoropa,* there are additional papillae lateral to the BFA and BRA.

Eleutherodactylus

The direct developing embryo of *Eleutherodactylus* essentially lacks all larval features; all that is visible on the buccopharyngeal floor are naked gill bars, a very large tongue anlage, and a large esophageal funnel.

Among direct developers, *Eleutherodactylus* constitutes an extreme for loss of larval features. Only the hylid genera *Cryptobatrachus* and *Hemiphractus,* of the forms studied to date, are similar in having such a loss of larval features.

Eupsophus

A high number of papillae are anterior to the buccal pockets and several large papillae are centrally located in the BFA. A single knob is in the prenarial arena. Other than these few features, the larvae are typical pond tadpoles.

Formas and Pugin (1978) found *E. roseus* larvae under flat stones in a water-filled excavation next to a slow-flowing river.

Hylodes

The buccal papillae are unusually attenuate. There are but two lingual papillae. The branchial baskets are relatively dorsoventrally compressed, particularly medially. There are multiple rows of postnarial papillae. The buccal foor has an unusually high number of papillae laterally in a cluster extending toward the BRA. The lateral-ridge papillae are unusually large.

Among genera examined in this study, *Hylodes* larvae are most similar to *Crossodactylus* and *Megaelosia. Hylodes* and *Megaelosia* can only be differentiated by such details as the number of lingual and postnarial papillae, overall size, and the curvature (i.e., interior bowing) of the buccal floor and roof. Both *Hylodes* and *Megaelosia* can be distinguished from *Crossodactylus* by fewer medial papillae, a papillate edge over the dorsal velum running more horizontally in *Hylodes* and *Megaelosia* (curving backward in *Crossodactylus* (Figure 63*c,d*)), proportionally less of a gap between the dorsal velum halves, and a V-shaped ridge in the prenarial region in *Hylodes* and *Megaelosia* (absent in *Crossodactylus*).

The attenuate nature of the papillae, relative low density for the gill filters, small lungs, and down-turned beak together characterize, morphologically, tadpoles associated with flowing water. *Hylodes* larvae occur in small- to moderate-sized rocky streams with turbulent, swift water.

Hylorina

Large papillae occur in the middle of the BRA. The branchial baskets are unusually large. There are many buccal floor and roof papillae with particularly extensive papillation in the buccal floor area, including up to 15 papillae in the prepocket area and an extensive row of papillae posteromedial to the buccal pockets.

In spite of the above characteristics, the tadpole has the morphology of typical pond tadpoles. Cei (1980:286) reported *Hylorina* to breed in open, flooded grassland ponds. Diaz and Valencia (1985) state that *Hylorina* breeds in temporary pools.

The specimen examined is in poor shape, precluding distinguishing it further from other telmatobiines with large branchial baskets, such as *Atelognathus* and *Eupsophus.*

Lepidobatrachus

An irregular cluster of pustules is in front of the tongue anlage. The buccal floor and roof papillation is extremely reduced, including the absence of a median ridge, lateral-ridge papillae, and postnarial papillae. The ventral velum is medially divided into separate left and right halves. Branchial food traps and gill filters are absent, but there are raker-like projections on the gill bars. The glottis is large and fully exposed.

The reduction of papillation and loss of mucous-entrapment surfaces and gill filters signify that these larvae have an obligate, carnivorous, macrophagous diet. Cei (1968:144) reported on *L. llanensis* larvae with invertebrates in the gut. Rudolpho Ruibal, who provided us with lab-raised specimens, reported (pers. comm.) that cannibalism was common in the laboratory. According to Ruibal, "they will not feed on anything but live food, and it has to be 'big enough' to excite them."

Leptodactylus

Several features unite the species examined. All have well-developed lungs. The infralabial papillae are small and simple (Figure 53*a,b*). The range in number of lingual papillae is unusually large (0–4). BRA, BFA, and lateral-ridge papillae are few and simple. All species examined have large, deep branchial baskets with dense gill filters. The fourth filter plate is more vertical ventrally and more horizontal dorsally than in most other larvae. The glottis is open, nearly or fully exposed, with thin glottal lips (in *pentadactylus* the glottis is smaller and the lips thicker). The prenarial arena is wide, with a transverse ridge that is often indented medially. The internal nares are transversely oriented. One or two postnarial papillae are on each side, only one of which is large and distinct; the large one (except in *knudseni* and *pentadactylus*) tends to be medially directed, sickle-shaped, and usually nearly as large as the lateral-ridge papillae. All have a small median ridge (Figure 61*a,b*).

Several features distinguish the species examined, the most obvious of which is the number of lingual papillae (Figure 53*a,b*). Variation also exists in the amount of papillation of the midportion of the dorsal and ventral vela—*L. chaquensis* and *wagneri* are the most papillate, *knudseni* and *pentadactylus* the

least, and the other species are intermediate. *Leptodactylus knudseni* and *pentadactylus* have more cup-like postnarial papillae than the other species examined (Figure 61*b*). *Leptodactylus wagneri* has less dense gill filters than the others. From overall comparisons, *knudseni* and *pentadactylus* are the most distinctive; *wagneri* is somewhat distinctive, but is quite similar to *chaquensis*. The differences among *L. fuscus, gracilis,* and *mystacinus* are slight—such that they generally fall within the range observed for intraspecific variation.

The internal oral features are consistent with a typical pond-larval diet and morphology. The larvae of *chaquensis, fuscus, gracilis, mystacinus,* and *wagneri* were all collected from temporary or semi-permanent ponds. The larvae of *knudseni* and *pentadactylus* also inhabit temporary ponds, but the larvae of *pentadactylus* (and presumably *knudseni,* based on similar external morphology) are facultative carnivores (Heyer, McDiarmid, and Weigmann, 1975).

Macrogenioglottus

The lateral pair of lingual papillae is larger than the medial pair (Figure 52*c*). There are papillae in the middle of the BFA. There is a lot of sculpturing on the free edge of the ventral velum. The prenarial papilla is very large. The median ridge is large and semicircular.

The morphology is that of a pond larva. The larvae were collected from a temporary oxbow pond 30 × 6 meters and less than a meter deep (Abravaya and Jackson, 1978).

Megaelosia

The region anterior to the tongue is extremely long with the ventral floor bowing downward sharply. The lingual papillae are long (Figure 52*d*). In almost all other features, *Megaelosia* is most similar to *Hylodes* (see above) but differs in having four rather than two lingual papillae. Similarities of these larvae to other genera are discussed with *Hylodes*. *Megaelosia* tadpoles are externally not unusual, except for their size. A vast array of internal oral papillae as seen in *Megaelosia* most often characterizes stream-adapted tadpoles (e.g., Figures 52*d*, 61*c*). Our *M. goeldii* larvae were in fact collected from fast-flowing water in moderately large mountain streams.

Odontophrynus

The infralabial papillae are relatively small. A moderate number of papillae occur within the BFA and prepocket area. The midportion of the ventral velum is transversely oriented and has supernumerary papillae. The branchial baskets are relatively large and deep. The median ridge is triangular-shaped. The lateral-ridge papillae are lobster claw-shaped (Figure 61*d*).

The two species examined differ only in fine details—*O. occidentalis* has a more distinct, transverse ridge in the prenarial arena and has more papillae than *O. americanus*.

Compared to *Leptodactylus*, the lateral-ridge papillae are larger and the postnarial papillae are smaller in *Odontophrynus* (Figure 61*a,b,d*). Otherwise it is difficult to distinguish the larvae of *Odontophrynus* from many other generalized leptodactylid tadpoles, such as *Eupsophus* and *Leptodactylus*.

The larval morphology is that of a pond tadpole. Cei reported that *O. americanus* larvae occur in temporary pools and lagoons (1980:303) and the larvae of *O. occidentalis* occur in natural pools beside streams (1980:308).

Paratelmatobius

The internal oral morphology is very distinctive, including a multipapillate tiara on the tongue (Figure 53*c*), and multitudinous, uniform, BFA and BRA papillae in a very narrow band (Figure 56*b*).

The only other tadpole with the BFA and BRA papillae in such sharply delineated rows and of such uniform size and shape is *Rhinoderma darwinii*. These two genera are, however, distinguished by many other characters, such as: no lingual papillae in *Rhinoderma* in contrast to supernumerary lingual papillae in *Paratelmatobius;* more numerous papillae overall in *Paratelmatobius;* a hidden glottis in *Paratelmatobius* versus an exposed glottis of *Rhinoderma;* and a large prenarial arena and far posterior position of the nares and median ridge in *Paratelmatobius* in contrast to a more typical arrangement of these features in *Rhinoderma*. The differences between these two forms suggest that the similar arrangement of BFA and BRA papillae is due to convergence.

The shallow branchial baskets with two filter cavities and reduced filter mesh further suggest a tadpole that lives in flowing water with a somewhat macrophagous diet. The tadpole was collected from a roadside rivulet (Heyer, 1976).

Physalaemus

The infralabial papillae are relatively small and simple, but touch on the midline. Overall, there is relatively little papillation. The ventral vela have slight marginal papillation. There is little or no imbrication of the third filter plate over the third filter cavity. The roof is distinctive in having postnarial papillae that are larger than the lateral-ridge papillae.

Physalaemus larvae are similar to many other medium- and small-sized leptodactylid pond larvae. *Physalaemus* larvae differ from *Leptodactylus* larvae by the shape of the third filter plate and cavity; from *Odontophrynus* in having fewer buccal floor and roof papillae; from *Alsodes* by the relatively taller, second filter plate and in having fewer papillae in general; from *Batrachyla* by the shape of the median ridge and less papillation on the middle portion of the ventral velum; from *Caudiverbera* by total size, fewer serrations on the margin of the ventral velum, and taller median ridge; and from certain *Pleurodema* by fine details that are less than the differences among species within *Pleurodema* (see below).

The two species of *Physalaemus* examined differ most in

terms of the amount of imbrication of the third filter plate, density of the filter mesh, and exposure and size of the glottis. *Physalaemus pustulosus* has only two filter cavities in each branchial basket. The total gill-filter surface area of *P. petersi* is slightly larger than that of *pustulosus*. Overall, the differences between the two species are slight, but the two differ as much from each other as either does from *Pleurodema brachyops, bufonina,* or *borellii*.

In overall morphology, the larvae look like generalized pond types with the notable exception of the lack of imbrication of the third filter plate over the third filter cavity. Their large lungs suggest a strong dependence on aerial respiration. Larvae of both species came from temporary ponds or swamps and the larvae of *P. pustulosus* are often found in temporary pools of extremely small size, such as puddles formed from cattle hoof prints.

Pleurodema

The species examined fall into three fundamental groups that are not easily united by obvious features. Each of these groups is discussed separately.

Pleurodema borellii—brachyops—bufonina

There are two pairs of small, non-abutting, infralabial papillae (Figure 54). There are four lingual papillae. The general buccal floor and roof papillation is of medium to low density (Figure 56*c*). The ventral velum has a gently curved semicircular edge with asymmetrical papillation medially. There are two filter cavities per side in dorsal view (Figure 56*c*). The prenarial arena has a horizontal ridge or row of pustulations. The internal nares are relatively transverse. The postnarial arena is large and open with one obvious pair of larger papillae. The lateral-ridge papillae are small and not too complex. The pressure cushions are large and globose.

Overall these larvae are morphologically more similar to *Alsodes, Batrachyla,* and *Physalaemus* than to the other two groups of *Pleurodema*.

With the exception of having but two filter cavities per side, the larval structures are those found in typical pond tadpoles. All three species are found in temporary ponds, but the eggs of *bufonina* are laid in strings, while those of *borellii* and *brachyops* are placed in a foam nest (Cei, 1980; Duellman and Veloso, 1977).

Pleurodema cinerea

There are two lingual papillae. There is a moderately large number of buccal floor papillae arranged in a posteriorly directed "V" (Figure 56*d*). The nares are obliquely oriented. The median ridge is small. The lateral-ridge papillae are very large with finger-like processes.

None of the characters in the above suite is particularly diagnostic. In terms of overall branchial basket structure, *P. cinerea* is most similar to *Atelognathus, Eupsophus, Hylodes, Hylorina, Leptodactylus,* and *Odontophrynus*. *Leptodactylus* larvae have less buccal papillation than *P. cinerea*. *Hylodes* has more extensive papillation on the buccal roof and dorsal and ventral vela, and has a more flattened branchial basket. The lateral-ridge papillae of *cinerea* are simpler than in the other genera with similar branchial-basket structure.

The larval features are those found in other typical pond larvae. The larvae occur in temporary rain pools; the eggs are laid in a foam nest (Cei, 1980:362).

Pleurodema nebulosa

The BFA and BRA papillae are organized in a central patch rather than bounding defined arenas and the BFA and BRA papillae are recurved with thick bases and caudally directed apices. The free edges of the ventral velum are recurved and lack papillae; however, the central portion forms an unusual apron overhanging the glottis. Secretory pits or ridges are absent.

The inner oral morphology of *P. nebulosa* is very distinctive among leptodactylids and is as different from the other *Pleurodema* examined as from all other genera studied. There are no external clues to the bizarre, internal, oral morphology of *P. nebulosa*.

The lack of organized secretory pits and ridges, together with but two filter cavities and the unusual buccal papillation and ventral velum, suggests something other than a normal pond tadpole. Among pond larvae only discoglossids and pelobatids have similar branchial food trap morphology. Larvae of the Asian pelobatid genus *Megophrys* have a somewhat similar recurved ventral velar margin (Wassersug, 1980). *P. nebulosa*'s branchial baskets are also somewhat similar to those of pelobatids which have a single-filter cavity (= a bowl-like design). We are unable to predict the habitat or feeding type, as we have not encountered this kind of larval morphology previously. Mares et al. (1977) reported that the desert-dwelling species has a very brief larval life (about 10 days) and that the larvae are carnivorous and cannibalistic under stress. In retrospect, such features as the posteriorly directed BFA and BRA papillae may be interpreted as functioning to direct large or active prey into the esophagus. *P. nebulosa* appears convergent with pelobatids that breed in seasonally arid environments.

Proceratophrys

The infralabial and lingual papillae are branched (this latter condition is unique among the larvae we have examined (Figure 53*d*)). There are many tall, attenuate papillae on the buccal floor and roof; the largest papillae arise from a ridge-like base. The nares are predominantly transversely oriented. The postnarial papillae are large and numerous. The lateral-ridge papillae are huge hand-like structures with many elongate fingers. The dorsal velum is strongly fringed medially.

These larvae are similar only to *Crossodactylus* and *Hylodes* of the South American leptodactylid tadpoles examined. *Proceratophrys* larvae are easily distinguished from *Crossodactylus* and *Hylodes* by the branching lingual papillae, absence of an elongate ridge in the prenarial arena, and transverse orientation of the nares.

The two species examined show interesting differences. In *P. boiei,* the lungs are twice as large, the branchial baskets deeper, and papillae are consistently fewer in number than in *P. appendiculata.*

The elongation and proliferation of buccal papillae in both species suggest a stream association. *Proceratophrys appendiculata* appears to be specialized for living in faster-flowing water than *boiei* and appears to be less specialized for microphagous suspension feeding. Izecksohn et al. (1979) reported *P. boiei* from ponds; Peixoto and Cruz (1980) reported *P. appendiculata* from streams. The diets are unreported.

Pseudopaludicola

There are three lingual papillae with the two lateral papillae larger than the medial one (Figure 54). The buccal floor and roof papillae are very tall, although not numerous, and they lack much terminal elaboration. There is but a single-filter cavity and the branchial baskets are flattened, especially medially. The lung buds are small.

The larva of *Crossodactylus,* the only genus examined with similar features, has one more lingual papilla and one more filter cavity per side than does *Pseudopaludicola.*

The dorsoventral flattening of the branchial baskets and elongate buccal papillation suggests that the larvae live in flowing water. Our tadpole sample was collected from shallow, slowly running water in a boggy area. Cei (1980:412) indicated that Argentinian populations of *P. falcipes* are pond dwellers, however.

Rhinoderma

The tongue anlage is well developed (earlier than in most other tadpoles) and the larval lingual papillae are reduced. The BFA and BRA papillae are organized into a precise, U-shaped, papillate band. The gill filters are very reduced. The branchial baskets are very shallow. The glottis is fully exposed. The esophageal funnel is very broad. The nares are far lateral. The median ridge is relatively large, and postnarial papillae and lateral-ridge papillae are absent.

