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

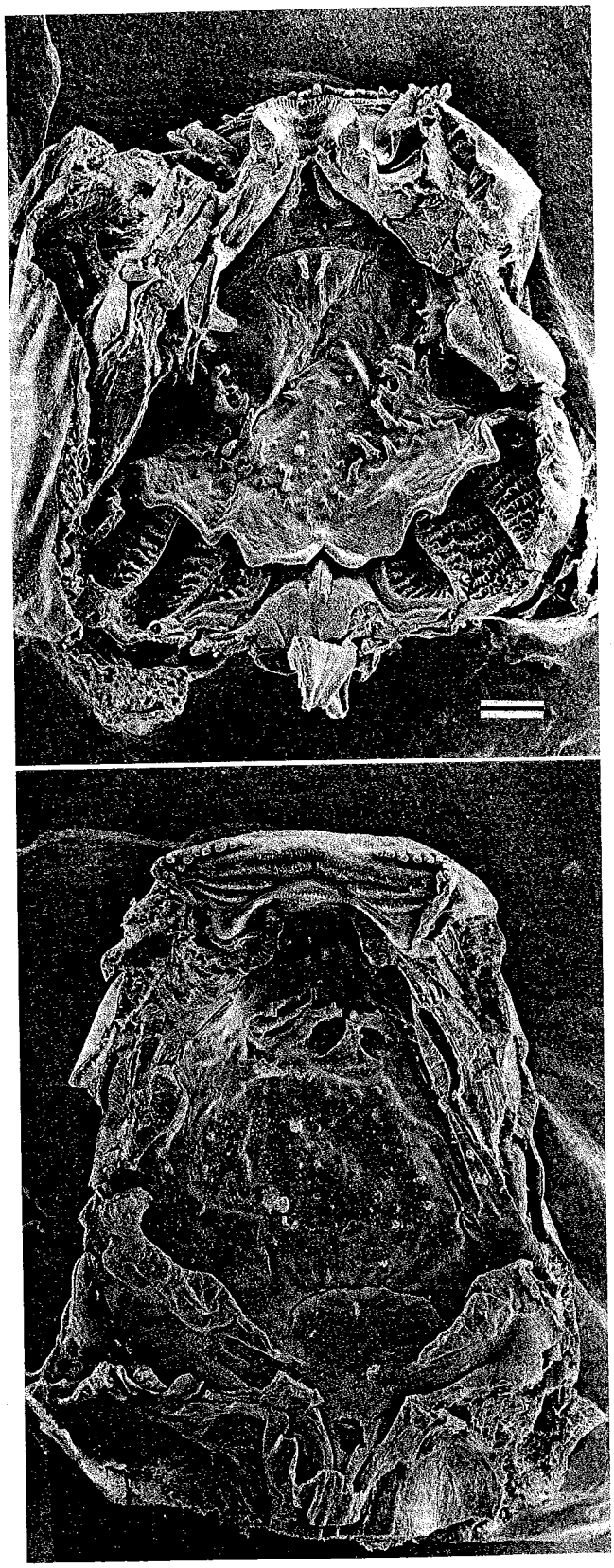


FIGURE 43.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Heleioporus* species; scale line = 400 μm.

