

Notes on the tadpole of *Phrynohyas resinifictrix* (GOELDI, 1907). Buccopharyngeal and external morphology of a tree hole dwelling larva (Anura: Hylidae)

Bemerkungen zur Kaulquappe von *Phrynohyas resinifictrix* (GOELDI, 1907).
Buccopharyngeale und äußere Morphologie einer baumhöhlenbewohnenden Larve
(Anura: Hylidae)

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KURZFASSUNG

Äußere Gestalt, Mundfeld und buccopharyngeale Strukturen der wenig bekannten baumhöhlenbewohnenden Larve von *Phrynohyas resinifictrix* (GOELDI, 1907) werden beschrieben und mit den entsprechenden Bildungen bei anderen arboricoler Hylidenlarven verglichen.

Die Ausprägung der Buccopharyngealregion weist bei *P. resinifictrix* im allgemeinen auf deutliche Reduktion jener Strukturen hin, die in Zusammenhang mit microphager, filtrierender Ernährungsweise und Kiemenatmung stehen. Die bemerkenswerte Größe von Glottis und Lungen ist mit vermehrter Luftatmung, weitere Modifikationen sind mit macrophager Ernährungsweise korreliert. Aufgrund ihres Darminhaltes sind die Larven detritusfressende (nekrophage), gelegentlich fleischfressende (zoophage) Formen, offensichtlich makrophage Generalisten.

ABSTRACT

External morphology, oral disk, and buccopharyngeal structures of the little known tree hole dwelling larva of *Phrynohyas resinifictrix* (GOELDI, 1907) are described and discussed in comparison with corresponding structures of other arboreal hylid larvae.

Buccopharyngeal features of *P. resinifictrix* in general show clear reduction of structures associated with microphagous filter-feeding and branchial respiration; marked development of glottis and lungs are correlated with increased areal respiration; special modifications are associated with macrophagous nutrition. According to the larval gut contents *P. resinifictrix* is a detritivorous (necrophagous), facultatively carnivorous (zoophagous) form, apparently a macrophagous generalist.

KEYWORDS

Phrynohyas resinifictrix, tadpole, morphology

INTRODUCTION

Phrynohyas resinifictrix (see cover illustration), a hylid frog restricted to scattered localities in lowland primary forests (ZIMMERMANN & HÖDL 1983; HÖDL 1991), was described first by GOELDI (1907) from the lower Amazon Basin (Maracanã River, Brazil). Later on, this treefrog predominantly was synonymized (MÜLLER 1912; MIRANDA-RIBEIRO 1926; MERTENS 1957; DUELLMAN

1956, 1970, 1971, 1977; CEI 1980) with *Phrynohyas venulosa* (LAURENTI, 1768), a species widespread in Middle and South American open lowlands, but similar in adult morphology.

Specific distinctiveness of the taxon *P. resinifictrix* was discussed by LUTZ (1973), but was not definitely recognized before LESCURE (1976), who specified morphological, ecological and ethological

differences between *resinifictrix* and *venulosa*.

Furthermore, coloration, pattern and calling behaviour of *P. resinifictrix* were analyzed and found to be different from that in *P. venulosa* (ZIMMERMANN & HÖDL 1983; HÖDL 1991).

While the larva of *P. venulosa* was described in detail (PYBURN 1967; ZWEIFEL 1964; DUELLMAN 1970; CEI 1980), nothing is known about the tadpoles of other *Phrynohyas* species except that of *P. resinifictrix*, to the knowledge of which comparatively little has been hitherto contributed:

GOELDI (1907) reported on the frog's reproductive behaviour high up in the trees of the rain forest: The mature animal was said to line tree cavities with resins (*resinifictrix*!), gathered by the animal from resinous trees, and, after this, should lay its eggs into these sealed, water-filled cavities, where the tadpoles develop.

Apparently, the doubts of subsequent scientists referred to the story as a whole, not only to the active use of resin, which in fact was reported erroneously (e. g. MÜLLER 1912; WUNDER 1932; MERTENS 1957; LUTZ 1973; ZIMMERMANN & HÖDL 1983).