The only other leptodactyloid genus that even remotely resembles *Rhinoderma* is *Paratelmatobius,* (see above).

Rhinoderma darwinii, the only species examined in the genus, has a tadpole that does not feed on particulate matter, although it may ingest some mucus from the mouth of the brooding adult. Many larval features are maintained, although reduction is evident in the filter-feeding apparatus.

Telmatobius

There are two or three lingual papillae. There is a great number of buccal floor papillae laterally, particularly anterior and posterior to the buccal pockets. The branchial baskets are large with dense gill filters. The third filter cavity is capped by the third filter plate. The secretory ridges of the branchial food traps are not smooth and continuous. The glottis is small, but lung buds are large. The prenarial arena is relatively smooth. The nares are obliquely oriented. There is a high number of papillae in the postnarial arena. The lateral-ridge papillae are relatively small flaps. The median ridge is small. The BRA is oval and well defined.

None of the above features distinguish larvae of *Telmatobius,* although it is unusual for a tadpole to have this amount of papillation without a few of the papillae being either large or elaborate.

Telmatobius larvae are most similar to larvae of *Atelognathus, Eupsophus, Hylorina, Macrogenioglottus, Odontophrynus,* and *Pleurodema cinerea* in that they all have branchial baskets with much imbrication of the third filter plate over the third filter cavity and have many buccal papillae. *Telmatobius* represents an extreme for these characters in this grouping, however. *Atelognathus* has fewer papillae on the roof and a very tall median ridge. *Eupsophus* has one more lingual papilla than *Telmatobius* and the filter baskets are flatter in *Telmatobius* than in either *Eupsophus* or *Hylorina. Macrogenioglottus* has a fringe on the dorsal velum and has prenarial papillae. *Odontophrynus* has one more lingual papilla than *Telmatobius;* the branchial baskets are larger and deeper in *Odontophrynus;* the median ridge is larger and the margin of the ventral velum is more papillate in *Odontophrynus;* the glottis is smaller and more hidden in *Telmatobius.* The larva we have examined that is most similar to *Telmatobius* is that of *Pleurodema cinerea,* but *Telmatobius* differs in having fewer papillae on the dorsal roof and more obliquely oriented nares.

Larvae of the two species of *Telmatobius* are more similar to each other than to any other larvae we examined, particularly with regard to tongue anlage, general shape of the papillary fields, and overlapping of the third filter plate. Some differences between the two species include more papillation on the ventral velum; more branched infralabial papillae; and larger median ridge in *marmoratus.* These kinds of differences are representative of species (not species group) differences based on our experience with other genera.

The larvae of *Telmatobius* morphologically are typical of pond tadpoles. The larvae of *T. marmoratus* occur in high montane streams and lagoons (Cei, 1980:263).

Thoropa

Another specimen of *T. petropolitana* was dissected to examine variation in certain features noted previously (Wassersug and Heyer, 1983). This specimen had cb 1 with 5 filter

rows, cb 2 with 6, cb 3 with 7, cb 4 with 5. The lung buds were very small, about 25% the length of the buccal floor and uninflated. The postnarial ridge had two papillae with terminal bifurcations, but the entire structure was more of a single ridge than a row of papillae. We counted 8 or 9 BRA papillae on each side. The glandular zone was distinct with a length of about 1/6 the length of the buccal floor and it had a distinct, wavy, anterior margin. The dorsal velum was interrupted on the midline and the posterior margin of the dorsal velum is more papillate than crenulate.

The two species of *Thoropa* examined share the following features (compare Figure 51 of *T. miliaris* with fig. 1 in Wassersug and Heyer, 1983, of *T. petropolitana*). The prelingual area is narrow and long. The infralabial papillae are palp-like (Figure 53*e*). There is only a moderate number of BFA and BRA papillae, but they are exceptionally long and attenuate. The ventral velum margin is irregularly sculptured. The branchial baskets are extensively compressed dorsoventrally and they have a reduced number of filter rows and a highly porous filter mesh. The branchial food traps lack secretory ridges. The prenarial arena is elongate with an elongate arch-like structure. The nares are obliquely oriented. The postnarial papillae are small, simple, and organized on a single ridge parallel to the nares. The lateral-ridge papillae are relatively small and simple (Figure 62). There is a large median gap between the left and right portions of the dorsal velum.

Thoropa shares with *Crossodactylodes, Cycloramphus, Pseudopaludicola,* and *Rhinoderma* depression of the branchial baskets and virtual loss of the filter cavity between the third and fourth filter plates. The pattern of papillation on the tongue, buccal floor, and area lateral to the median ridge (and including the shape of the median ridge) readily distinguish *Thoropa* from *Crossodactylodes, Pseudopaludicola,* and *Rhinoderma. Thoropa* larvae are most similar to the feeding larvae of *Cycloramphus* (see above under *Cycloramphus*).

The differences observed between the two species of *Thoropa* are minor and about the same as those observed between either and *Cycloramphus izecksohni* (Figure 50).

We (Wassersug and Heyer, 1983) previously proposed that the unique set of features observed in *Thoropa* defined a subaerial, larval, adaptive pattern.

Australian Leptodactyloids

Crinia

There are two small pairs of infralabial papillae. The free edge of the dorsal velum lacks distinct peaks over the filter cavities. The fourth filter plate is oriented horizontally and is much larger than the third filter plate, resulting in two, rather than three, filter cavities. The fourth filter plates from each side almost touch on the midline and, along with the ventral velum, completely obscure the glottis from dorsal view (Figure 55). The filter-mesh density is low. The lung buds are extremely small. There is little in the way of papillae/pustulations in the postnarial arena. The dorsal velum is continuous across the midline.

The only similar Australian form is *Pseudophryne bibronii;* both have the same distinct morphology of the branchial baskets, glottis, and general shape of the dorsal and ventral vela. *Pseudophryne* has more papillation along the midportion of the vela, and larger infralabial and prenarial papillae; it lacks lingual papillae and has fewer BFA and BRA papillae than *Crinia.*

The presence of two rather than three filter cavities per side, together with the low filter-mesh density, suggests that *C. tasmaniensis* is not a typical pond larva; its other features are those found in typical pond larvae, however. Martin (1967:108) reported embryos collected from "the bottom of a shallow pool (2–8 cm deep) fed by a small rivulet."

Heleioporus

There are two lingual papillae. There are many BFA papillae but no BRA papillae. The ventral velum has crenulations but lacks distinct papillae, particularly medially. The filter-mesh density is low. The edges of the second and third filter cavities are straight such that the three filter cavities are of approximately subequal size (Figure 56*e*). There is a single pair of large postnarial papillae. The median ridge is tall and narrow. The dorsal velum is broadly divided on the midline (Figure 63*b*).

Heleioporus can be distinguished from other Australian forms examined by the presence of BFA but absence of BRA papillae, together with low-density filter mesh and almost subequal-sized filter cavities. *Heleioporus* is more similar in the narial region to *Limnodynastes, Megistolotis, Mixophyes, Platyplectron,* and *Taudactylus* than to *Crinia* and *Pseudophryne.*

The filter mesh is of too low a density for a normal, microphagous, pond tadpole. Lee (1967) reported that western Australian *Heleioporus* lay their eggs in a foam mass in dry burrows that later flood. The larval diet is unreported. While the habitat for the *Heleioporus* larvae described herein is unknown, adults of this genus breed in banks along both standing and flowing waters (Lee, 1967; Martin, 1967; Littlejohn and Martin, 1967). The slight reduction in oral surface features seen in *Heleioporus* compared to other Australian tadpoles may reflect a trend away from aquatic larval development as suggested by Martin (1970). Certain egg-brooding hylids of the genus *Gastrotheca* (i.e., *G. gracilis* and *G. orophylax*) have larvae and embryos that develop from similarly sized eggs and closely resemble the *Heleioporus* larva internally (see figs. 10, 14 in Wassersug and Duellman, 1984).

Limnodynastes

The second pair of infralabial papillae are more posterior than in other tadpoles. There are two lingual papillae. The

postnarial papillae are very large and sickle-shaped. The lateral-ridge papillae are identical in shape to, but smaller than, the postnarial papillae. The median ridge is semicircular. Small papillae lie posterior to the dorsal velum.

None of these features is particularly noteworthy; all are within the realm of intrageneric variation rather than at the level desirable to distinguish between genera. *Limnodynastes* is most similar to *Megistolotis, Platyplectron,* and *Taudactylus.* The combination of relative size and shape of the postnarial and lateral-ridge papillae, together with the crescentic shape of the median ridge distinguishes *Limnodynastes* larvae from these others.

The morphological features are those found in typical pond tadpoles. Martin (1965:149) reported *L. tasmaniensis* "in deep water in permanent ponds and swamps."

Megistolotis

Several features cannot be determined in detail due to the poor condition of the specimen. The overall determinable morphology is very similar to that found in *Limnodynastes, Platyplectron,* and *Taudactylus. Megistolotis* is the only member of this group to have claw-shaped, lateral-ridge papillae.

The morphological features are those found in typical pond tadpoles. Tyler et al. (1979) reported that the species breeds in rock pools in an escarpment where, during the frequent rains, the pools fill and overflow. These authors stated that two conditions must be met for larvae to survive in this habitat: first, they must be able to endure conditions temporarily resembling mountain torrents and, second, survive in ponds with a serious deficiency of suitable nutrient material. The authors stated that *Megistolotis* has highly efficient suctorial mouthparts to deal with torrential flow and that the larvae are cannibalistic in the laboratory and presumably in nature when food is limited. We find no particular specializations for this way of life in the internal oral anatomy.

Mixophyes

There are no lingual papillae. There is a high number of buccal floor papillae. The filter plates are large, with the third filter plate obscuring the third filter cavity from dorsal view. The prenarial arena is large with a predominant, longitudinal, median ridge. The lateral-ridge papillae are as large or larger than the median ridge and have finger-like processes. The dorsal velum has a papillate margin but is broadly interrupted on the midline.

The lack of lingual papillae, two filter cavities per side in dorsal view, and long prenarial area distinguish *Mixophyes* from all other Australian tadpoles examined.

Most features are those seen in other typical pond tadpoles, except for the high number of buccal floor papillae, the obscuring of the third filter cavities, and the uninflated lungs, which fit a stream association. Watson and Martin (1973) indicate that *Mixophyes* has stream tadpoles and the larval external morphology is very typical of other stream-adapted tadpoles.

Platyplectron

There are two lingual papillae (Figure 53*f*). For an animal of this size (~12 mm), it has a large number of buccal floor papillae. The branchial baskets are large and have tall filter plates (Figure 56*f*). There are three postnarial papillae (Figure 62). The median ridge is tall. There are many BRA papillae.

Platyplectron is similar to *Limnodynastes, Megistolotis,* and *Taudactylus* in buccal and pharyngeal anatomy to the point of having the same crescentic pustulate arch in the prenarial arena. The only feature that differentiates *Platyplectron* from the others is the inflated lung condition.

The morphology is that found in typical pond tadpoles. Barker and Grigg (1977) indicated that eggs are laid in foam nests in rain pools in desert habitats.

Pseudophryne

There is one large pair of infralabial papillae. Lingual papillae are absent. There are relatively few, tall, BFA and BRA papillae. The velar margins are smooth laterally but distinctly papillate medially. The fourth filter plate is oriented horizontally and is much larger than the third, resulting in two distinct filter cavities per side. The fourth filter plates from each side almost touch on the midline and, along with the ventral velum, completely obscure the glottis from dorsal view. The filter-mesh density is low. The lung buds are extremely small. There is little in the way of papillae/pustulations in the postnarial arena. The dorsal velum is continuous across the midline with long finger-like papillae on the margin.

See *Crinia* (p. 74) for comments.

As with *Crinia,* most of the features of *Pseudophryne* are characteristic of pond larvae, while a few features, such as small lung buds, clearly are not. *Pseudophryne* eggs are laid on land with intracapsular embryonic development, followed by a pond larval stage (Watson and Martin, 1973).

Taudactylus

There are two lingual papillae. There are few BRA papillae and no prepocket papillae. A large vomeronasal pit occurs at the median edge of the internal nares. The narial-valve projection is very large. Postnarial papillae are absent. The dorsal velum is continuous across the midline.

Taudactylus is most similar to *Limnodynastes, Megistolotis,* and *Platyplectron,* but differs by the large size of its narial-valve projection together with the absence of postnarial papillae.

The internal oral morphology is most similar to that seen in typical pond tadpoles. The only other group that we know with a vomeronasal pit and very narrow secretory ridges in the

branchial food traps is the Microhylidae. This suggests that *Taudactylus* may be specialized for microphagy, which is also corroborated by the low number of buccal papillae. The tadpoles are found in forest creeks (Liem and Hosmer, 1973). Liem (pers. comm.) commented that these tadpoles are found in clear side pools rather than in the main current, and that they do not have particularly specialized suctorial oral discs. Internally and externally these tadpoles resemble stream-associated tadpoles, such as those of *Colostethus nubicola*, which have an oral disc slightly expanded into a funnel.

Ontogenetic Variation

Viertel (1982) and Wassersug (1976b) have shown that within species, the number and complexity of papillae increase noticeably from hatching to about Gosner stage 26 and then remain relatively stable through stage 39–40. Although not always possible, we made every attempt to examine specimens in the mid-30 stage of development to minimize the effects of ontogenetic variation. We attempt throughout the rest of this paper to discuss and compare those features that we believe are not attributable to ontogenetic variation.

Although we have not examined large developmental series specifically to evaluate ontogenetic variation in each leptodactyloid genus, one example dramatically indicates that the larval morphology is stable as demonstrated in other studies (Wassersug, 1976b). Of the two specimens of *Megaelosia goeldii* that we examined, one was stage 25, 21.8 mm SVL, the other stage 37 and 54.7 mm SVL; this represents more than a 15-fold increase in mass, yet the oral morphologies, including the number and complexity of papillae in these two specimens, was to our eyes almost identical. The differences were equal to or less than those between any two tadpoles from closely related species.

Individual Variation

The amount of individual variation encountered has been very slight. The degree of variation observed between individuals within species has been of the same magnitude as the right versus left side variation within a single specimen.

There are two sources for incorrectly interpreted variation: (1) distortion of shape due to preservation, dissection, and microscopic preparation; (2) actual errors in counting and measuring. Concerning the latter, counting the number of filter rows in a dissection is difficult to do on a wet specimen in a consistent fashion. Since the branchial baskets are complex and typically deep structures, the specimen must be manipulated constantly to keep the area in focus, and filter rows below the ventral velum exposed. An effort was made to count only rows that were complete—i.e., that continued ventrally to the bottom of a filter plate surrounding a gill slit—but there is an element of subjectivity concerning what is a complete filter row. Repetitive counts on a freshly dissected specimen vary within 1 or 2 rows. Similarly, a gradation exists in size of common buccal surface projections, ranging from pustules to papillae in any area. Papillae counts on wet specimens may be influenced by the degree of staining and whether intermediate-sized structures are counted as pustulations or papillae. Thus, BFA papillae may differ by one or two counts if done on different days in those specimens with many papillae, of which several are intermediate in size. SEM preparations allow much greater precision in such counts; but not all specimens can be prepared for SEM examination, nor have all specimens so prepared survived intact. SEM specimens are fragile and subsequent dissections are highly destructive.

We recognize that we may be underestimating the degree of intraspecific variation, as nearly all of the individuals of the same species came from a single sample and thus could be siblings. This may account for some of the striking similarities observed, where even oral asymmetries have been identical among specimens examined. Nevertheless, the fact remains that in the cases where more than one individual of a species has been examined, variation has been minimal (Table 1).

Character Variation

In the course of our work, we found certain features, described by us and previous workers, to be either so vague as to be meaningless, or to not show any meaningful patterns of variation. We propose that future work not include study of the following characters.

The general internal shape of the floor and roof of the mouth of tadpoles is easily affected by the plane of dissection and manipulation of wet specimens for pinning under a light microscope. Similarly, slight shrinkage of a specimen during drying for SEM preparation affects most severely the largest dimensions of a specimen.