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

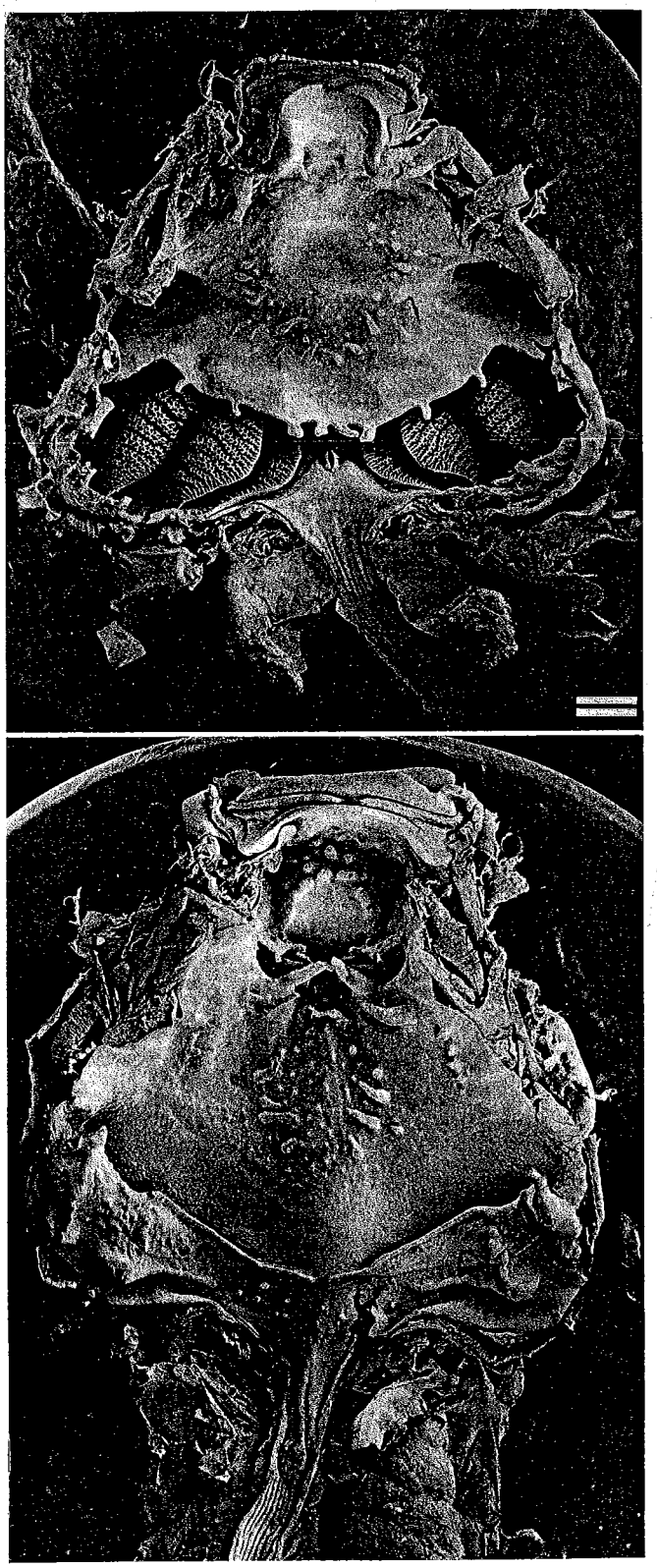


FIGURE 44.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Limnodynastes tasmaniensis;* scale line = 1 mm.

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

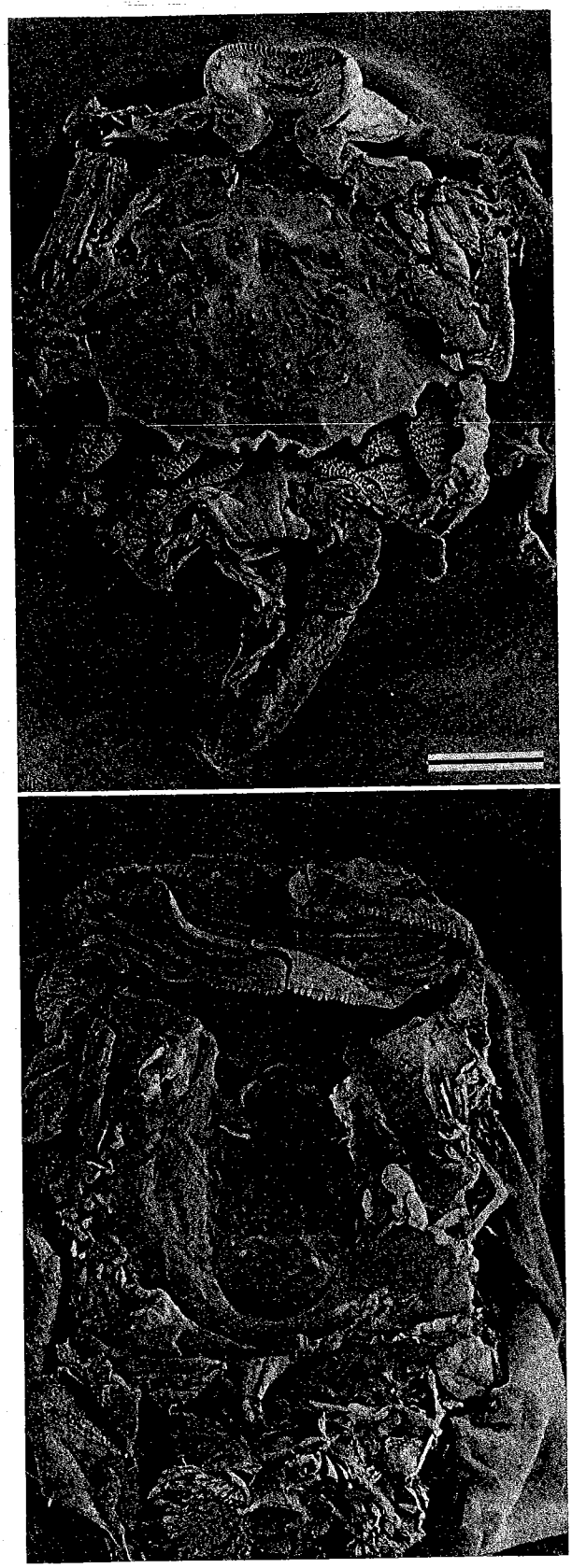


FIGURE 45.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Megistolotis lignarius;* scale line = 1 mm.