Thus, GOELI's observation con-

cerning the arboreal breeding site of *P. resinifictrix* was further on ignored.

As a matter of fact breeding in such ("nightly plugged and dayly reopened" - HÖDL 1991) tree cavities appears to be a very constant behavioural character of *P. resinifictrix* (HERO 1990; HÖDL 1991), whereas *P. venulosa* exclusively breeds in shallow temporary ponds on the ground (ZWEIFEL 1964; DUELLMAN 1970).

The well developed tadpole (GOSNER stage 39) of *P. resinifictrix* including a rough closeup of the oral disk were most recently depicted by HERO (1990), accompanied by some diagnostic morphological and chromatic characters.

Seven larvae of *P. resinifictrix*, generously entrusted to the author of this paper by W. HÖDL (Vienna), now give the opportunity to contribute to the morphology and to speculate on the biology of this little known tadpole.

For better understanding of peculiarities in *P. resinifictrix* larval morphology corresponding structures are compared to those of other hylid tadpoles which develop in tree holes or phythothelms as *Hyla dendroscarta* TAYLOR, 1940, *H. bromeliacea* SCHMIDT, 1933, *H. zeteki* GAIGE, 1929, *Anothea spinosa* (STEINDACHNER, 1864), and *Osteopilus brunneus* (GOSSE, 1851).

MATERIAL AND METHODS

On November 11th, 1988, 8 tadpoles of *P. resinifictrix* were collected from a treehole of the primary forest of Panguana, Peru, by W. HÖDL and M. HENZL. Descriptions of the locality and of the males' call sites (which probably are identical with the larval habitat) are given by ZIMMERMANN & HÖDL (1983) and by HÖDL (1991).

Seven tadpoles were immediately preserved in formalin (10%), one larva was kept until metamorphosis to guarantee correct determination. All of them are now stored in the Museum of Natural History

in Vienna (NMW 32779: 1-8).

Measurements were made with the optical digital display length-measuring unit WILD MMS 235. Micrographs were taken by means of scanning electron microscopy (ZEISS DSM 950) after ethanol desiccation, critical point drying, and gold sputter coating.

Terminology of the buccopharyngeal structures follows WASSERSÜG (1976, 1980), that of the external mouthparts and body proportions BOULENGER (1891) and GRILLITSCH (1984). Abbreviations are explained in figure legend 2.

RESULTS

External appearance

The tadpole of *P. resinifictrix* (well depicted in HERO 1990) is a typical hylid larva with the tail almost twice as long as the body, the upper caudal crest not markedly extending onto the back, the spiracular tube sinistral, ventrolateral, directing backward and upward, the vent tube opening median (as already stated by HERO 1990), sometimes describing a curve to the right; the eyes are in a moderate lateral position, not visible from below. In its body shape the well developed tadpole of *P. resinifictrix* is the typical lentic type, with a slightly attenuate and depressed trunk and a tail fin of moderate width, tapering to a (sometimes rounded) point. The larvae from Panguana show the following correlations of stages and sizes (Table 1):

Table. 1: Correlation of stages and sizes (TL mm) in seven *Phrynohyas resinifictrix* tadpoles of the Panguana series (NMW 32779: 1-7).

Tab. 1: Die Gesamtlänge (TL mm) in bezug zum Entwicklungsstadium bei den sieben *Phrynohyas resinifictrix* Larven der Panguana Serie (NMW 32779: 1-7).

Specimen No.	Stage	Size (TL mm)
1	28	21.0
2	32	27.7
3	35	28.5
4	36	30.1
5	36	30.3
6	37	31.0
7	38	34.3

The measurements taken from seven tadpoles of the Panguana series are listed in Table 2. These data were not further processed statistically because of the smallness of the series and the low number of specimens per stage.