The actual number of prepocket papillae is difficult to assess in most tadpoles because of the continuation of the prepocket papillary field with the BFA. A case could be made for no longer treating surface features in the prepocket and more medial regions of the buccal floor as independent. In all tadpoles that have BFA papillae, the largest ones are, invariably, immediately medial to the edge of the buccal pockets, thus little is gained by reporting this topographic fact in each description.

The dimensions of the buccal pockets are greatly altered by the plane of dissection and the standard pinning of a specimen for light microscope examination. It is very difficult to examine the floor of the buccal pockets in small larvae to decide whether the pockets are naturally perforated without producing artificial perforations in the regions. Gradwell (1972a,b) discussed the functional implications of a shunt or pharyngeal bypass through naturally patent buccal pockets. In neither the present study nor earlier studies have we been able to find any systematic patterns between the ecology or phylogeny of tadpoles and the character state of the buccal pockets, even

though we suspect that such patterns exist given the profound implication to respiration and feeding of patent buccal pockets (i.e., a bypass for water around, rather than through the branchial baskets). The problem here may lie in errors in assessing the state of this character.

Except where the ventral velum has an exceptionally odd shape, the spicular support of the velum is difficult to determine objectively on surface examination, since it is an underlying skeletal feature rather than a surface characteristic. We have found little variation that does not simply reflect the size of the velum in the tadpoles that we examined.

The distinctiveness of the laryngeal disc is another feature that depends on the underlying skeleton rather than surface anatomy. As with the spicules of the ventral velum, we have found it difficult to describe variation in this region in a consistent fashion; what intrafamilial variation we have found seems to be slight. The region around the glottis is greatly affected by the developmental stage and changes greatly near metamorphosis.

The amount that the glottis is covered by the ventral velum, as seen in dorsal view, appears greatly altered by slight changes in the pitch of a mounted specimen and by shrinkage of the velum. This character has clear implications for distinguishing higher taxa of anurans (Wassersug, 1984) but we no longer consider the slight variation seen between species in the same genus of great significance. On the other hand, the size of the glottis and particularly whether or not it is patent continues to be strongly related to the pulmonary anatomy of tadpoles. Invariably, a large open glottis correlates with large inflated lungs and pulmonary ventilation in a tadpole.

The profile of the esophageal funnel of tadpoles depends solely on the size and shape of the branchial baskets; as such it is not an independent character and its appearance is altered by minor shifts in the plane of dissection.

Much of the variation in the prenarial arena of tadpoles is consistent among and within genera in ways that make it useful for diagnosing species. However, clearly the morphological complexity in this region relates to the development of the adult vomerine skeletal region, rather than the ecology of the larvae; at least, we have been unable to relate the observed variation in leptodactyloid larvae to their ecology.

The surface morphology of the narial region and the postnarial arena, in general, is extremely complex in most free-living larvae. This region is both difficult to expose in a tadpole without some damage to surface structures and difficult to describe comparatively. We have avoided basing species and generic diagnoses on these features.

Lateral-roof papillae are very variable; these structures appear to be the dorsal equivalent of the prepocket papillae on the buccal floor. As with the floor, it was difficult to distinguish the lateral-roof papillae from the more medial and more extensive BRA field. If the plane of section is high, lateral-roof papillae are easily destroyed.

The distinctiveness of the glandular zone in tadpoles seems to be consistent within species and highly variable among species. The appearance of this character is easily affected by the quality of the staining in wet specimens and that, in turn, by the quality of the preservation of the specimens. Because many museum specimens stain in an uneven and unpredictable fashion, we do not consider the glandular zone a useful feature for specific or generic diagnoses. The state of the glandular zone does, however, consistently reflect extremes in feeding ecology. Tadpoles, which have abandoned microphagous suspension feeding, not surprisingly, have reduced the secretory tissue field of both the branchial food traps and the buccal roof.

The dorsal pressure cushions and the ciliary groove are the structures that define the roof and lateral margins respectively, of the branchial baskets. As such these structures are most likely to be damaged in any dissection designed to expose the branchial baskets. For that reason alone they are not a reliable source of characters for generic and specific taxonomic diagnoses. Furthermore, the size and shape of pressure cushions merely and invariably reflect the size and shape of the filter cavities into which they descend. Variation in the ciliary groove is associated with the distinction between microphagous and macrophagous larvae (present in the former and absent in the latter). Not surprisingly, the ciliary groove is also shallow or lost in non-feeding larvae. However, beyond that we have been unable to discern any variation in this structure that helps to either distinguish between tadpoles or to understand their ecology.

The following are characters and character fields for which we find variation to be important in delimiting taxa and/or understanding ecologies of leptodactyloid tadpoles.

The number of infralabial papillae varies within a rather narrow range, the total number between 0 and 12 (Figures 52–54; Table 1). The most common number encountered in larvae of other families is 2 (Viertel, 1982; Wassersug, 1980). Within the leptodactyloids, the most common number is 4. Because of the relatively low variability observed, the variation that is observed is considered significant.

The number of lingual papillae (Figures 52–54) is easy to determine in tadpoles by simply inserting scissors into the right and left corners of the mouth and cutting back. The roof need not be completely separated from the floor to expose the tongue anlage. With a single exception (*Paratelmatobius* with 11), the number of lingual papillae ranges from 0 to 4 (Table 1). Most other tadpoles have a range of lingual papillae from 0 to 4 (Inger, 1985; Wassersug, 1980). The variation in this character is considered to be significant, due to the low overall variability observed in tadpoles in general. Unexpected and uncommon, odd numbered patterns (i.e., 1 and 3) were found to be consistent within species.

The numbers of infralabial and lingual papillae appear to be independent from each other and from the numbers of other buccal papillae (Figures 52–54). Otherwise, overall correlation of the general buccal papillae (i.e., the BFA, prepocket, BRA,

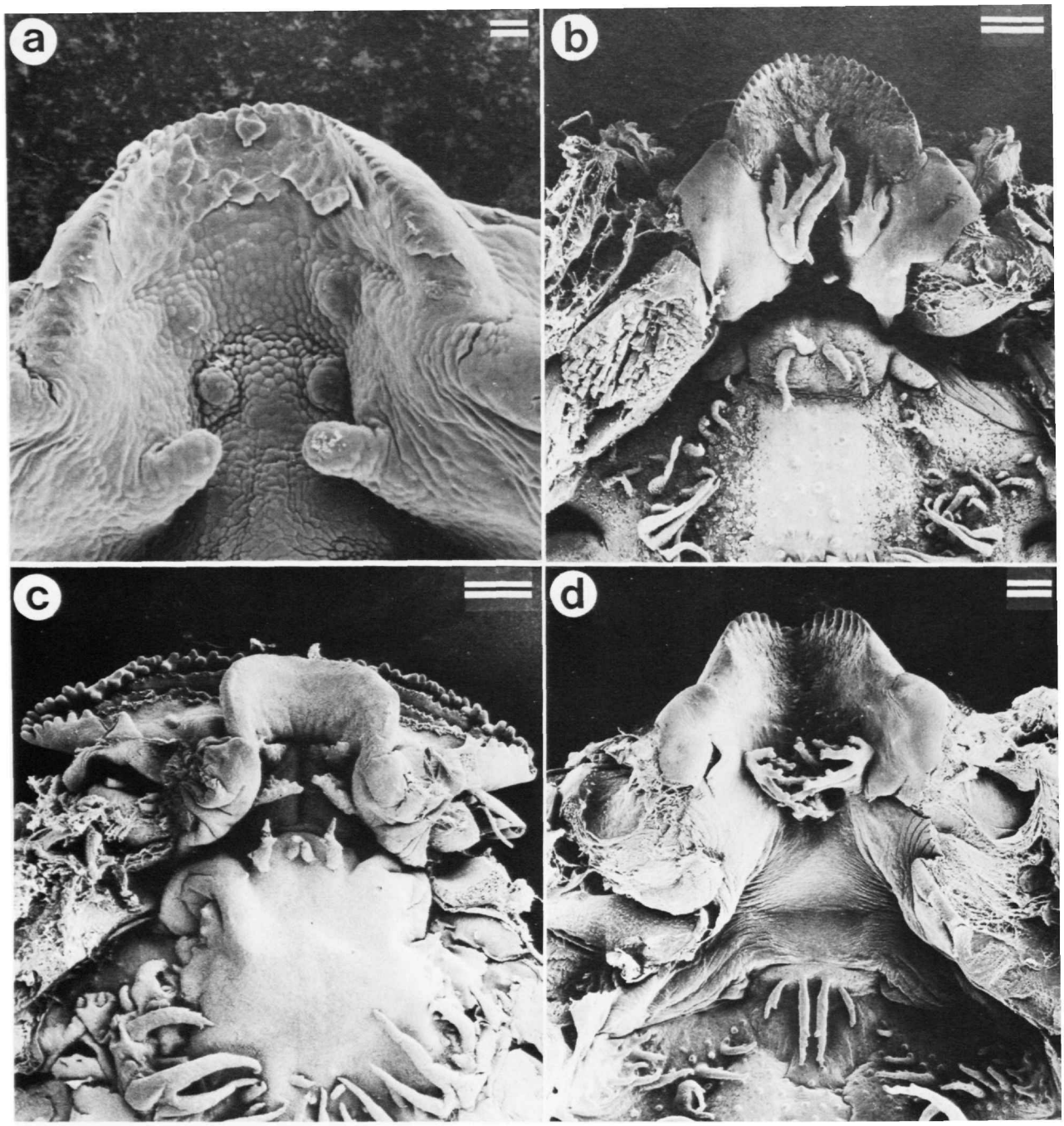


FIGURE 52.—SEM micrographs of front of floor of mouth in dorsal view for selected leptodactylid larvae: (*a*) *Adenomera marmorata* (scale line = 40 μm); (*b*) *Crossodactylus gaudichaudii;* (*c*) *Macrogenioglottus alipioi;* (*d*) *Megaelosia goeldii.* Scale lines for *b–d* = 400 μm. Compare with Figures 53 and 54. Note the variation in infralabial and lingual papillae from the reduction in non-feeding *Adenomera* larva to proliferation and elongation of papillae in stream-adapted *Crossodactylus* and *Megaelosia.*

postnarial, and lateral-ridge papillae) exists: an elaboration in number or complexity of any one field generally signals an overall elaboration of buccal papillation in the other fields. The precise number of these papillae may not be taxonomically useful, but contrasts between ranges of numbers are. Most of the larvae examined have a field of 10–30 BFA papillae per side arranged in a U-shaped pattern (e.g., Figures 55, 56). This is matched above by about 5–15 BRA papillae, arranged in the same configuration as the BFA papillae. On average across species, BRA papillae number 54% of the BFA papillae. Either higher or lower numbers of BFA and BRA papillae are unusual; as is radical difference in the arrangements of BFA and BRA papillae from floor to roof. An example of the general type of correlation seen in papillae number is that, without exception, species with high numbers of prepocket papillae have moderate to high numbers of BFA papillae. The correlations seen in these characters may reflect a common, underlying factor regulating development.

Most of the species have well-developed papillae on the edge of the ventral velum that are oriented directly over the dorsal edges of the underlying filter plates (Figures 55, 56). Presumably, this arrangement functions somehow in the normal filter-feeding process, perhaps to help direct water into the individual filter cavities. Most tadpoles that lack marginal velar papillae are carnivorous or non-feeding. On the basis of this character, we would predict that tadpoles, such as *Proceratophrys appendiculata* and *Crinia tasmaniensis*, are not predominantly microphagous suspension feeders.

Usually, medial papillae on the ventral velum lie over the glottis and act to deflect currents away from the glottis (e.g., Figures 55, 56). Because the absence of these papillae is rare, that condition is considered significant. Such absences are often associated with an enlarged, open glottis and suggest an early commitment to pulmonary respiration.

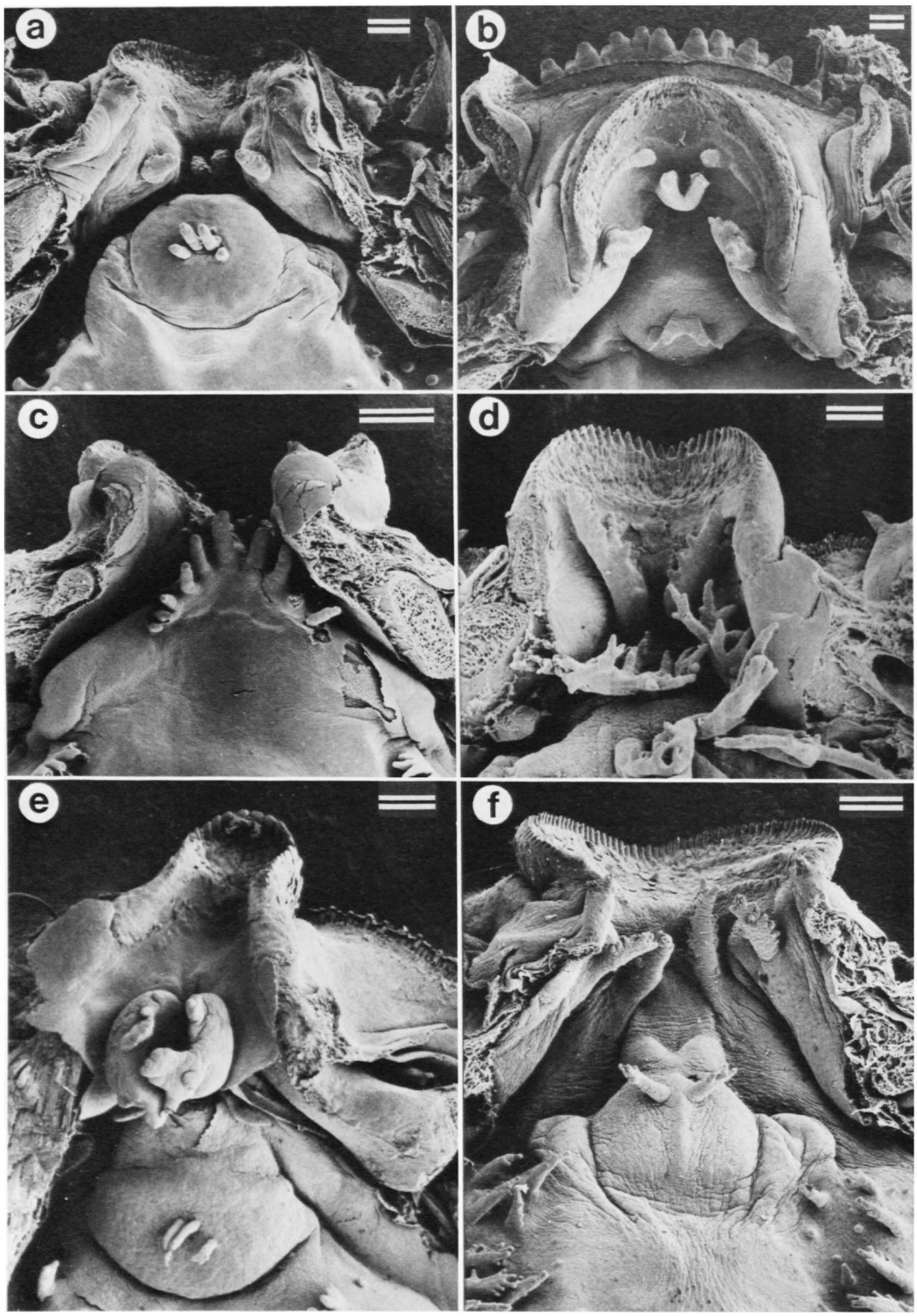
All tadpoles that are capable of suspension feeding have secretory tissue on the margins and under surfaces of the ventral velum (Figures 57–60). In most tadpoles, this tissue is organized such that secretory pits are on the free edge of the velum and secretory ridges are on the underside of the ventral velum (the branchial food traps). The presence of secretory tissue in the branchial food traps that specifically lacks the ridge pattern has been postulated to be the generalized situation in tadpoles because it characterizes all free-living archaeobatrachian tadpoles (including pelobatids), except pipids (Wassersug and Rosenberg, 1979). The absence of the secretory ridges, or of the entire branchial food traps, in the non-feeding tadpoles of *Adenomera*, *Cycloramphus*, *Eleutherodactylus*, and *Rhinoderma*, the carnivorous tadpoles of *Ceratophrys*, *Lepidobatrachus*, and *Pleurodema nebulosa* (Figure 60*a*,*b*), and the subaerial tadpoles of *Cycloramphus* and *Thoropa* is likely due to secondary loss of these structures, rather than retention of a primitive pattern. Similarly, the condition in the bromeliad-dwelling *Crossodactylodes* is likely due to dietary specialization and represents a secondarily derived condition. Sokol (1981) claimed that secretory ridges are absent in the larvae of *Telmatobius culeus* but we have found weak ridging in *Telmatobius jelskii*, *T. marmoratus*, and all other telmatobines (e.g., see Figures 57*c*, 59). We know of no reports on the diet or feeding habits of *T. culeus;* thus we cannot say whether the absence of ridging in *Heleophryne* and possibly some *Telmatobius* is the expression of a primitive tadpole pattern or secondary loss due to dietary specialization.