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

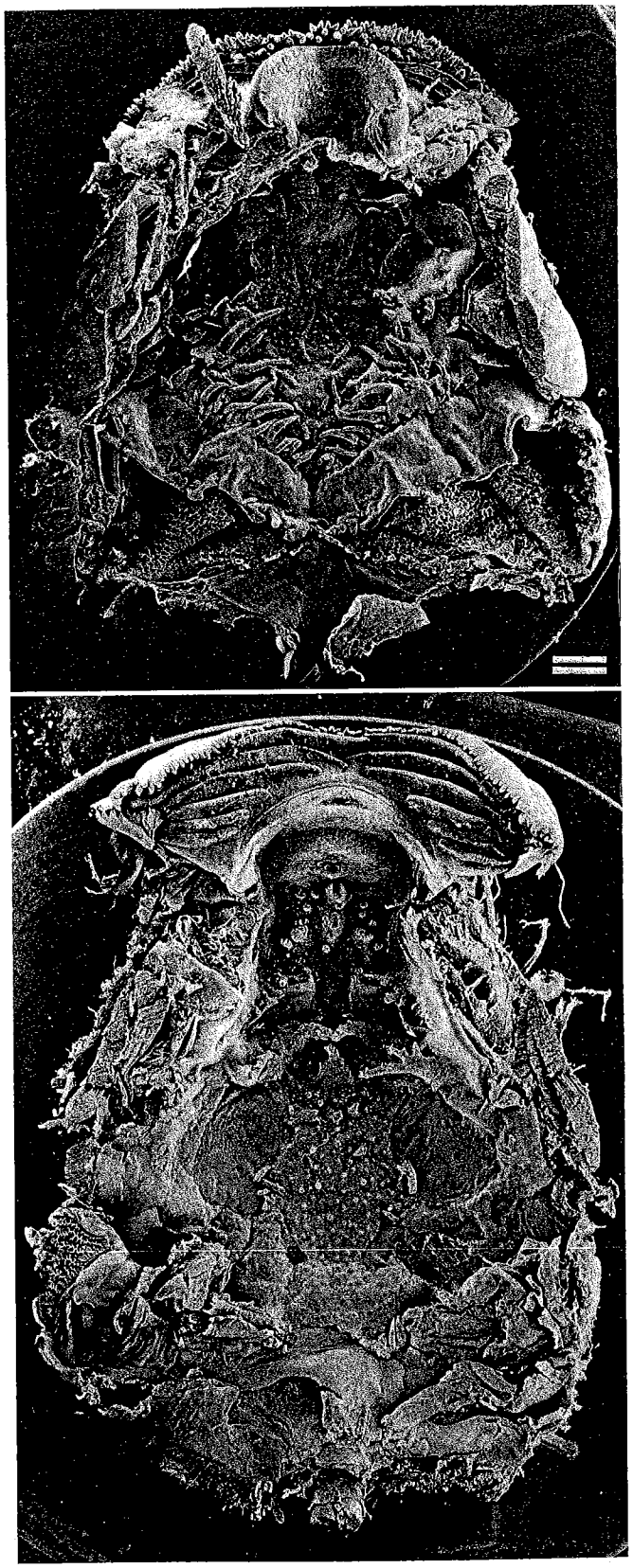


FIGURE 46.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Mixophyes balbus;* scale line = 1 mm.

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

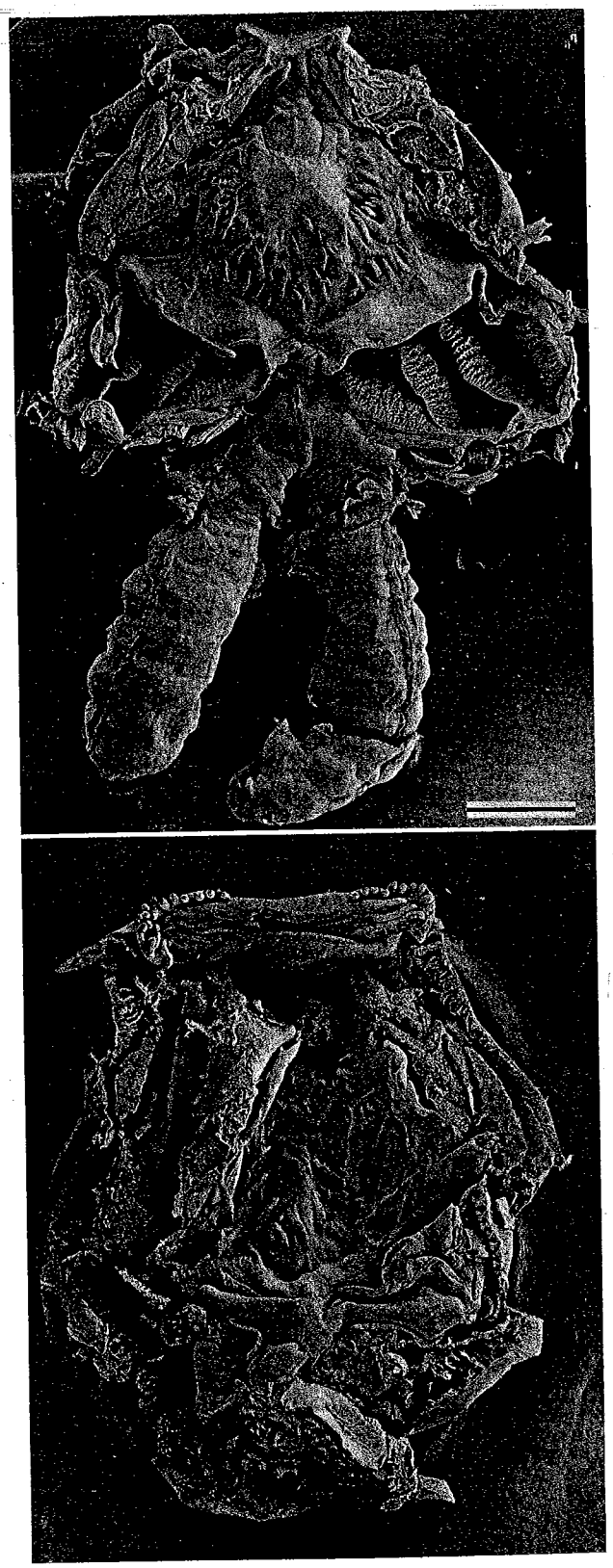


FIGURE 47.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Platyplectron ornatus;* scale line = 1 mm.