Comparison of the data of Table 2 with the metric values given by ZWEIFEL (1964) and PYBURN (1967) reveals the following differences between *P. resinifictrix* and *P. venulosa* larvae:

Comparable developmental stages seem to be longer in *P. venulosa* than in *P.*

resinifictrix. This is true in particular for stages >30, where the differences in total length (TL) were found to be around 5.0 mm at any given stage. The maximum TL known for *P. venulosa* larvae (49.4 mm, stage 41 - ZWEIFEL 1964) exceeds that of *P. resinifictrix* tadpoles (38.7 mm, stage 39 - HERO 1990) by 10.7 mm. In early developmental stages (<30) it appears to be the reverse situation.

Ratio VT/SV which represents the proportion of body and tail varies from 1.5 to 1.77 in *P. resinifictrix*, and from 1.61 to 2.19 in *P. venulosa* (calculated from data of ZWEIFEL 1964 and PYBURN 1967), indicating a comparably longer tail in the latter species.

Ratio DT/SV which indicates the relative depth of the tail was found to range from 0.59 to 0.74 in *P. venulosa*, and from 0.48 to 0.54 in *P. resinifictrix*, the latter being the species with the less deep tail fin.

In *P. resinifictrix* the diameter of the eye bulb (DE) is some 60% smaller than in comparable stages of its congener.

The coloration, not well preserved in the formalin specimens, is said to be dark olive on the body, silvery on the belly, and transparent on the tail fin (HERO 1990).

Dark blotches on the dorsum as can be seen in the drawing in HERO (1990) were not found among the specimens on hand, but, to a variable extent, there were fine brown sprinkles all over the body and tail forming a slight reticulation on the upper caudal crest, and some pigment aggregations in the region of the spiraculum and the vent tube.

One of the specimens collected on November 11th by HÖDL & HENZL measured 14.4 mm from snout to vent on November 28th, the day it completed metamorphosis. This TL observed is assumed to be close to the lower limit of the TL of newly metamorphosed froglets of *P. resinifictrix*, as the tadpole was kept in the original tree hole water until metamorphosis without additional food supply.

Table 2: Morphometric data of seven *Phrynohyas resinifictrix* tadpoles of the Panguana series (values given in mm). N - specimen number, TL - total length, SV - snout-vent-length, VT - distance: vent - tip of tail (= length of tail), DT - maximum depth of tail, UC - maximum depth of upper crest, LC - maximum depth of lower crest, SU - distance: snout - insertion of upper crest, SS - distance: snout - spiracle, VS - distance: vent - spiracle, PP - interpapillary distance, NN - internarial distance, RN - rostral distance, NP - naris-pupillary distance, DN - diameter of naris, DE - diameter of eye bulb, OD - width of oral disk, UR1(2) - first (second) upper tooth row, UR1(2)I - median interruption of first (second) upper tooth row, UR2F - fragment of second upper tooth row, LR1(2-4) - first (second - fourth) lower tooth row, LR1(2-4)I - median interruption of first (second - fourth) lower tooth row, (numbers in parentheses) - number of fragments, MP - number of marginal peribuccal papillae, IMP - number of inframarginal papillae.

Tab. 2: Meßwerte von sieben *Phrynohyas resinifictrix* Larven der Panguana Serie (Längen in mm). N - laufende Nummer, TL - Gesamtlänge, SV - Kopf-Rumpf-Länge, VT - Schwanzlänge, DT - Schwanzhöhe, UC - Maximalhöhe des oberen Schwanzsaumes, LC - Maximalhöhe des unteren Schwanzsaumes, SU - Entfernung: Schnauzenspitze - Insertion des oberen Schwanzsaumes, SS - Entfernung: Spirakulum - Schnauzenspitze, VS - Entfernung: Spirakulum - After, PP - Pupillenabstand, NN - Nasenlochabstand, RN - Entfernung: Nasenloch - Schnauzenspitze, NP - Entfernung: Nasenloch - Pupille, DN - Nasenlochdurchmesser, DE - Augendurchmesser, OD - Mundfeldbreite, UR1(2) - erste (zweite) obere Zahnreihe, UR1(2)I - mediane Unterbrechung der ersten (zweiten) oberen Zahnreihe, UR2F - Teilstück der zweiten oberen Zahnreihe, LR1(2-4) - erste (zweite - vierte) untere Zahnreihe, (Ziffern in Klammern) - Anzahl der Teilstücke, MP - Anzahl randständiger Mundfeldpapillen, IMP - Anzahl submarginaler Mundfeldpapillen.