In typical tadpoles the branchial baskets are moderately deep, with the third filter plate tipped at about a 45° angle and slightly overlapping the fourth filter plate such that three filter cavities are clearly visible in dorsal view on each side (Figure 56). The most consistent trend in leptodactyloid larvae is for consolidation or reduction of the filter cavities. The loss of a filter cavity in dorsal view always involves the second and third cavities and is structurally derived in three distinct fashions: (1) the third filter plate is exceptionally large and tall, and overlies the fourth filter plate, completely obscuring the third filter cavity from dorsal view (e.g., *Pleurodema cinerea*, Figure 56*d*); (2) the third filter plate is large but has little vertical height and is instead horizontally oriented. Here the third filter plate abuts with the base of the fourth filter plate so that the second and third filter cavities represent a single functional cavity (e.g., *Paratelmatobius lutzii*, Figure 56*b*); (3) the fourth filter plate is normally oriented, the branchial baskets are relatively deep, but the third filter plate is small and has a very low vertical profile. The result again is that the second and third filter cavities form a single functional unit (e.g., *Pleurodema brachyops*, Figure 56*c*). In the latter two arrangements loss of a filter cavity in dorsal view is usually, but not always (e.g., *Crossodactylus*), accompanied by the branchial baskets being shallow. This flattening of the branchial baskets with reduction of filter cavities is typical of sub-aerial (Wassersug and Heyer, 1983) and stream-associated leptodactyloid larvae.

The number of filter rows per ceratobranchial does not show discrete variation. Most tadpoles examined have about the same number of filter rows, especially when individual variation is taken into account. No larvae examined in this study had particularly high counts compared to those in obligate, midwater, suspension-feeding tadpoles, such as *Xenopus* and most *Microhyla* (Wassersug, 1980).

Two trends appear in tadpoles with a reduced number of filter rows. In most, the lower number of rows correlates with a low-density of the filter mesh; that is, there is a trend away from suspension feeding and toward either not feeding, or feeding selectively on large, individual food particles. Only two larvae with low numbers of filter rows have an average density for the gill-filter mesh: *Pseudopaludicola* species and *Thoropa petropolitana*.

An expected positive correlation is observed between the density of filter mesh and the increased complexity of the folding pattern of the filter rows. The exceptions, all of which have relatively low-density filter mesh and tertiary or quaternary folding patterns, are *Heleophryne*, *Alsodes*, and


a
b
c
d
e
f

Pseudophryne.

The size, shape, and complexity of the median ridge is quite variable (Figures 61, 62). Morphological variation in this conspicuous anatomical feature is not easy to interpret in either a phylogenetic or functional sense. Median ridge morphology is useful in making comparisons among genera, as fine details of the ridge are often strikingly similar among species within a genus.

The dorsal velum is discontinuous across the midline in the leptodactyloids examined except in *Heleophryne, Pleurodema borellii, Pleurodema nebulosa, Crinia, Pseudophryne,* and *Taudactylus.* All of the New World stream leptodactyloids have a papillate medial edge on the dorsal velum, but other New World and Australian leptodactyloid pond tadpoles also have papillate medial margins (Figure 63). The African stream larva *Heleophryne,* however, lacks papillae on the medial edge of the ventral velum.

Lung development in leptodactyloid larvae varies both between and within genera, but is consistent within species. Variation here correlates extremely well with ecology (see below); viz., large lungs are found in tadpoles that occur in small ponds and pools, while larvae that are found in fast-flowing water have reduced lungs.

Ecological Correlates

The correlation of tadpole internal oral anatomy with larval habitats and diets is strong. Most leptodactyloids can be placed into one of five categories based on internal oral anatomy: generalized suspension feeding, pond tadpole; tadpoles living in flowing water; macrophagous carnivorous tadpoles; subaerial tadpoles; and non-feeding tadpoles. The basic categories and associated suites of internal oral features are based on study of non-leptodactyloid tadpoles (Wassersug, 1980; Inger, 1985). Thus, it is instructive to note the generality of the previous work as applied to the leptodactyloids. The compositions of these ecological groupings are: typical pond tadpoles—*Alsodes, Atelognathus, Batrachyla, Caudiverbera, Eupsophus, Hylorina,* most *Leptodactylus, Macrogenioglottus, Odontophrynus, Physalaemus, Pleurodema* (except *nebulosa*), *Proceratophrys boiei, Telmatobius, Limnodynastes, Platyplectron;*

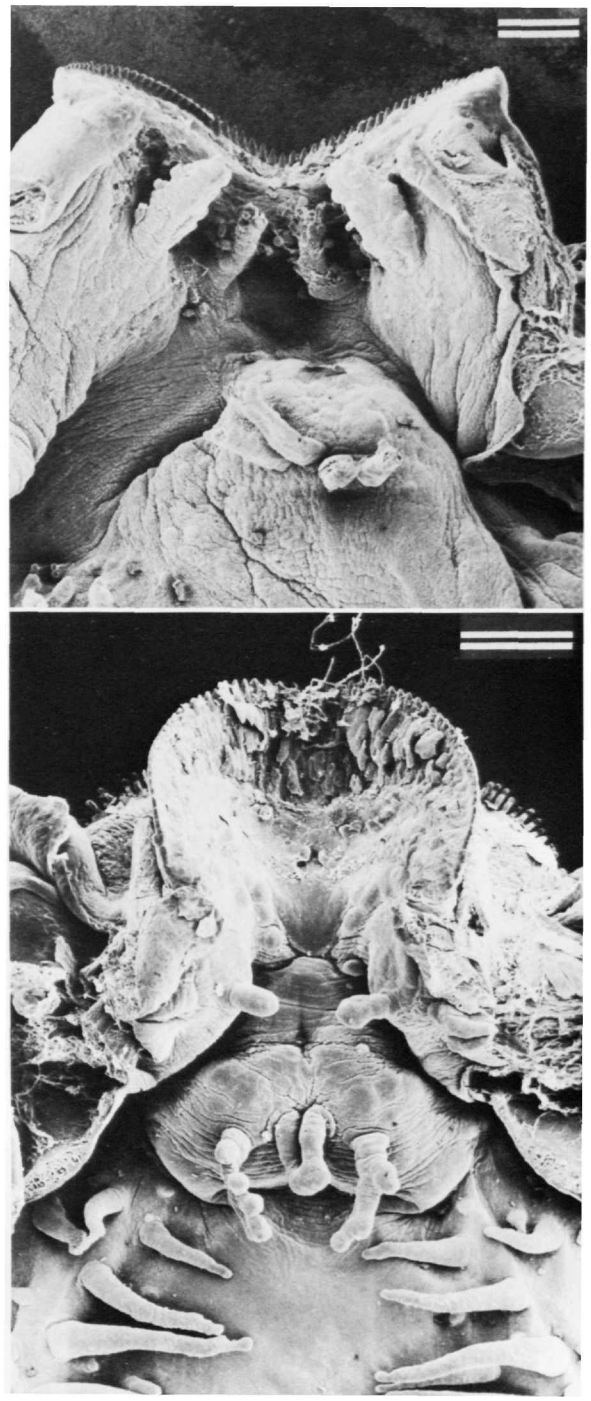


FIGURE 54.—SEM micrographs of front of mouth in dorsal view for two leptodactylid larvae: *Pleurodema borellii* (above) and *Pseudopaludicola* species (below). Scale lines for both = 200 μm. Compare with Figures 52 and 53. Note that *Pseudopaludicola* has only two infralabial papillae and three lingual papillae.

FIGURE 53.—SEM micrographs of front of floor of mouth in dorsal view for selected leptodactyloid larvae: (*a*) *Leptodactylus gracilis;* (*b*) *Leptodactylus knudseni;* (*c*) *Paratelmatobius lutzii;* (*d*) *Proceratophrys appendiculata;* (*e*) *Thoropa miliaris;* (*f*) *Platyplectron ornatus.* All scale lines = 200 μm. Compare with Figures 52 and 54. The fact that in some pictures the lower jaw is depressed (e.g., *L. gracilis*) or elevated (e.g., *L. knudseni*) is insignificant. Note that most tadpoles have four infralabial papillae while *Thoropa* has two. The number of lingual papillae range from two in *L. ornatus* to eleven in *Paratelmatobius.* Stream forms, such as *Proceratophrys,* typically have longer, more elaborately branching papillae. Branching of these papillae, however, appears unique to this genus among leptodactylids. The two representatives of the genus *Leptodactylus* are similar in having small, simple papillae in this region. They differ, however, in number of infralabial and lingual papillae. The lingual papillar pattern in *Paratelmatobius* is unknown in other anurans.

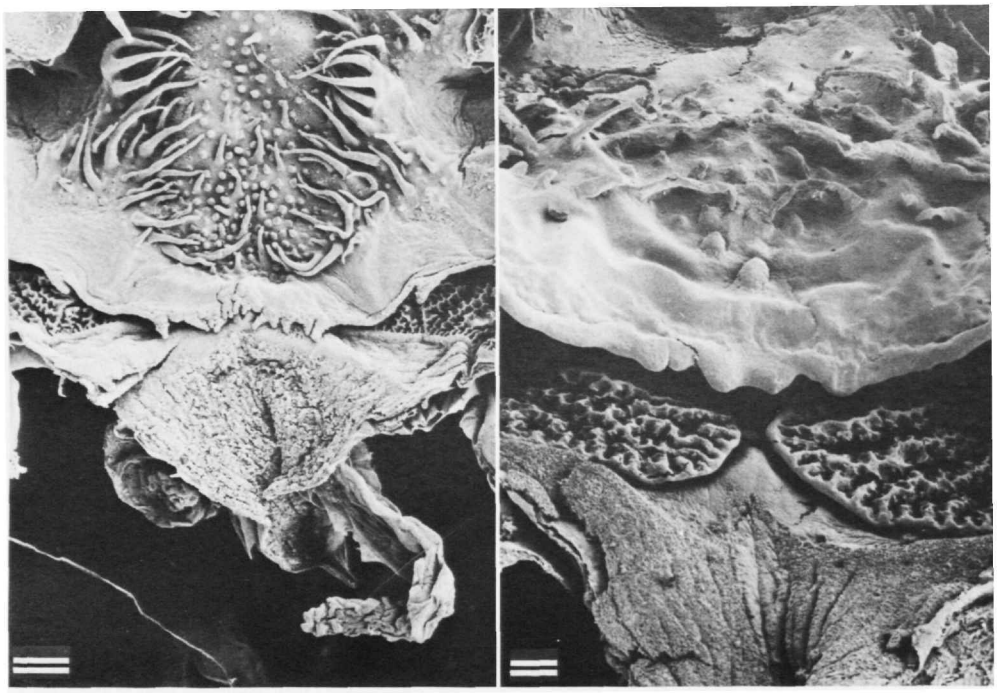


FIGURE 55.—SEM micrographs of posteromedial portion of buccal floor and pharynx in dorsal view for *Crossodactylus* species (left) and *Crinia tasmaniensis* (right). Scale lines = 400 μm and 100 μm, respectively. Note variation in amount of papillation on buccal floor. *Crossodactylus* is unusual in having a fringe on posterior ventral velum. *Crinia* (and *Pseudophryne*) are exceptional among tadpoles examined in medial convergence of their 4th filter plates.

stream or flowing-water tadpoles—*Crossodactylus, Hylodes, Megaelosia, Paratelmatobius, Proceratophrys appendiculata, Pseudopaludicola;* macrophagous carnivores—*Ceratophrys, Lepidobatrachus;* subaerial tadpoles—*Cycloramphus izecksohni, Thoropa;* non-feeding tadpoles—*Adenomera, Cycloramphus stejnegeri, Eleutherodactylus. Rhinoderma darwinii* may be included in this last group although its tadpoles could conceivably receive some nutrition from the ingestion of mucus secreted by the brooding adult.

Not all larvae show such a good match between predicted habitat/ecology based on morphological features with actual habitat preferences. Larvae of *Mixophyes* and *Taudactylus* are stream dwellers, but do not show all the internal oral features predicted for stream forms. In contrast, *Crinia* and *Pseudophryne* larvae are reported to live in ponds, but have morphological features more suggestive of stream forms. The *Heleophryne* tadpole is internally quite unlike most stream-associated neobatrachian larvae. However, it closely resembles, internally and externally, the torrent-adapted *Ascaphus* larva and shares some features, such as reduced buccal papillation, with the neobatrachian torrent-adapted *Amolops* (Ranidae).

The suite of features observed in *Crossodactylodes* was understandable only by knowing that the tadpoles lived in bromeliads. We would not have predicted that habitat based on the internal oral anatomy alone. Other arboreal tadpoles however, do have morphological features indicative of dietary specialization, most commonly macrophagy (Lannoo et al., in press).

Within *Leptodactylus, L. knudseni* and *pentadactylus* were notably distinct from the other typical pond larval *Leptodactylus* examined (e.g., Figure 53*a,b*). Apparently, the more specialized morphologies of *knudseni* and *pentadactylus* correlate with facultative carnivory (Heyer et al., 1975); but again, this dietary capability was not predictable to us based on larval anatomy that we examined.