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;

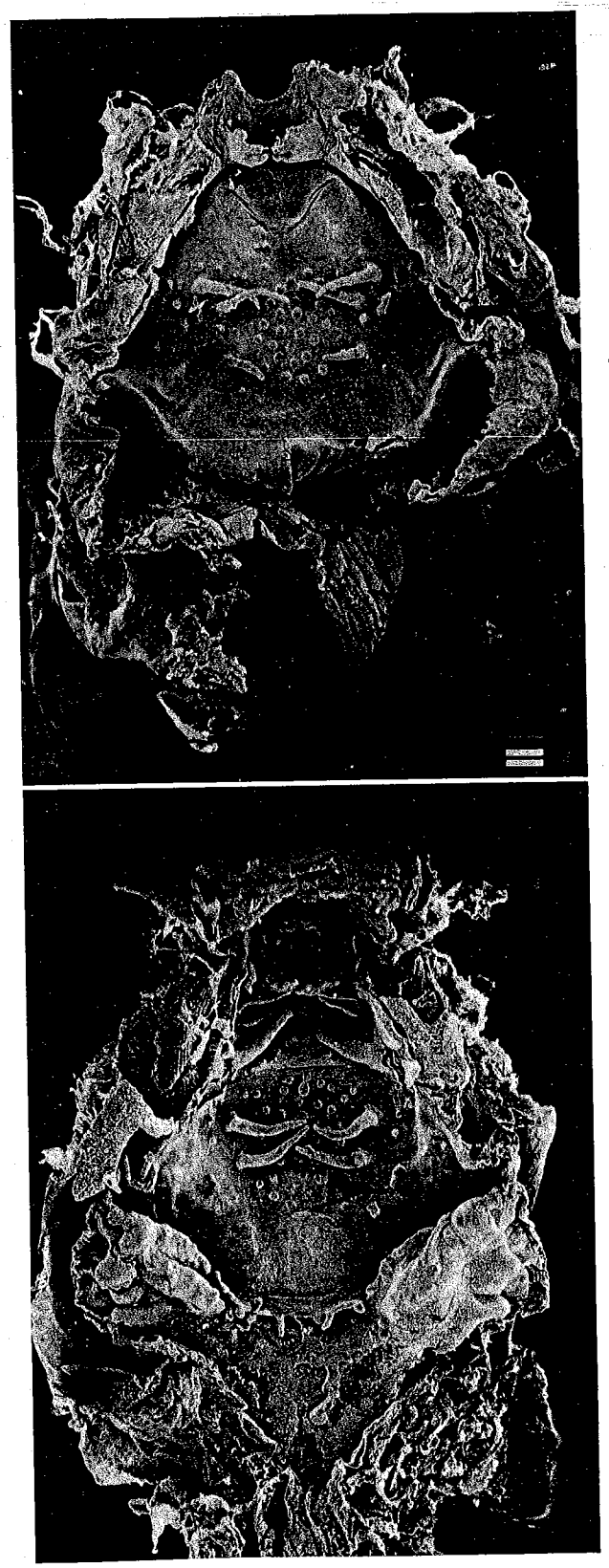


FIGURE 48.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Pseudophryne bibronii;* scale line = 2 mm.