N	TL	SV	VT	DT	UC	LC	SU	SS	VS	PP	NN	RN	NP	DN	DE	OD
1	21.0	8.4	12.6	4.0	1.0	0.7	4.2	4.5	3.9	2.7	2.5	1.3	1.2	0.2	0.6	1.7
2	27.7	10.4	17.3	5.6	1.7	1.5	7.6	5.7	4.7	4.0	3.3	1.3	1.7	0.4	1.1	2.5
3	28.5	10.8	17.7	5.6	1.5	1.8	7.3	5.8	5.0	4.0	3.0	1.2	1.6	0.3	1.0	1.8
4	30.1	11.6	18.5	5.8	1.6	1.8	4.8	6.7	4.9	4.4	3.2	1.7	1.7	0.3	1.2	2.5
5	30.3	11.7	18.6	5.7	1.4	1.8	6.7	6.4	5.3	4.3	3.3	1.5	1.7	0.3	1.1	2.4
6	31.0	11.7	19.3	6.2	1.8	1.8	7.5	7.0	4.7	4.4	3.1	1.4	1.8	0.3	1.2	2.6
7	34.3	12.4	21.9	6.6	1.7	1.8	7.0	6.7	5.7	4.3	3.5	1.6	1.4	0.4	1.3	2.6

N	UR1	UR1I	UR2F	UR2I	LR1	LR1I	LR2	LR2I	LR3	LR3I	LR4	LR4I	MP	IMP
1	1.42	0.0	0.55	0.36	0.80	0.0	0.91	0.0	0.88	(3)	-	-	60	10
2	2.20	0.0	1.29	0.10	1.40	0.0	1.47	0.0	1.17	0.0	1.48	(5)	56	16
3	1.41	0.0	0.76	0.30	1.13	0.0	1.05	0.0	1.05	0.0	-	-	57	10
4	2.14	0.0	1.11	0.34	1.38	0.0	1.65	0.0	1.29	0.0	-	-	57	7
5	2.19	0.0	1.07	0.22	1.42	0.0	1.52	0.0	1.35	0.0	-	-	59	8
6	2.19	0.0	1.15	0.32	1.39	0.0	1.42	0.0	1.43	0.0	1.28	(4)	63	16
7	2.22	0.0	1.15	0.42	1.71	0.0	1.72	0.0	1.65	0.0	1.37	(5)	81	28

Oral disk (Fig. 1)

The moderate sized oral disk is located anteroventrally displaying a round elliptical contour when fully expanded (not as in HERO 1990). Except for a narrow dorsal (upper) median gap, the margin of the oral disk is bordered completely by papillae arranged, mostly alternating, in one to three rows. From the lateral corner of the oral disk a medially directed row of 5 to 7 submarginal papillae is extending towards the lateral basis of the keratinized beak on each side, pretending a dense papillation of the lateral peribuccal area in the not expanded oral disk. Between 13 and 22 papillae per mm line the posterior margin; all marginal papillae show dark cores.

The upper jaw sheath is broadly arched, the lower somewhat V-shaped. Both have broad dark keratinized edges which

are finely serrate with 40 to 45 acutely pointed keratodonts per mm. The height of serration is about 45 µm. Jaw musculature in larval *P. resinifictrix* appears not to be extremely heavy, but has not been studied in detail.