Pleurodema nebulosa stood out in the morphological analysis as being very different from other *Pleurodema* or, for that matter, leptodactyloid pond larvae in general. For example, secretory ridges on the ventral surface of the ventral velum are absent in this species (Figure 60). When the specimens were being examined, we did not recall the larval habitat or diet of *P. nebulosa* and were unable to predict where the larvae might live or what they might eat, aside from the observation that it did not seem to be a typical pond tadpole. Mares et al., (1977)

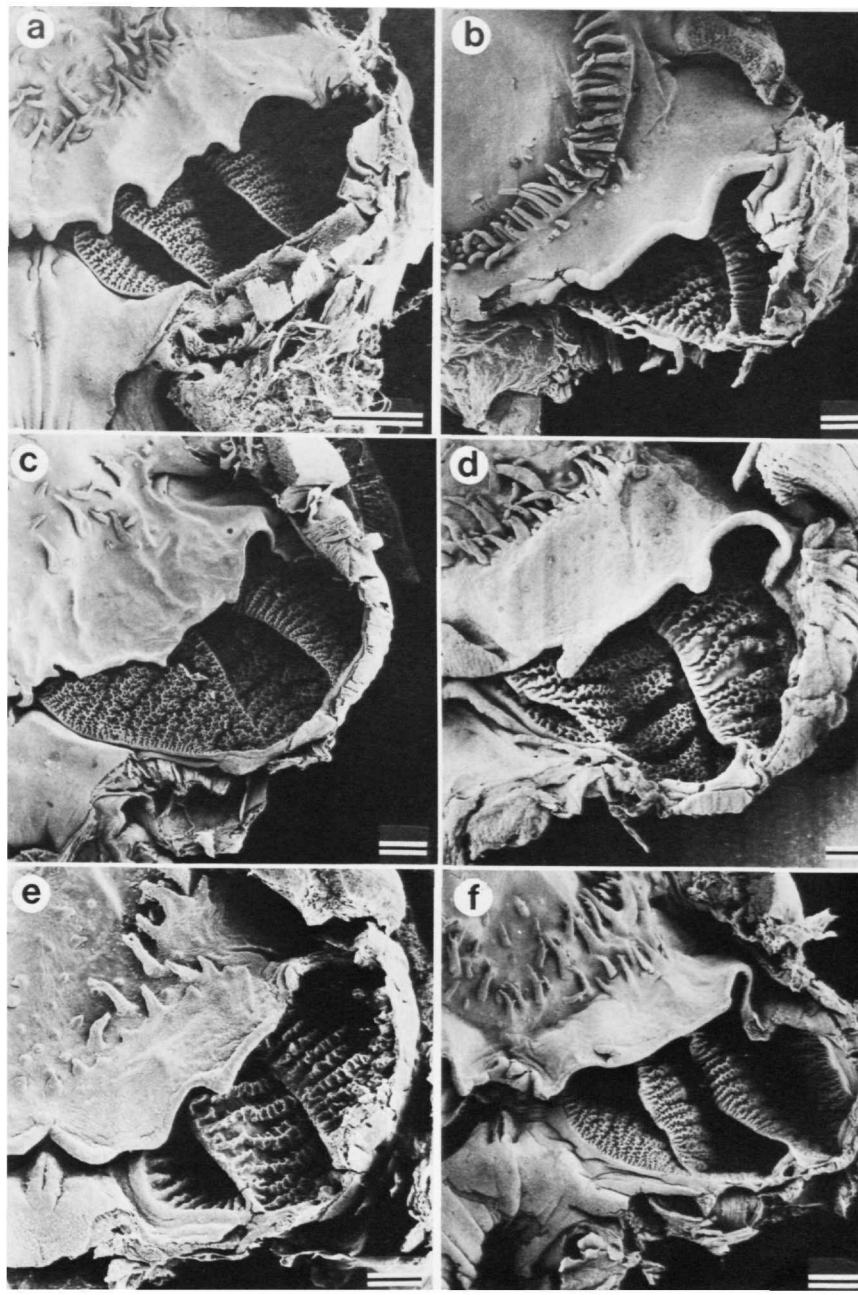


FIGURE 56.—SEM micrographs of branchial baskets in dorsal view for selected leptodactyloid larvae: (*a*) *Atelognathus reverberii* (scale line = 1 mm); (*b*) *Paratelmatobius* (scale line = 200 μm); (*c*) *Pleurodema brachyops* (scale line = 400 μm); (*d*) *Pleurodema cinerea* (scale line = 200 μm); (*e*) *Heleioporus* species (scale line = 400 μm); (*f*) *Platyplectron ornatus* (scale line = 400 μm). All are right branchial basket except for *b*, which is a left basket printed in reverse to orient with other figures. Note that tadpoles vary in height and orientation of filter plates and filter-mesh density. There may be two (e.g., *b,c,d*) or three (e.g., *a,e,f*) major filter cavities visible in this view. Interspecific variation in *Pleurodema* branchial morphology is great (e.g., *c,d*) compared to species in other genera.

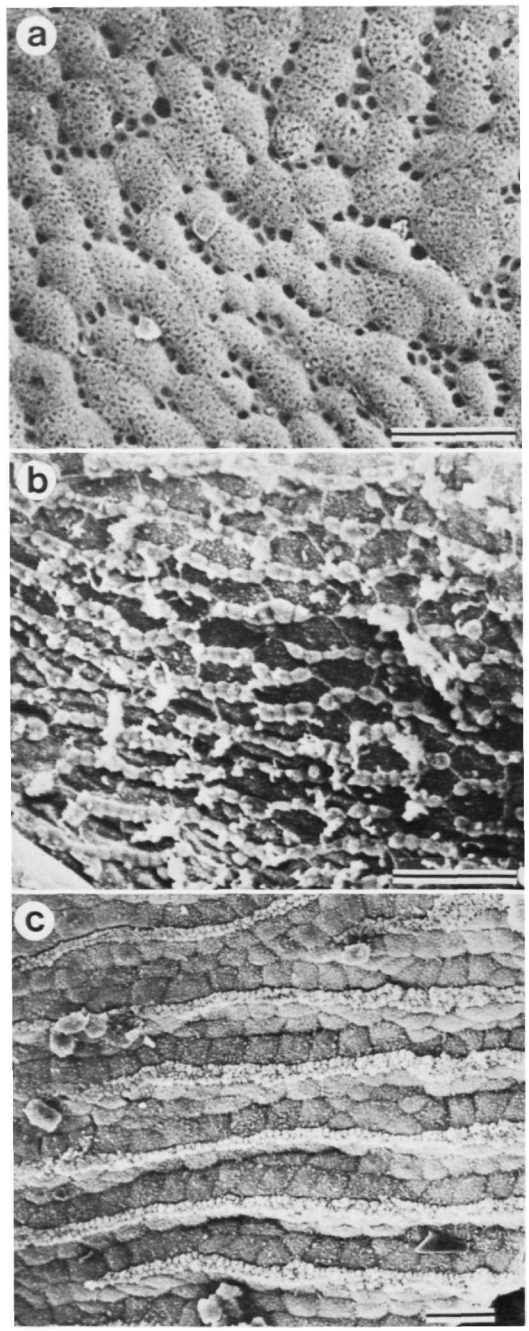


FIGURE 57.—SEM micrographs of secretory tissue in branchial food traps: (*a*) *Heleophryne natalensis;* (*b*) *Crinia tasmaniensis* and (*c*) *Hylorina sylvatica.* All scale lines = 20 μm. Note that secretory cells are numerous in all three species but are not organized into ridges in *Heleophryne.* Absence of ridges is a feature that *Heleophryne* shares with most archeobatrachian genera; however, whether it is a primitive feature in this leptodactyloid genus is not known. *Crinia* and *Hylorina,* as representative tadpoles of Australian and American leptodactyloid radiations, both show the ridged pattern.

commented at length on the convergence of *P. nebulosa* with *Scaphiopus* of the North American deserts. Both have very short larval periods, breed in very ephemeral desert ponds, are carnivorous, and if stressed, cannibalistic. *Pleurodema nebulosa* clearly is not an obligate carnivore like *Lepidobatrachus,* since it retains most of the suspension feeding structures (such as gill filters) seen in generalized tadpoles. On the other hand, the absence of secretory pits and secretory ridges on the branchial food traps certainly correlates with a macrophagy. Presumably, *P. nebulosa* and *Scaphiopus,* compared to other pond larvae, have specialized in terms of being able to feed on large, individual food items at the expense of efficiency in entrapping small, microscopic particles. Interestingly, besides lacking secretory ridges in the branchial food traps, both *P. nebulosa* and *Scaphiopus* (Wassersug, 1980) share a peculiar feature: a convex shape to the free lateral margins of the ventral velum. While both *P. nebulosa* and *Scaphiopus* have a rather well-developed filter-mesh apparatus, the mesh is much finer in *Scaphiopus.* Buccal papillation differs as well in these two taxa.

Heleioporus has too low a filter-mesh density for typical microphagous pond tadpoles. Although *Heleioporus* larvae occur in ponds, their natural diet is unknown; thus, we do not consider *Heleioporus* a typical pond tadpole.

The tadpoles of *Megistolotis* have been associated with both streams and ponds (rocky pools) in nature, yet can be cannibalistic in the laboratory. Nevertheless, we found that the internal oral anatomy is typical of pond larvae.

Leptodactyloid larvae collectively seem to embrace most specializations for habitat and diet found in anurans. However, this diversity does not hold up when considered on a continental basis. Africa has but one genus of leptodactyloid and all species have stream-adapted larvae. The American leptodactyloids lack at least two major tadpole types that were identified previously: oophagous arboreal larva (Lannoo et al., in press); and the obligate, microphagous suspension feeder (Wassersug, 1980). Concerning the former type, arboreal dendrobatids and hylids seem to have filled this niche in Central and South America. Concerning the latter, American leptodactyloids generally co-occur with pipids and microhylids, most of which have specialized microphagous larvae. Phyllomedusine hylids also are common in the Neotropics in association with leptodactylids and they also have tadpoles particularly adapted for midwater microphagy (Wassersug, 1980). Pipids and phyllomedusine treefrogs are absent in Australia, and microhylids are a minor part of the Australian herpetofauna, both in terms of numbers of species and geographic distribution. It is puzzling that *Taudactylus,* which occurs in stream habitats, has the extremely narrow secretory ridges in the branchial food traps that typically characterize obligate, microphagous, suspension feeders (Wassersug and Rosenberg, 1979). As we have examined only a small portion of the myobatrachids, we do not know the full extent of the

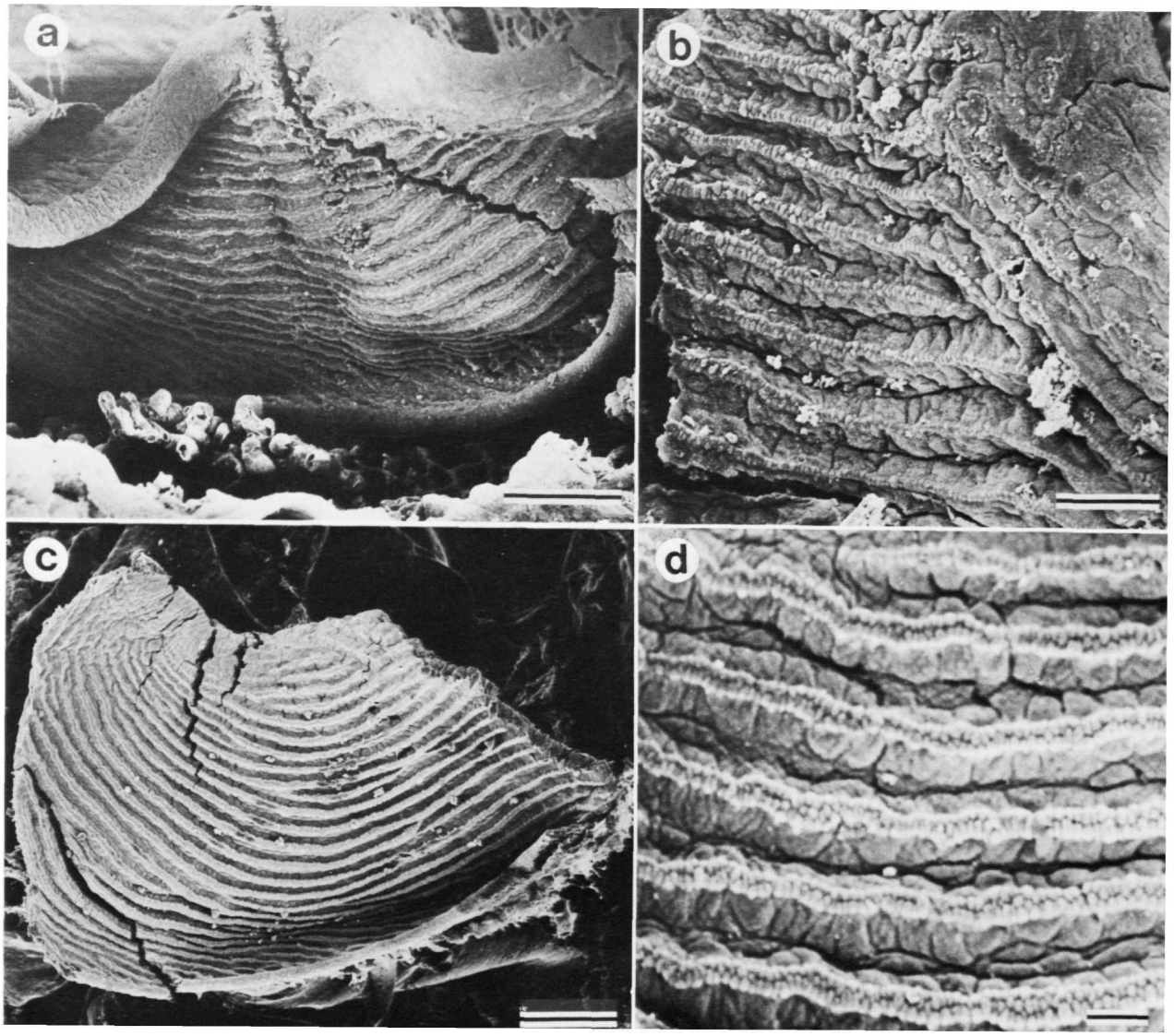


FIGURE 58.—SEM micrographs of branchial food traps (left) and secretory ridges at higher magnification (right) of *Proceratophrys appendiculata* (*a* and *b*) and *Megistolotis lignarius* (*c* and *d*). From *a* to *d* scale lines = 100 μm, 40 μm, 100 μm, and 20 μm, respectively. Since both of these tadpoles and other stream associated leptodactyloid larvae have secretory ridges in branchial food traps, it is unlikely that absence of such ridges in *Heleophryne* (Figure 57*a*) is an adaptation to flowing water.

Australian diversity of larval types.

It is worth emphasizing the very high degree of correlation of internal oral features with larval habitat and diet, and that leptodactyloid larvae in general show the same patterns found in other anuran families (e.g., see Inger, 1985). Most of the exceptions observed involve larvae specialized for living in extreme habitats, such as the desert pond-dwelling *Pleurodema nebulosa* (Figure 60*a,b*) or the bromeliad inhabiting *Crossodactylodes*. Few larvae that inhabitat these specialized environments have been examined to date (but see Lannoo et al., in press). Study of more species of desert-pond larvae and arboreal larvae may result in recognition of morphological features that can characterize each of these as another major larval type.

Formas (1981a) reported the results of a phenetic analysis comparing external larval morphologies and ecological characteristics for the leptodactylid larvae inhabiting the temperate forests of Chile. He found a good correlation between external

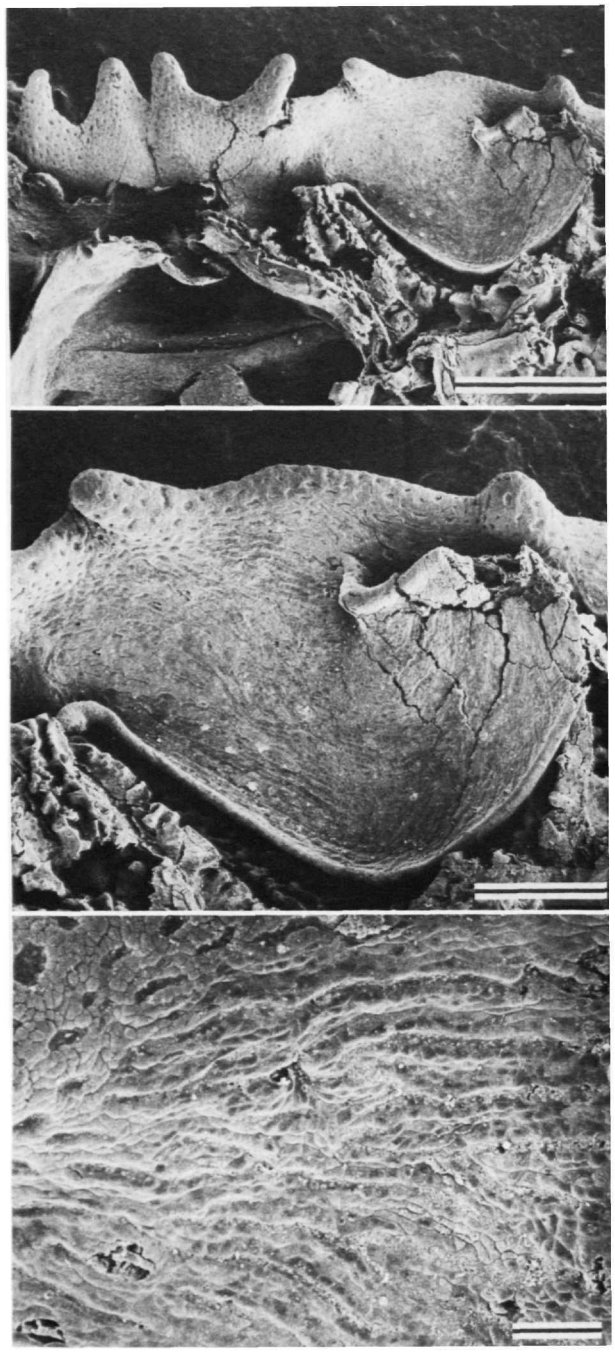


FIGURE 59.—SEM micrographs of branchial food traps and secretory ridges of *Alsodes monticola* larva at three different magnifications. From top to bottom scale lines = 1 mm, 400 μm, and 100 μm. *Alsodes*, like all other telmatobiine tadpoles examined, has secretory ridges in the branchial food traps (contra Sokol, 1981).