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,

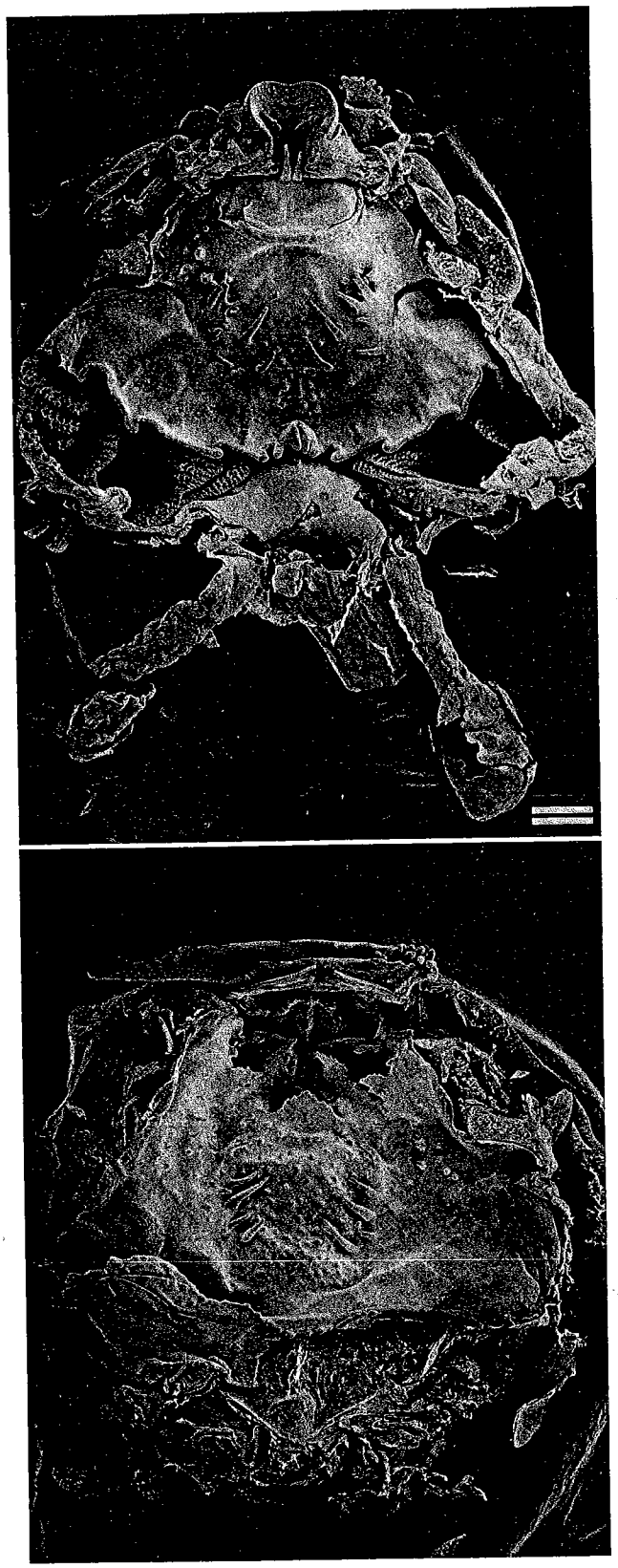


FIGURE 49.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Taudactylus diurnus;* scale line = 400 μm.

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 *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	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	–	+
Proceratophrys 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 *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	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 izecksohni	none under 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	+
Odontophrynus occidentalis	9	12	11	9	dense	tertiary	+
Paratelmatobius lutzii	10–11	12	9	5	low	tertiary	+
Physalaemus petersi	11	10	10	7	dense	quaternary	+
Physalaemus pustulosus	8	12	11	7	dense	tertiary	+
Pleurodema borellii	10	10	10	7	dense	some quaternary	+
Pleurodema brachyops	11	10	11	7	dense	some quaternary	+
Pleurodema bufonina	10	12	10	8	dense	some quaternary	+
Pleurodema cinerea	10	11	8	7	average	tertiary	+
Pleurodema nebulosa	8–13	11	9–10	8–10	average	tertiary	–
Proceratophrys appendiculata	6–8	7–8	5–8	4	less than average	tertiary	+
Proceratophrys 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)
Telmatobius marmoratus	12	11	11	9	average	some quaternary	+ (weak)
Thoropa miliaris	<4	5	7	4	low	tertiary	–
Thoropa 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	Dorsal velum: Papillate medial edge
Megaelosia goeldii	2–3	average	complex	1	15	–	+
Odontophrynus americanus	3	large	simple	1	8–15	–	+
Odontophrynus occidentalis	3	large	simple	1	8–15	–	+
Paratelmatobius lutzii	3	large	complex	1	~50	–	+
Physalaemus petersi	2	average	simple	1	6	–	–
Physalaemus pustulosus	2	average	simple	1	6	–	–
Pleurodema borellii	3	average	complex⁻	1	7	+	–
Pleurodema brachyops	3	average	complex⁻	1	4–5	–	–
Pleurodema bufonina	3	average	complex⁻	1	4–5	–	–
Pleurodema cinerea	5	small	complex	1	10–15	–	+ (tiny)
Pleurodema nebulosa	2	large	simple	1	18–20	+	–
Proceratophrys appendiculata	5–6	small	complex	1	30–35	–	+
Proceratophrys 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	–	–
Telmatobius marmoratus	6–7	average	simple⁺	1	8–10	–	–
Thoropa miliaris	1–2	small	complex	1	3–4	–	–
Thoropa 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

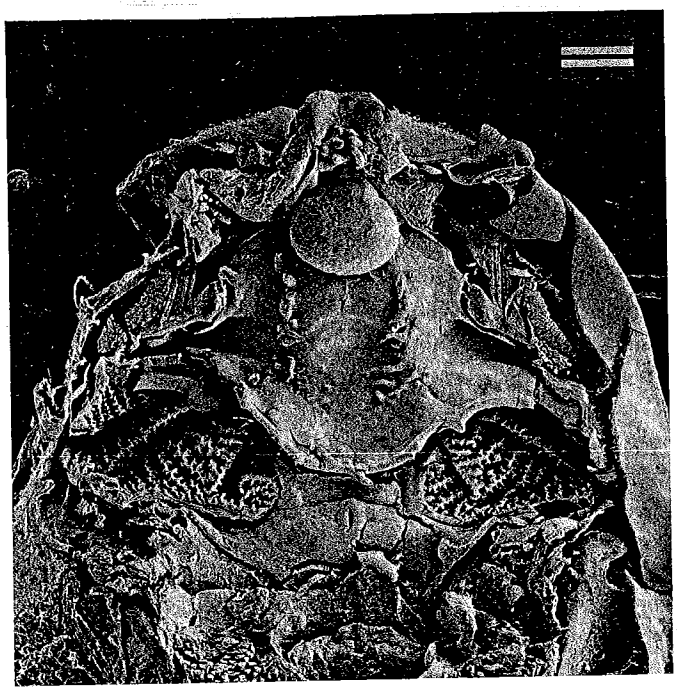


FIGURE 50.—SEM micrograph of floor of oral cavity of *Cycloramphus izecksohni;* scale line = 400 μm.

