

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

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ABSTRACT

Wassersug, Richard J., and W. Ronald Heyer. A Survey of Internal Oral Features of Leptodactyloid Larvae (Amphibia: Anura). *Smithsonian Contributions to Zoology*, number 457, 99 pages, 66 figures, 1 table, 1988.—The internal oral anatomy of larvae from 34 genera (52 species) of leptodactyloid larvae are examined and described. These represent most of the South American leptodactylid genera plus *Heleophryne* from Africa and a sample of both myobatrachine and limnodynastine genera from Australia.

Full descriptions are provided for at least one species of each genus and additional species comparisons are made as appropriate. Comparative synopses, which emphasize unique or unusual features, are also presented for each genus.

In general, larval oral morphologies are distinctive at the generic level, but specific features correlate better with ecology than with phylogeny. Nevertheless, certain phylogenetic conclusions are possible based on the larval data, which are discussed in detail. Major evolutionary trends in leptodactyloid larval internal oral anatomy are discussed that involve elaboration or simplification of surface structures.

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

*Richard J. Wassersug
and W. Ronald Heyer*

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.

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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

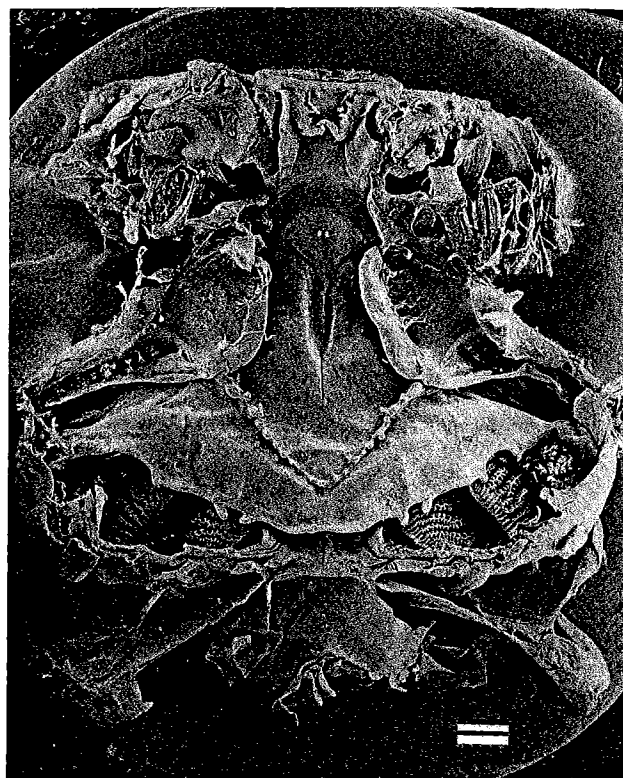


FIGURE 1.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Heleophryne natalensis*; scale line = 1 mm.

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 57a). 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

NOMENCLATURE 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 52a). 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

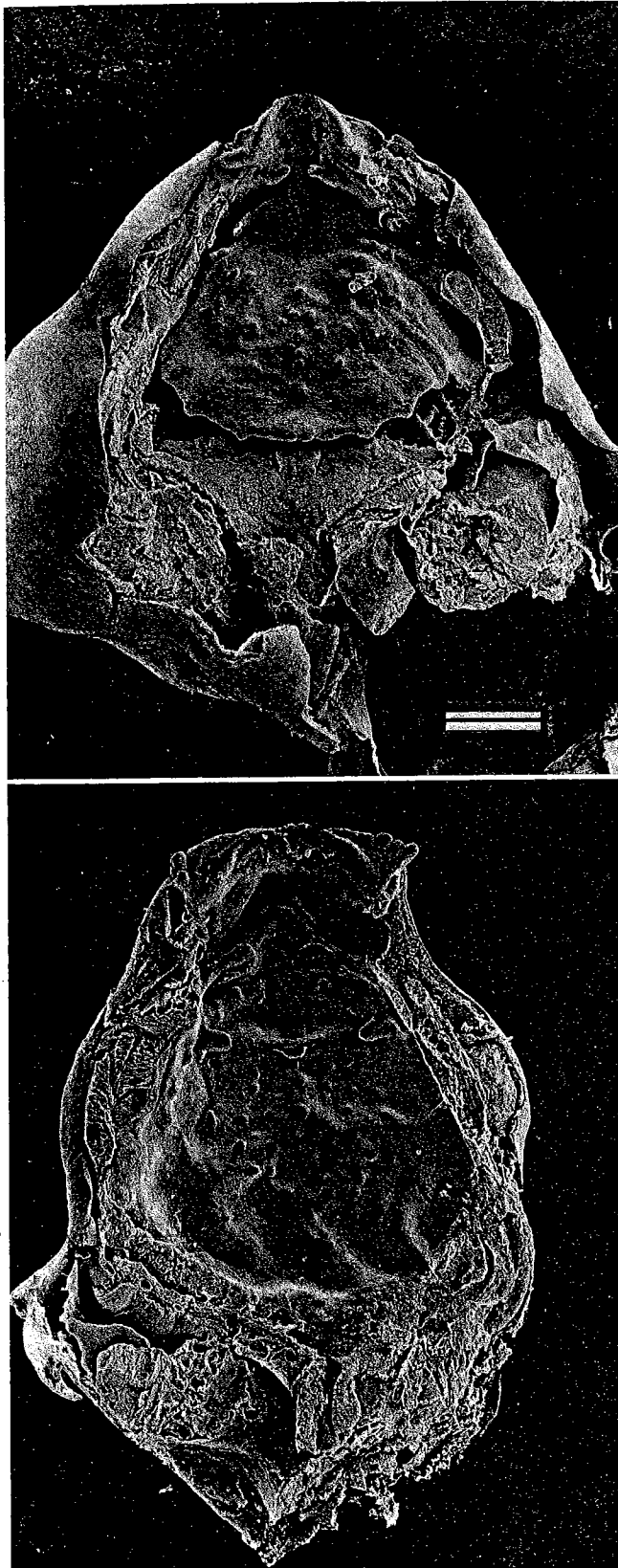


FIGURE 2.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Adomera marmorata*; scale line = 400 μ m.

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