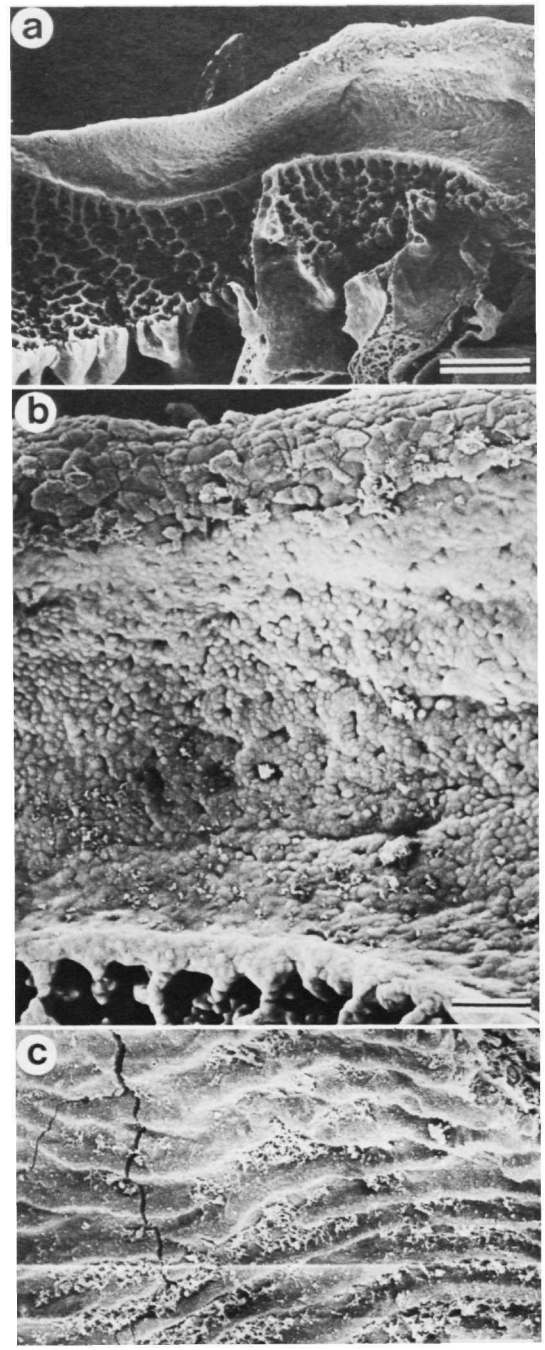


FIGURE 60.—SEM micrographs of branchial food traps of: (*a*) *Pleurodema nebulosa;* (*b*) secretory tissue of that food trap at higher magnification compared to; (*c*) secretory tissue of branchial food traps of *Pleurodema brachyops*. Scale lines = 200 μm, 40 μm, and 40 μm respectively. Of the *Pleurodema* examined, *P. nebulosa* is unique in lacking secretory ridges in branchial food traps. In this and other features *P. nebulosa* appears to be convergent with desert-adapted *Scaphiopus*, and distinct from other *Pleurodema*.

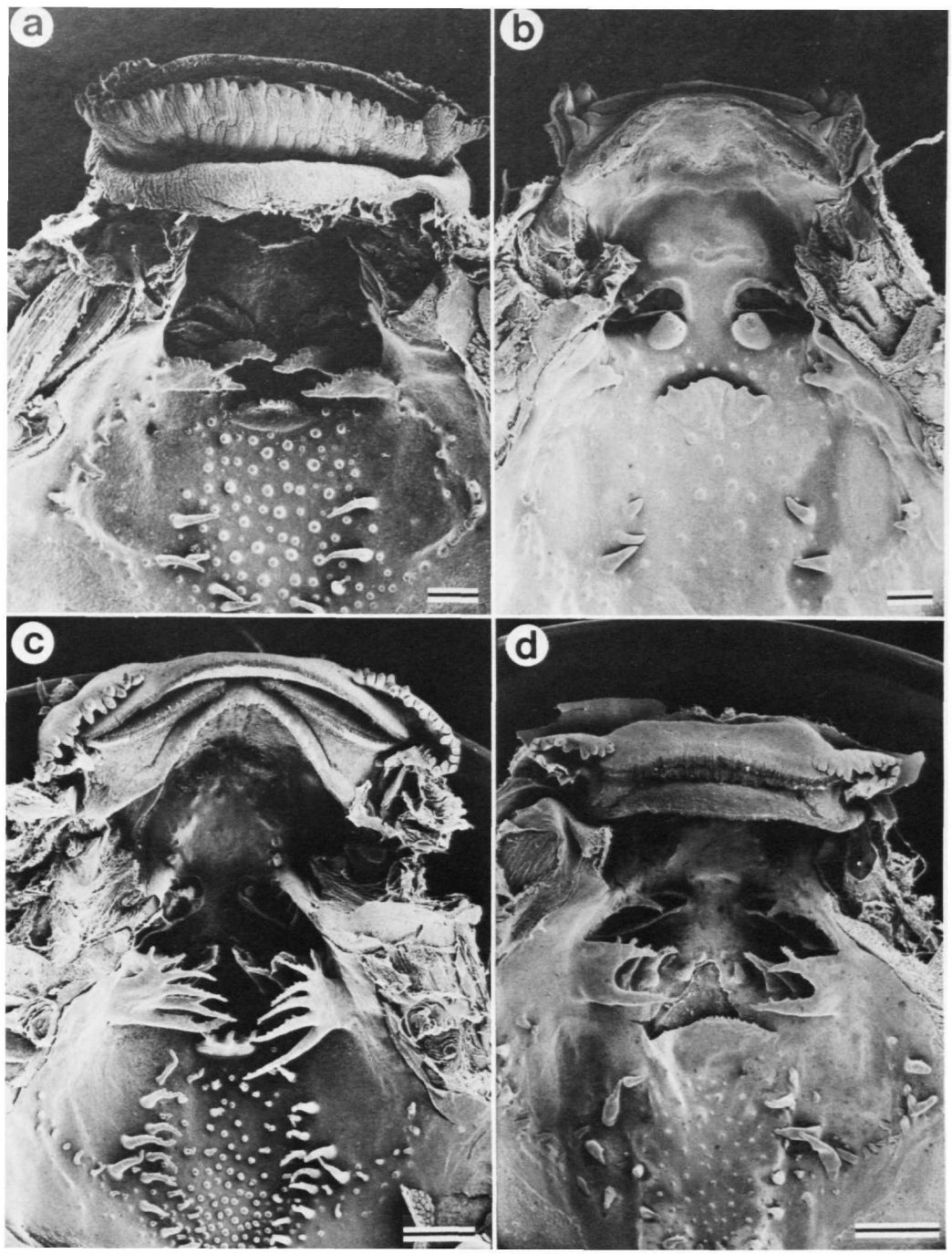


FIGURE 61.—SEM micrographs of front of roof of mouth in ventral view for selected leptodactyloid larvae: (*a*) *Leptodactylus fuscus;* (*b*) *Leptodactylus knudseni;* (*c*) *Megaelosia goeldii;* and (*d*) *Odontophrynus americanus.* Scale lines = 400 μm for *a* and *b*, 1 mm for *c* and *d*. Note the differences in postnarial papillae, median ridge, and lateral-ridge papillae in *L. fuscus* vs. *L. knudseni.*

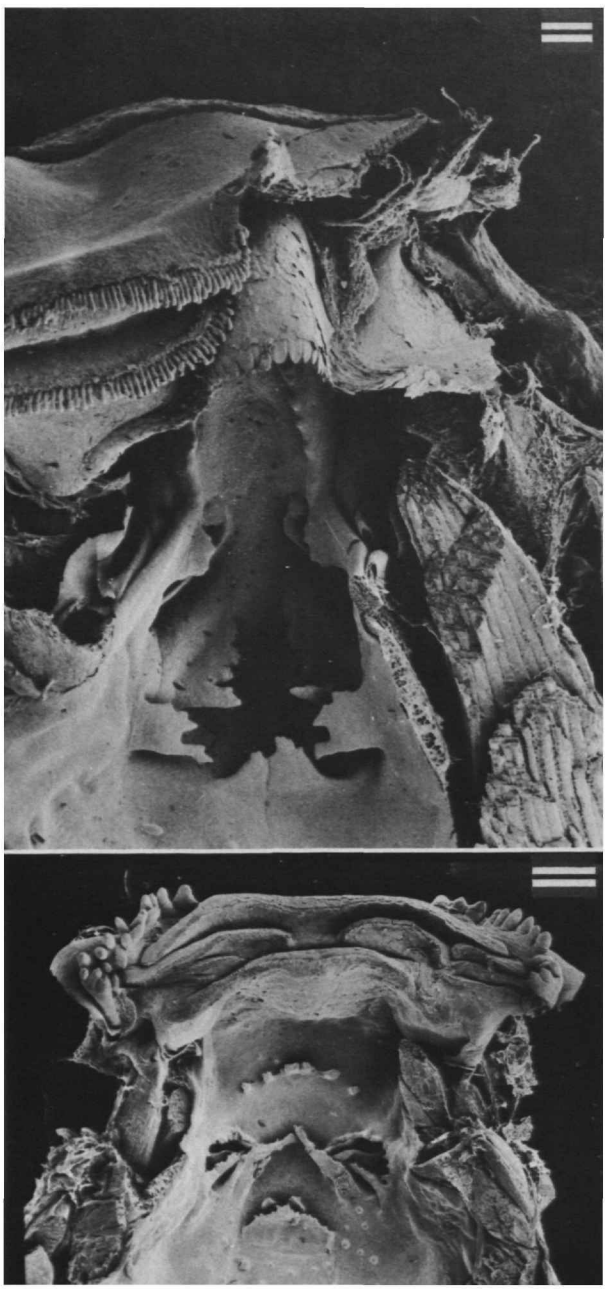


FIGURE 62.—SEM micrographs of front of roof of mouth in ventral view of *Thoropa miliaris* (above) and *Platyplectron ornatus* (below). Scale lines = 200 and 400 μm respectively.

larval morphology and the ecological conditions. Both external and internal features are necessary to understand the ecological correlates, however. For example, Formas (1981a) found that externally, *Eupsophus* tadpoles are distinctive from *Alsodes*, *Batrachyla*, and *Caudiverbera*. The distinctive external *Eupsophus* morphology correlates with a habitat of living in crevices or small caves under rocks. Internally, we find no distinctive differences within this group. Alternatively, the larvae of *Proceratophrys appendiculata* and *boiei* are externally almost identical. Internally, they demonstrate differences that correlate with differences in standing- versus flowing-water habitats.

PHYLOGENETIC CORRELATES

Any phylogenetic inferences must be proposed within the framework of the preceding discussions on ontogenetic, individual, and intraspecific variation. The most difficult factors to separate in this study are ecological and phylogenetic. The clearest correlation of internal oral anatomy for leptodactyloid larvae is with larval ecology. Because of this correlation, parallelism and convergence are common in larval evolution, making phylogenetic interpretation difficult. For example, two species that have features characteristic of stream larvae may have those features because they shared a common stream-dwelling ancestor, but it may be just as likely that the features were independently derived due to convergent adaptations to stream life. In too many cases, information is inadequate to resolve the question of whether morphological similarities are due to convergence or to common ancestry.

Another limitation of these data for phylogenetic analysis is the central and common occurrence of the typical pond tadpole in leptodactyloid evolution. We infer that the primitive leptodactyloid tadpole was a typical pond larval type (see below). If this is true, one would not expect to find much, if any, phylogenetic information within the larvae of taxa that retain this generalized larval type.

Within these constraints, internal oral anatomical features do suggest some phylogenetic patterns.

Inter-Continental Leptodactyloid Relationships

Taxonomically, the leptodactyloids have been treated at one extreme as a single family (e.g., Tyler, 1979) and at the other extreme as three separate families (e.g., Savage, 1973), each occurring in a separate continent. One of our initial interests in undertaking this project was to determine if there were any internal oral features of larvae that would resolve the relationships among the African, South American, and Australian leptodactyloids. Zoogeography suggests a Mesozoic Gondwanan origin for the leptodactyloids, but the fossil record is of little help in establishing the time of origin. In a recently proposed phylogeny for the Anura based on sixteen characters (Duellman and Trueb, 1986) the Australian forms clustered with the African leptodactyloid (*Heleophryne*), whereas the South American forms were more derived. These authors (p. 475) noted, however, unresolved polytomies: depending on

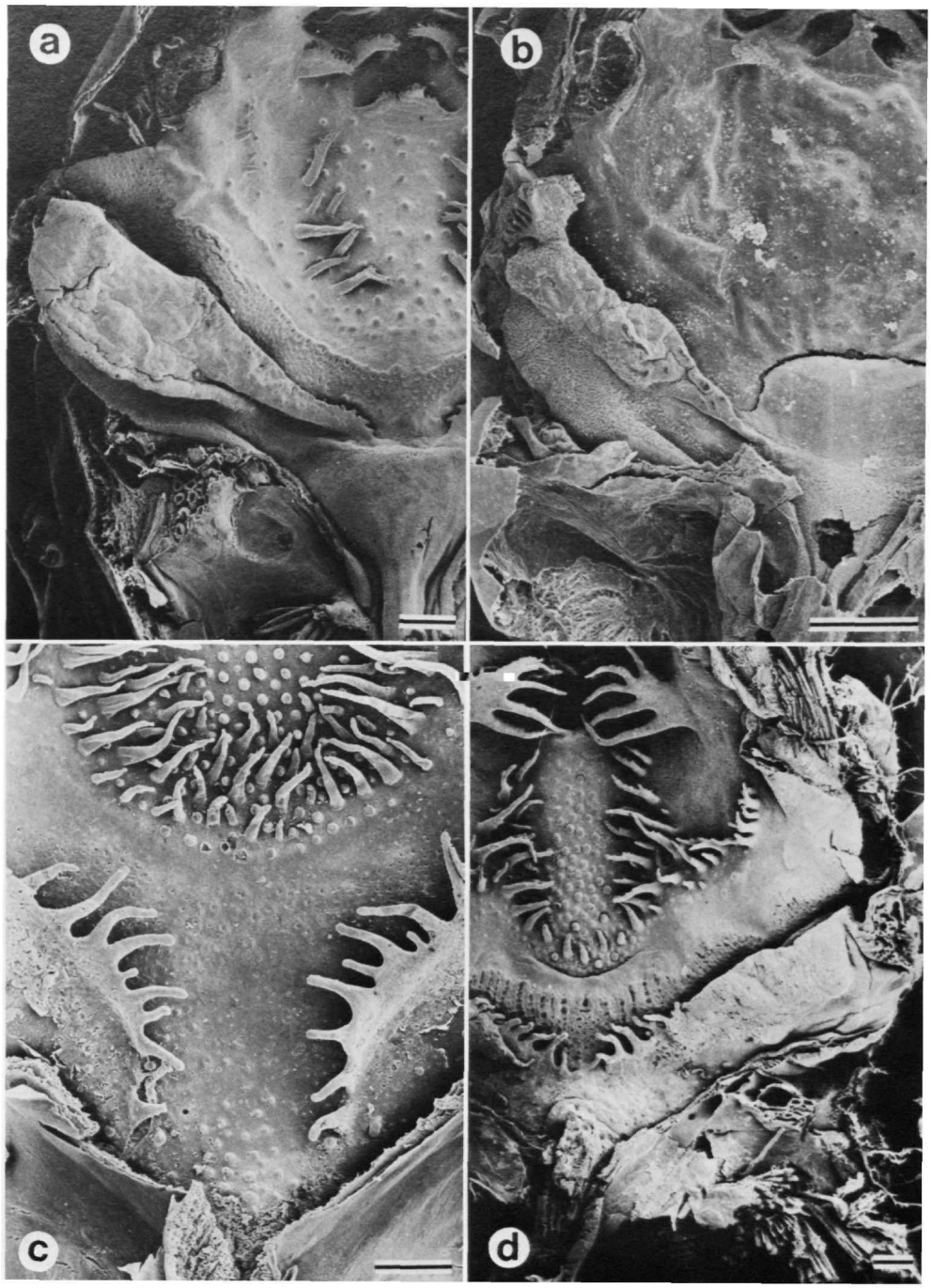


FIGURE 63.—SEM micrographs of posterior portion of buccal roof and pharynx in ventral view for selected leptodactyloid larvae: (*a*) *Alsodes monticola*, right side; (*b*) *Heleioporus* species, right side; (*c*) *Crossodactylus* species, midline; (*d*) *Hylodes* species, left side. All scale lines = 400 μm. Tadpoles vary in having few (e.g., *Heleioporus*) to many (e.g., *Crossodactylus*) buccal-roof papillae. Dorsal velum is unfringed in *Heleioporus* and heavily fringed in *Crossodactylus* and *Hylodes*. Other differences include size and distinctness of secretory zone in front of dorsal velum, and breadth of ciliary groove behind dorsal velum.