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

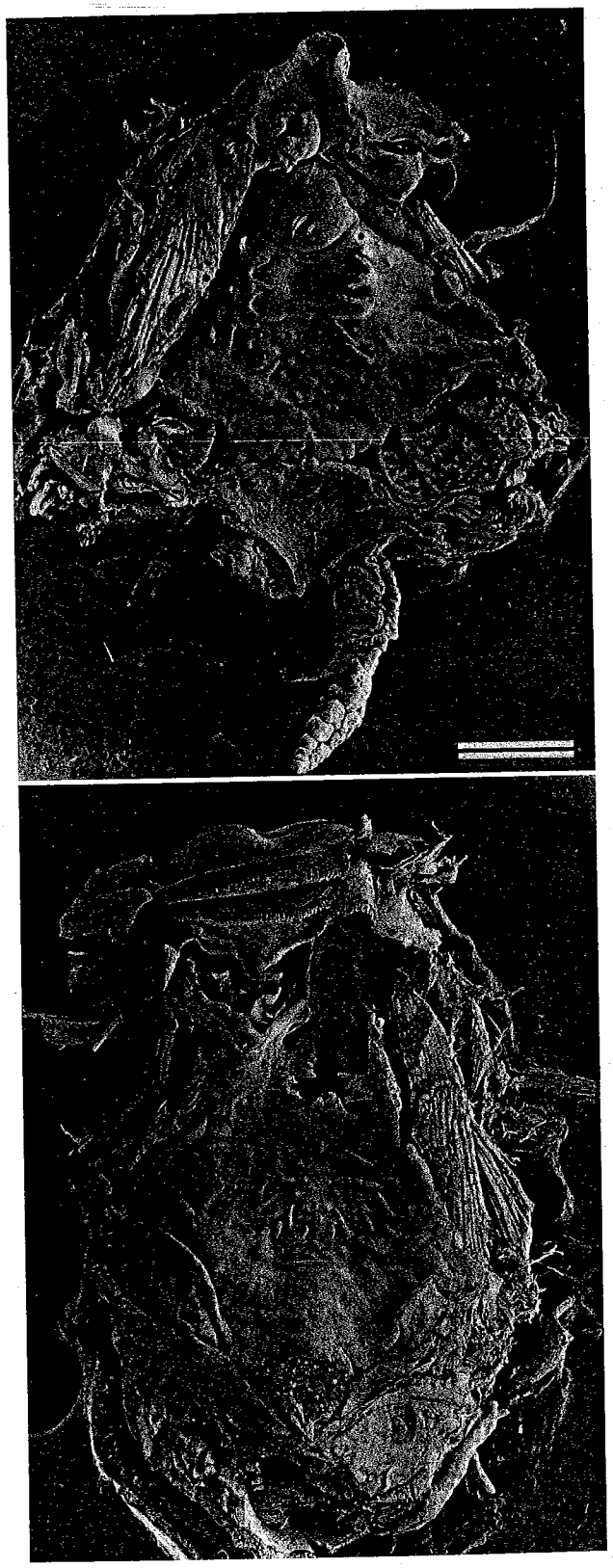


FIGURE 51.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Thoropa miliaris;* scale line = 1 mm.

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,

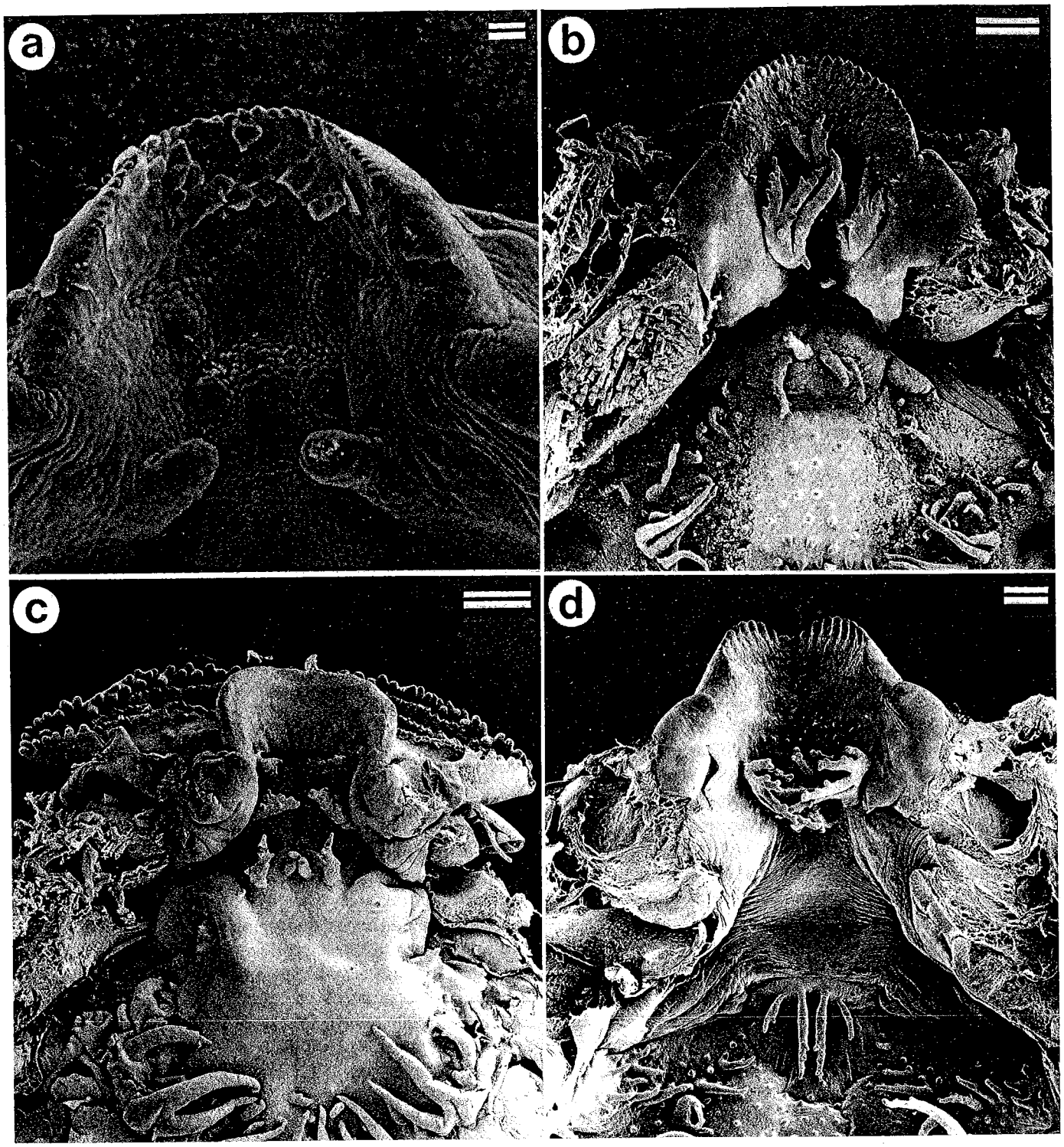


FIGURE 52.—SEM micrographs of front of floor of mouth in dorsal view for selected leptodactylid larvae: (*a*) *Adenomera marmorata* (scale line = 40 μm); (*b*) *Crossodactylus gaudichaudii;* (*c*) *Macrogenioglottus alipioi;* (*d*) *Megaelosia goeldii.* Scale lines for *b–d* = 400 μm. Compare with Figures 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.

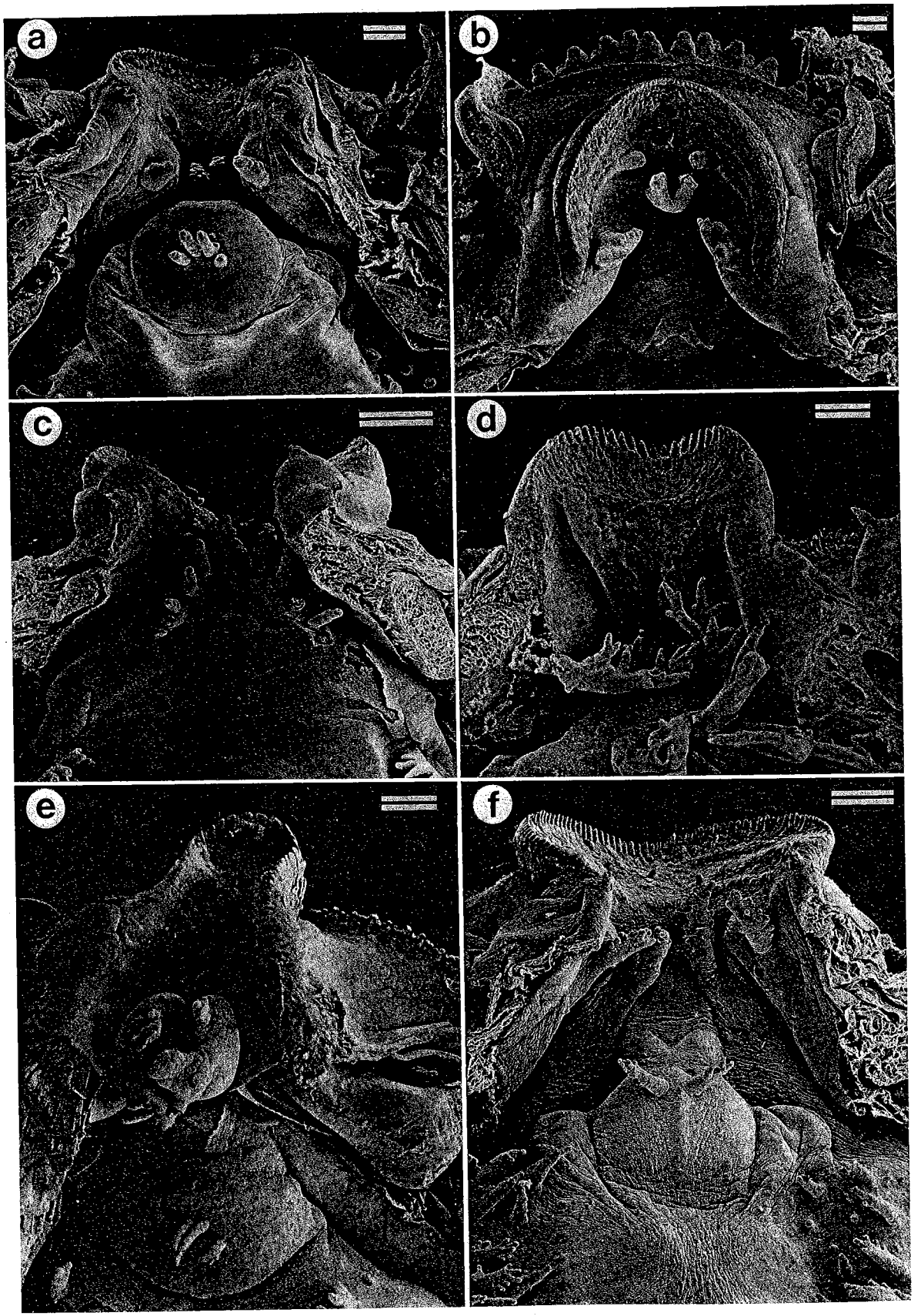
All tadpoles that are capable of suspension feeding have secretory tissue on the margins and under surfaces of the ventral velum (Figures 57–60). In most tadpoles, this tissue is organized such that secretory pits are on the free edge of the velum and secretory ridges are on the underside of the ventral 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;*