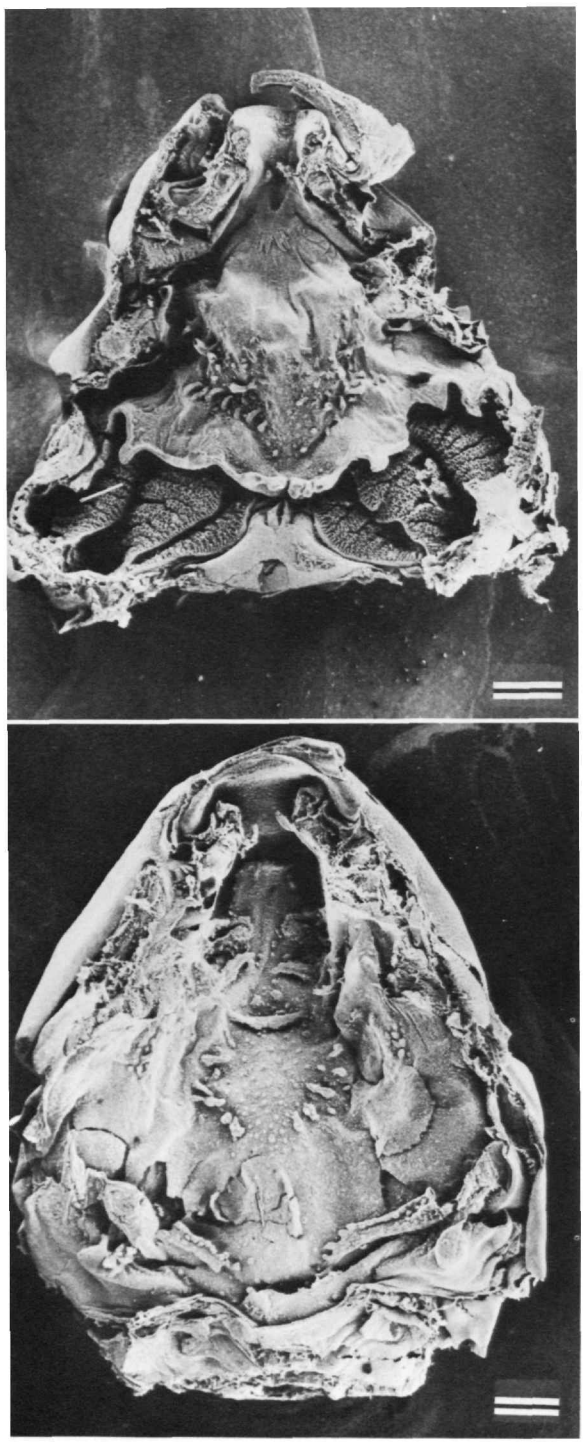


FIGURE 64.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Litoria alboguttata;* scale lines = 1 mm.

how one interpreted a single character (amplectic position) certain South American leptodactylids, e.g., *Batrachyla* and *Pleurodema,* fell in with the myobatrachids of Australia and the Australian forms overall could cluster with the Leptodactylidae rather than the Heleophrynidae. Regrettably, we do not find any single, derived, larval character-state that defines any one of these three groups.

Heleophryne presents a special problem, as there is but a single genus with a clearly specialized, stream larval type. Features unique to *Heleophryne* larvae include the longitudinal orientation of the internal nares, and the pair of ridges on each side in the area of the buccal roof where lateral-ridge papillae occur in other tadpoles. It is not clear, however, whether these features indicate a separate origin at the familial level or are specializations for stream life within the genus. The absence of secretory ridges in the branchial food traps (Figure 57*a*) is a feature that distinguishes *Heleophryne* from other stream-adapted leptodactyloid larvae and is similar to the pattern common, but not unique, to archaeobatrachian frogs (Wassersug and Rosenberg, 1979). *Heleophryne* tadpoles are, in fact, quite similar to *Ascaphus* tadpoles. *Heleophryne* shares with *Ascaphus* the following internal features: a V-shaped BFA with the BFA papillae arising from a common ridge, reduced buccal-roof papillation, cup-like structures in the infralabial region, and no secretory ridges in the branchial food traps. Both of these tadpoles externally have large oral disks specialized for holding onto rocks in torrential streams. Most of these features are clearly convergent. Some, for example, the reduced buccal papillation and cup-like structures in the infralabial region, also characterize other torrent-adapted tadpoles such as those of *Amolops* (Inger, 1985). Whether the absence of secretory ridges in the branchial food traps is due to convergence or retention of a primitive pattern in *Heleophryne* cannot be determined, but the somewhat similar *Amolops* clearly has the ridges (Wassersug, pers. obs.). Overall internal oral anatomy of the larvae argues neither for nor against a close relationship of *Heleophryne* with the South American and Australian leptodactyloids.

There are greater radiations of larval types in both South American and Australian leptodactyloids. At the generic level, our sample of South American leptodactyloids is good; our sample of Australian leptodactyloids is much poorer. The samples, however, are adequate to draw the following two conclusions. First, no single larval feature unequivocally defines either group in relation to the other. Second, two pieces of evidence suggest that the radiations have occurred independently in each continent. The number of lingual papillae have been used by other workers to delineate taxonomic groups; e.g., in Europe, brown frog and green frog larvae can be distinguished on this character (Viertel, 1982); in South America most hylids have two lingual papillae whereas *Gastrotheca* has four (Wassersug, 1980; Wassersug and Duellman, 1984). All of the Australian leptodactyloid larvae examined have two lingual papillae, whereas most of

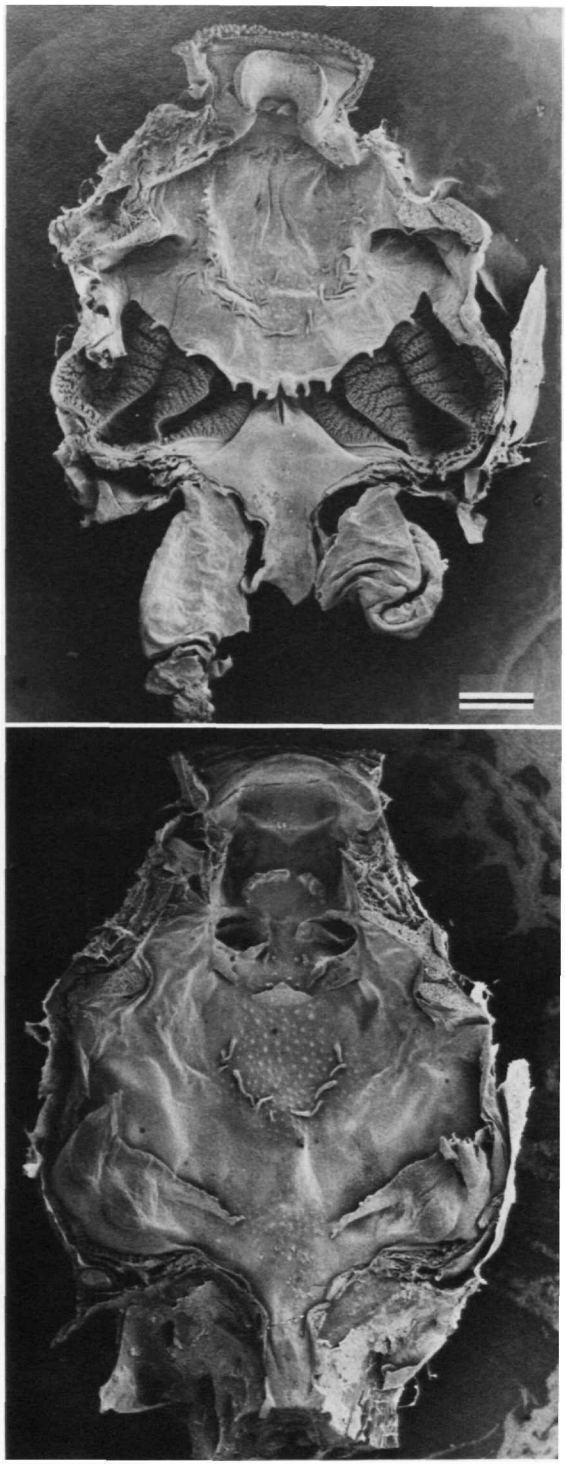


FIGURE 65.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Cyclorana australis;* scale line = 1 mm.

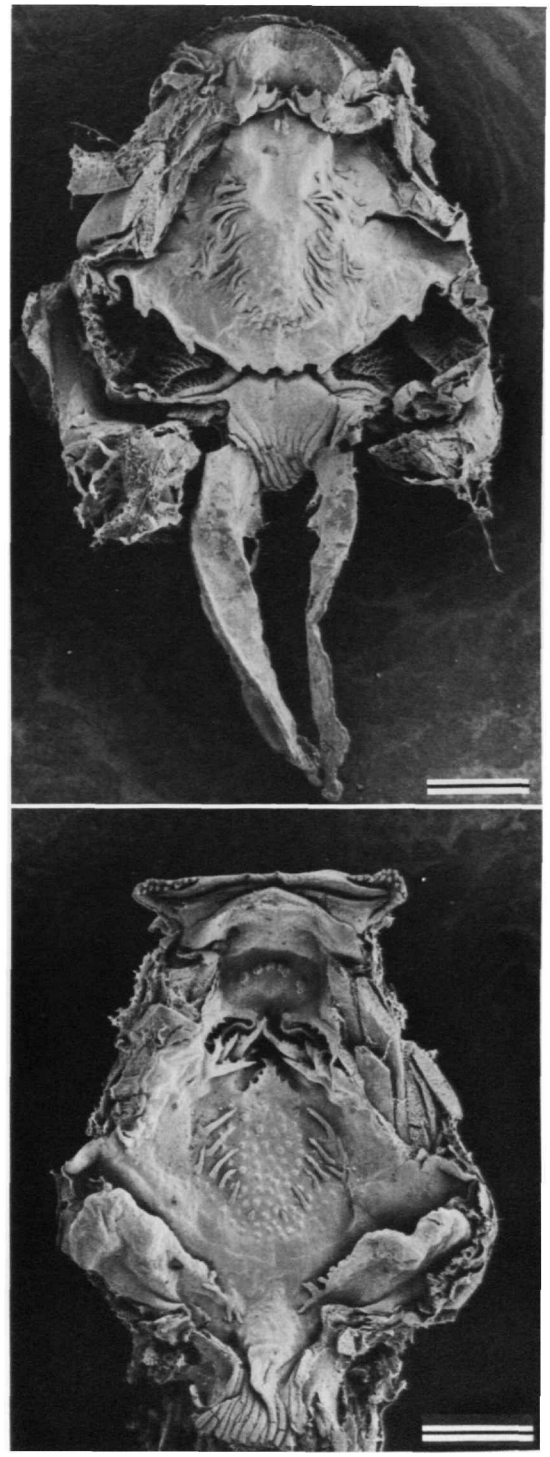


FIGURE 66.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Colostethus whymperi;* scale lines = 1 mm.

the South American larvae have four (Figures 52–54). Whether two or four is the primitive pattern, the most parsimonious explanation for the variation seen in lingual papillae is that separate radiations have occurred in South America and Australia.

The South American stream larvae, for which we have the most data, show the same suites of morphological specializations seen in other families. Similarly, South American leptodactyloids in general show the same extremes of morphology evidenced by carnivorous, subaerial, or non-feeding larvae in other families (Wassersug, 1980). The Australian larvae we examined do not fit nearly as well into these categories; of the tadpoles discussed in the ecological correlates section (above) that did not show easily interpretable congruence of habitat with internal oral anatomy, most were Australian. For example, the larva of *Mixophyes* is clearly an externally specialized stream-dwelling tadpole. Yet internally most of the features are not different from those characteristic of typical pond larvae. Similarly, *Taudactylus diurnus* larvae are reported (Liem, pers. comm.) from fast-flowing streams yet, except for slight expansion of the oral disc, they show little morphological specialization for life in currents, either externally or internally. This non-concordance of habitat, external morphology, and internal oral morphology suggests a different evolutionary pattern or a shorter period of evolutionary response.

Relationships Involving the Australian Leptodactyloids

The sample of Australian leptodactyloids is not extensive enough to adequately characterize the radiation in Australia. However, the sample does allow some comparisons and predictions.

Lynch (1973) suggested that certain pelobatids were closely related to cycloranine leptodactyloids among the Neobatrachia. The larval features examined herein argue against such relationships. The pelobatids (sensu lato) have a single-filter cavity per side and lack secretory ridges on the branchial food traps (Wassersug, 1980; Wassersug and Rosenberg, 1979). All of the Australian taxa examined (including both myobatrachines and cycloranines [= limnodynastines]) have well-developed secretory ridges in the branchial food traps and have either two or three filter cavities per side. The Australian leptodactyloids demonstrate less similarity to pelobatids than does either *Heleophryne* in South Africa or telmatobine leptodactylids in South America.

Historically, the genus *Cyclorana* has been included either in the Australian leptodactyloids or the Australian treefrogs (Hylidae or Pelodryadidae, depending on author). Currently, authorities agree that *Cyclorana* is a member of the Australian tree frog assemblage (for example, Maxson et al., 1982). We have examined one species of *Litoria, L. alboguttata* (Figure 64), and one species of *Cyclorana, C. australis* (Figure 65). Both of these larvae externally have a typical pond morphology. The most striking feature that they share is 4–6 lingual papillae. This is unlike any of the myobatrachid larvae that we examined. It will be interesting to see if this difference in lingual papillae will hold up with additional sampling of pelodryadids and myobatrachids.

The few species examined support the two major groupings of Australian leptodactyloids recognized by all authors: the myobatrachines and limnodynastines (although the genus *Rheobatrachus* has been placed in a separate subfamily, the Rheobatrachinae, by some authors, e.g., Heyer and Liem (1976), others, such as Frost (1985), group this genus with the limnodynastines). *Crinia* and *Pseudophryne* have peculiar branchial basket morphologies with the fourth filter plates from each side almost in contact on the midline (Figure 55). This arrangement, unusual among all tadpoles examined, is associated with little lung development and is totally unexpected in pond larvae. More myobatrachines should be examined to determine whether this character defines the group.

Relationships Involving the New World Leptodactyloids

Lynch (1973), among others, has proposed a close relationship between the family Dendrobatidae and the subfamily Elosiinae (*Crossodactylus, Hylodes, Megaelosia*) of the family Leptodactylidae, deriving the former from the latter. In addition to two species of *Colostethus* examined previously (Wassersug, 1980), we examined *Colostethus whymperi* (Figure 66). *Colostethus nubicola, subpunctatus,* and *whymperi* are very distinct from each other. *Colostethus subpunctatus* and *whymperi* are presumably pond-dwelling tadpoles, whereas *C. nubicola* is a funnel-mouthed tadpole that lives in shallow-stream pools. There are no larval features that argue for or against close relationships among the dendrobatids and elosiines. All of the elosiines have stream-adapted larvae; thus it is reasonable to assume that, if the dendrobatids were derived from elosiines, the ancestral dendrobatid had a stream larva. *Colostethus whymperi* shows some features associated with stream life, such as elongate BFA and BRA papillae, an elaboration of lateral-roof and postnarial papillae, and a papillate medial margin of the dorsal velum. Of these features, *C. subpunctatus* shares only the elongate BFA and BRA papillae; *C. nubicola* has none of these features. Thus, morphological traces of stream life are not evident in all dendrobatid tadpoles. Confirmation of whether dendrobatids are derived from elosiines must await a clearer understanding of phylogenetic relationships within the Dendrobatidae.