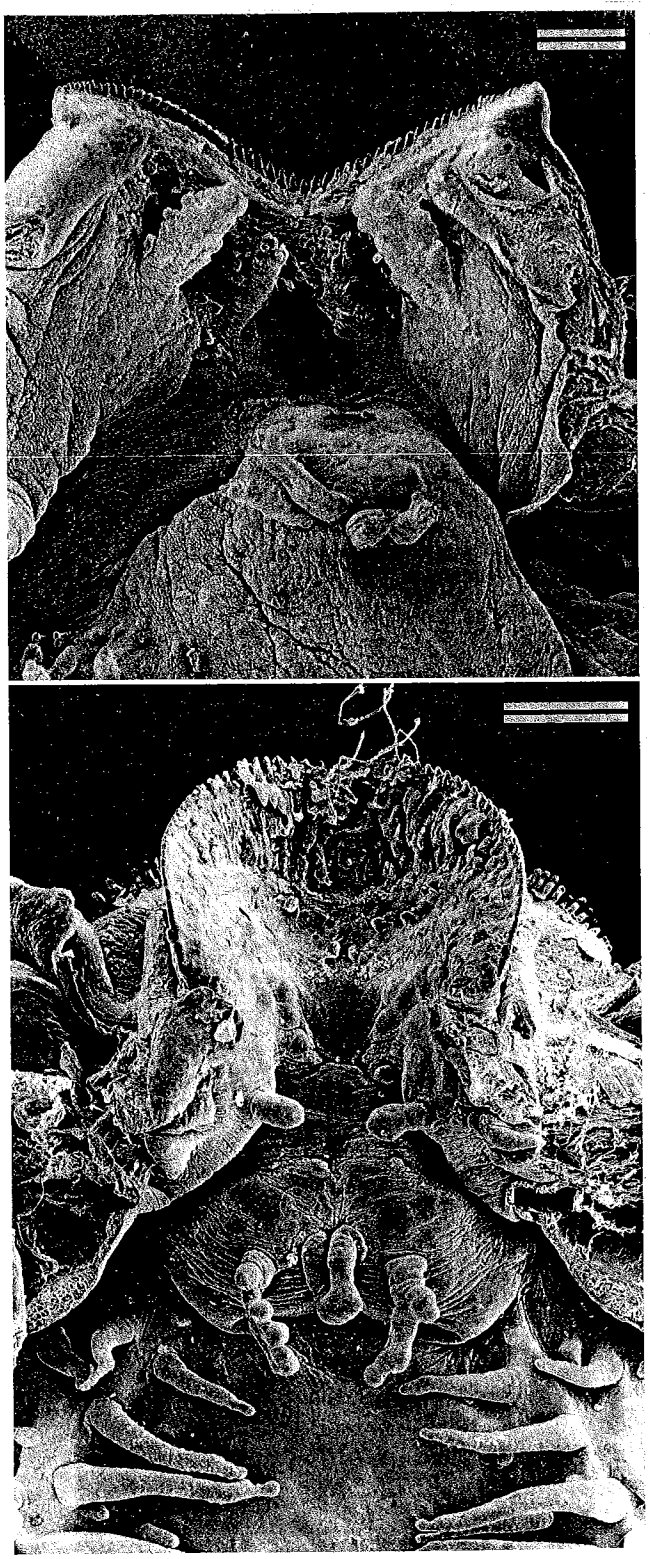


Figure 53.—SEM micrographs of front of floor of mouth in dorsal view for selected leptodactyloid larvae: (*a*) *Leptodactylus gracilis;* (*b*) *Leptodactylus knudseni;* (*c*) *Paratelmatobius lutzii;* (*d*) *Proceratophrys appendiculata;* (*e*) *Thoropa miliaris;* (*f*) *Platyplectron ornatus.* All scale 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 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.