The genus *Rhinoderma* is often considered to be the only member of the family Rhinodermatidae (e.g., Duellman, 1975). The non-feeding larva of *R. darwinii* has lost some features of free-living, feeding larvae, but still retains many. We have been unable to examine *R. rufum* larvae, which are free-living pond forms (Formas et al., 1975). The data available for *R.*

darwinii neither support nor refute recognition of the family Rhinodermatidae.

Internal oral features do not provide any conclusive information of relationships among the New World leptodactylid genera. However, they argue against certain associations proposed on other, more limited, morphological features. For example, based on other characters, the genera *Ceratophrys* and *Lepidobatrachus* are considered to be closely related, as are the genera *Odontophrynus* and *Proceratophrys*. However, there is considerable difference of opinion on the relationships between these two lineages. Lynch (1971) recognized *Ceratophrys* and *Lepidobatrachus* in the subfamily Ceratophryninae and placed *Odontophrynus* and *Proceratophrys* in a separate subfamily, the Telmatobiinae. Heyer (1975) thought that these two lineages were closely related. The tadpoles of all four of these genera are much more distinctive from each other than they are similar. There are few features that link either *Ceratophrys* with *Lepidobatrachus* or *Odontophrynus* with *Proceratophrys*, let alone any features that support any close relationship between these two lineages within the Leptodactylidae. It is no surprise that *Odontophrynus* tadpoles, which are typical pond larvae, are different from *Proceratophrys* larvae, which show many adaptations to living in flowing water.

It is noteworthy that both *Ceratophrys* and *Lepidobatrachus* have macrophagous carnivorous tadpoles. Yet these larvae are so different, particularly in their head shape and jaw design, that they most likely have been independently derived. The features that they share, such as reduced branchial baskets, reduced gill filters, large buccal floor area, and reduced buccal papillation, are characteristic of tadpoles specialized for macrophagy regardless of family. Adults of the genera *Cycloramphus* and *Thoropa* are quite distinctive, yet the feeding larvae of both genera are remarkably similar and distinctive in external morphology. This paradox led Lynch (1971) to place these two genera in separate subfamilies by emphasizing the adult characters and Heyer (1975) to consider *Cycloramphus* and *Thoropa* much more closely related by utilizing larval characters, in part. The internal oral features of feeding *Cycloramphus* and *Thoropa* larvae are very similar, differing only in trivial ways. Yet the morphological features do not unambiguously support or reject either the hypothesis that the larvae are similar because of common ancestry, or that the larval morphologies are convergent as a result of similar adaptations to the subaerial way of life. These two examples are discussed in detail because they illustrate where internal larval anatomy might have been expected to shed light on phylogenetic relationships at the intergeneric level. Using external larval features, Diaz and Valencia (1985) concluded that "*Alsodes, Telmatobius* and *Hylorina* form a group united at a high level of phenetic similarity and that *Batrachyla, Caudiverbera, Insuetophrynus, Telmatobufo* and *Eupsophus* do not show sufficient similarity to justify formation of [subfamilial] groups [with the telmatobiine leptodactylids]." Based on the larger array of morphological features that we have before us, we can neither support nor refute this suggestion. We find little evidence in the characters we examined for concluding that the first three genera are in any way closer phenetically or phylogenetically than are any of the latter genera.

A final example is the genus *Paratelmatobius*. The relationships based on adult morphology are enigmatic, as members of this genus have a peculiar mixture of primitive and derived character states (Heyer, 1975). The tadpole of *Paratelmatobius* is unique externally. The internal oral anatomy is as distinctive as any observed among leptodactyloids (Figure 28)—the tadpole data underscore the distinctiveness of *Paratelmatobius*, but provide no clue to its relationships with other genera of leptodactyloids.

In contrast to the little insight into suprageneric relationships given by the internal oral features of leptodactylid larvae, oral morphology does contain consistent phylogenetic information at the generic and specific levels. In almost all cases, there are similar features that unite members of the same genus. This subtle unity at the genus level is not easy to verbalize and is not always obvious within the standardized format of the written descriptions provided above. When either specimens, or good figures of specimens, are compared directly, it is easy in most cases to recognize members of the same genus. This is true, in the present sample, even for the two *Proceratophrys* examined, which occur in different habitats and apparently preferentially ingest different-sized particles.

The three exceptions to this general observation are instructive. Based on internal oral features, the larvae of *L. knudseni* and *L. pentadactylus* form a very distinctive grouping within the *Leptodactylus* species examined; the *L. wagneri* tadpole is distinctive, but somewhat similar to the tadpole of *L. chaquensis;* and the larvae of *L. fuscus, L. gracilis*, and *L. mystacinus* are very similar to each other (and are typical pond tadpoles). These groupings are identical to those proposed independently on other features (Heyer, 1969). Thus, larval features are useful for determining species groupings within the genus *Leptodactylus;* yet the total variation observed, while exceeding the variation seen in most other genera, is rather continuous and understandable within the context of a single genus.

The differences between the feeding and non-feeding larvae of *Cycloramphus* are striking, yet the non-feeding morphology is clearly derivable from the feeding morphology. In this case, based on only two species, a persuasive argument could be made that the relationships were at the generic, rather than specific level. Wassersug and Duellman (1984) described a morphocline in *Gastrotheca* ranging from the typical pond tadpole morphology to an extreme non-feeding tadpole morphology similar to that seen in *Eleutherodactylus*. Because of the example provided in *Gastrotheca*, we defer making any generic proposals for *Cycloramphus* based on larval morphology until the larvae of more species are studied.

Variation in the genus *Pleurodema*, based on species we

have examined, exceeds the degree of variation observed in all other leptodactyloid genera except *Cycloramphus*. The larvae of *P. nebulosa* are not only very different from the other *Pleurodema* species examined, but also distinctive among all leptodactyloid larvae. The distinctiveness of the internal oral features in part reflects the carnivorous feeding mode. *Pleurodema nebulosa* is a member of a species group that is distinctive within *Pleurodema* in lacking lumbar glands and living in desert regions (Cei, 1980; Duellman and Veloso, 1977). Based on the available tadpole data, we think that this species group should be elevated to the generic level. We refrain from formally proposing this action for two reasons. First, we have only examined five species of *Pleurodema*, only one of which is a member of the *P. nebulosa* species group. Second, a proposal should include members of the entire genus, especially considering the fact that the internal oral larval information for the other four species examined is at variance with relationships proposed on other characters. The internal oral anatomy of *P. cinerea* larvae differs from that seen in *P. borellii—bufonina—brachyops*. In the most recent treatment on relationships of *Pleurodema*, Duellman and Veloso (1977) indicated that *cinerea* and *borellii* were each other's closest relatives and that *brachyops* was a member of the same species group, but that *bufonina* was a member of a different species group. Clearly, more work is required to understand the relationships among the species currently placed in *Pleurodema*. *Pleurodema* is one case where examination of internal oral anatomy will provide useful phyletic information in determining relationships at the species group level.

Major Evolutionary Trends

The primitive leptodactyloid tadpole was a pond-dwelling, microphagous, suspension-feeding tadpole with keratinized mouthparts capable of substrate grazing. Evidence for this comes from outgroup comparisons with the sister-group families Bufonidae and Hylidae (Wassersug, 1980) and the fact that the primitive group of leptodactyloids in the New World, the Telmatobiines, are characterized by having generalized pond tadpoles.

There have been two major trends in the evolution of oral anatomy of leptodactyloid larvae: either elaboration or simplification of surface structures. Elaboration of buccal papillae, usually as proliferation and/or elongation, is seen in the stream-dwelling larvae. Interestingly, in the leptodactyloids we have surveyed, there has been no major hypertrophy of the branchial baskets or the gill-filter system as seen in obligate, microphagous-feeding tadpoles.

The most common trend has been simplification, either general or structure-organ specific. Apparently, simplification is a result of altering the normal larval development of specific oral features at different stages. Most of the simplified larval structures seen are morphologically similar to embryonic or early ontogenetic stages of tadpoles with typical pond morphology. However, the simplification of larval anuran anatomy can be achieved through the modification of a developmental program along more than one evolutionary pathway (Wassersug, 1980). For example, a particular larval feature in one species may appear to be incompletely developed in comparison to that of a sister species because (1) either the onset of, or rate of, embryonic development is retarded in relation to other features, or (2) the onset of, or rate of, metamorphosis is accelerated in relation to other features (see also Alberch et al., 1979). In anurans it is sometimes actually possible to distinguish between evolutionary pathways because of what could be called "developmental hysteresis," i.e., metamorphosis is not a simple reversal of larval development. A larval feature may look quite different halfway through its embryonic development than it does halfway through its metamorphosis. To determine the actual evolutionary pathway taken requires both good developmental series and confidence in the inferred phyletic relationships of the species in question. Unfortunately, we lack both for leptodactyloids.

A general developmental simplification in larval oral surface features is seen in two feeding specialists: non-feeding tadpoles and macrophagous tadpoles. The loss is extreme in the direct-developing *Eleutherodactylus*. The non-feeding *Adenomera* larva is less extreme and, in comparison to *Eleutherodactylus* and direct-developing gastrothecine hylids (Wassersug and Duellman, 1984), appears to have arrived at its simplified morphology by modification of the early embryology of a generalized leptodactylid larva. Simplification of the branchial basket and food trap structure is seen to a lesser extreme in larvae that feed on larger food items, such as in the subaerial larvae of *Cycloramphus* and *Thoropa*, some stream larvae, such as *Heleophryne*, the bromeliad larvae of *Crossodactylodes*, and the carnivorous *Ceratophrys* and *Lepidobatrachus* larvae. The structural simplification seen in *Lepidobatrachus*, in contrast to *Adenomera*, apparently is the type involving early onset of or accelerated metamorphosis (compare Figures 2 and 17). The wider mouth, eroded ventral velum, and enlarged anteriorly directed glottis in *Lepidobatrachus* are all features more characteristic of leptodactylid larvae near metamorphosis than of leptodactylid embryos.

Leptodactyloids show the same discordance of larval and adult morphological specializations observed in other groups of frogs. Starrett's Rule (Savage, 1981) may be paraphrased: the plainest of adult frogs often have the most unusual tadpoles, whereas the most bizarre adult frogs usually have ordinary tadpoles. *Macrogenioglottus* has a bizarre adult morphology involving very specialized locomotor and feeding adaptations. *Macrogenioglottus* tadpoles are very ordinary pond tadpoles. *Proceratophrys* are striking frogs, and the external morphology of the tadpoles is very ordinary, but the internal oral features are distinctive and betray a stream way of life. Some leptodactyloids (certain *Leptodactylus*) are ordinary as both

adults and larvae; others (such as *Paratelmatobius* and *Rhinoderma*) are distinctive both as adults and larvae. Clearly, the adult and larval stages represent, at one level, discrete units of selection in the leptodactyloid life cycle. At another level, however, the two stages of the life cycle must be coadapted, for the larva and adult of any species share a single genome. Understanding the nature of these coadaptations remains one of the major unsolved problems in anuran biology.

Summary and Conclusions

(1) Ontogenetic variation in internal oral morphology is relatively slight once a tadpole has developed the external larval features characteristic of the species.

(2) Individual variation is remarkably low for tadpoles from the same collection series. However, tadpoles from a single collection may be siblings, reducing the amount of genetic and consequently phenotypic variation.

(3) Several oral features described by previous workers were found to be too affected by preservation and dissection artifact or otherwise too variable to be of systematic use.

(4) Among the features found to vary little within species but vary considerably among species—and consequently to be of systematic value—are the number, size, shape, and position of the infralabial, lingual, and buccal floor papillae; the shape of the ventral velum; the presence or absence of secretory ridges in the branchial food traps; the size and shape of the filter plates (and the filter cavities between them); the number of filter rows and the density of the filter ruffles on the filter plates; the size and shape of postnarial papillae, median ridge, and lateral-ridge papillae on the buccal roof; the shape of the medial portion of the dorsal velum; and the extent of lung development.

(5a) The ecology of most, but not all, tadpoles that live in ponds or streams may be predicted from internal oral morphology even when external morphology gives little evidence of tadpole habitat. The extent and complexity of buccal papillation and particularly the extent of lung development are the features that best predict the flow regime in which tadpoles live. Stream tadpoles typically have large, prolific buccal papillae and little lung development.

(b) Leptodactyloid larvae can be sorted into the following ecological categories: generalized suspension feeding, pond tadpole; tadpoles living in flowing water; macrophagous carnivorous tadpoles; subaerial tadpoles; and non-feeding tadpoles. Africa has but one adaptive type of tadpole—a highly specialized version of the type associated with flowing water.

Our limited sample of Australian leptodactyloid larvae contains generalized suspension feeding pond tadpoles; tadpoles living in flowing water; and perhaps an obligatorily microphagous tadpole. The correlation of morphology with ecology in the Australian larvae examined is not as robust as in the South American larvae examined. The South American leptodactylid larvae show all of the ecological/morphological types listed above, but lack at least two major types recognized from other studies: an obligatorily microphagous tadpole type and an oophagous arboreal larval type. These tadpole types do occur in other New World anurans among hylids, microhylids, and pipids.

(6) Morphological observations with systematic and phylogenetic implications include the following.

(a) *Heleophryne* shares several morphological features, such as the absence of secretory ridges in its branchial food traps, with *Ascaphus* and certain other archaeobatrachian anurans. These features, however, may be convergent.

(b) Australian leptodactyloid larvae do not share any unique, derived features with pelobatid larvae.

(c) All Australian leptodactyloid larvae have two or fewer lingual papillae whereas South American leptodactyloid larvae typically have four lingual papillae, suggesting that the Australian forms represent a single, separate radiation.

(d) *Cyclorana* has 4–6 lingual papillae, unlike the Australian leptodactyloids examined, supporting non-larval based arguments for a non-leptodactyloid assigment of the genus.

(e) Most South American leptodactylids have similar, generalized pond larvae; consequently, oral morphology gives limited insight into the phylogenetic relations among genera. However, the morphology suggests that *Lepidobatrachus* and *Ceratophrys* represent two independent evolutionary lines with macrophagous carnivorous larvae. *Paratelmatobius* larvae are extremely different from other leptodactylids and are not close to any other genus examined. *Leptodactylus knudseni* and *L. pentadactylus* are most similar to each other and differ from other *Leptodactylus; L. wagneri* is distinct, but most similar to *L. chaquensis*. *Leptodactylus fuscus, gracilis* and *mystacinus* form a natural group, in support of previous suggestions. *Pleurodema nebulosa* larvae lack secretory ridges in their branchial food traps and differ in a variety of ways from all other *Pleurodema* at a level consistent with generic differentiation. Interspecific variation in pharyngeal morphology in the genus *Pleurodema* is great, suggesting several distinct species groups.

(f) Except for *Pleurodema nebulosa*, all telmatobine tadpoles examined have secretory ridges in their branchial food traps, a feature that distinguishes them from all pelobatids examined to date.

(7) The major evolutionary trends in leptodactyloid larval internal oral anatomy have involved either elaboration or simplification of surface structures. Elaboration has been through proliferation and/or elongation of structures. Elaboration of buccal papillae and concomitant reduction in the size of the lungs and branchial baskets (and density of the gill filters) characterizes tadpoles associated with flowing water. Simplification has been a more common pattern that may have occurred through a variety of evolutionary pathways. Overall

simplification typifies carnivorous tadpoles and non-feeding larvae as well as species with direct-development. The simplification seen in the non-feeding *Adenomera* appears to be due to a truncation of the development of normal larval features, whereas the simplification seen in the carnivorous *Lepidobatrachus* appears to be the result of premature metamorphosis of normal larval features.

(8) No obvious correlation of the degree of specialization between larvae and adults of the same species exists across the leptodactyloids. This underscores, at one level, that natural selection acts independently at these two stages of the life cycle. At another level, the two stages of the life cycle must be coadapted; understanding the nature of this coadaptation remains a major challenge.

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