In tadpoles of stages 28-41 there are two anterior labial tooth rows of about equal lateral extension; the first (UR1) is uninterrupted, a median gap in the second (UR2), variable in size, ranges from about 4% to 33% of the total row length, measured as if it was continuous. The (usually four) posterior tooth rows decrease slightly in length from the first (outermost) through the fourth; the outermost row (LR1) is the last to develop. In about 50% of the cases it is subdivided into isolated parts, and in the other 50% it is completely absent even in advanced developmental stages. A hardly visible median inter-

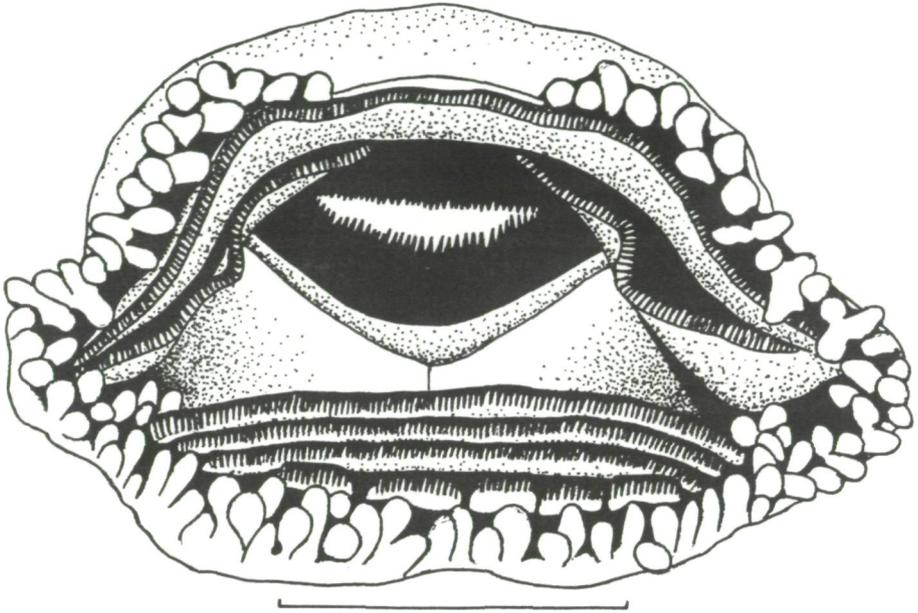


Fig. 1: Oral disk of *Phrynohyas resinifictrix* (GOELDI, 1907) (stage 38; Panguana, Peru). Bar represents 1 mm.

Abb. 1: Mundfeld von *Phrynohyas resinifictrix* (GOELDI, 1907) (Stadium 38; Panguana, Peru). Balkenlänge entspricht 1 mm.

ruption of the innermost lower tooth row (LR4) may or may not be present. According to HERO (1990) the tooth row formula is 2/3-5, meaning that the number of tooth rows in the lower lip varies from 3 to 5. The density of teeth is 55 to 65 per mm, and about the same in all rows. The total height of a single keratodont (Fig. 2) is about 40 μm ; its apical portion is spatulate with a margin formed by 12-13 acute denticles.

Tadpoles of *P. resinifictrix* can be distinguished from those of *P. venulosa* by their labial dentition and chromatic peculiarities (comparative data were taken out of ZWEIFEL 1964; PYBURN 1967; DUELLMAN 1970). The number of labial tooth rows in *P. venulosa* tadpoles of different localities varies from 3 to 4 in the anterior, and from 5 to 7 in the posterior labium. In all cases the innermost anterior (=superior, upper) tooth row is - to a variable extent - interrupted medially; the following tooth row is continuous, and the

(1-2) outermost tooth rows are frequently broken up into isolated parts but always present a wide median gap. In the lower (=posterior, inferior) labium the innermost tooth row is constantly bipartite with or without a very short median gap. The following rows may or may not be broken up into isolated parts which seems to occur most frequently in the outermost 2 - 3 tooth rows.

As far as the coloration is concerned, there is a clear longitudinal striation observed on the tail of tadpoles of *P. venulosa* which is not present in *P. resinifictrix*.

Buccal floor (Fig. 3)

In the buccal floor the prelingual area shows three more or less papilliform pustulations on each side (called ventral infrastroral papillae by VIERTTEL 1982). They are anteriorly directed and rise near

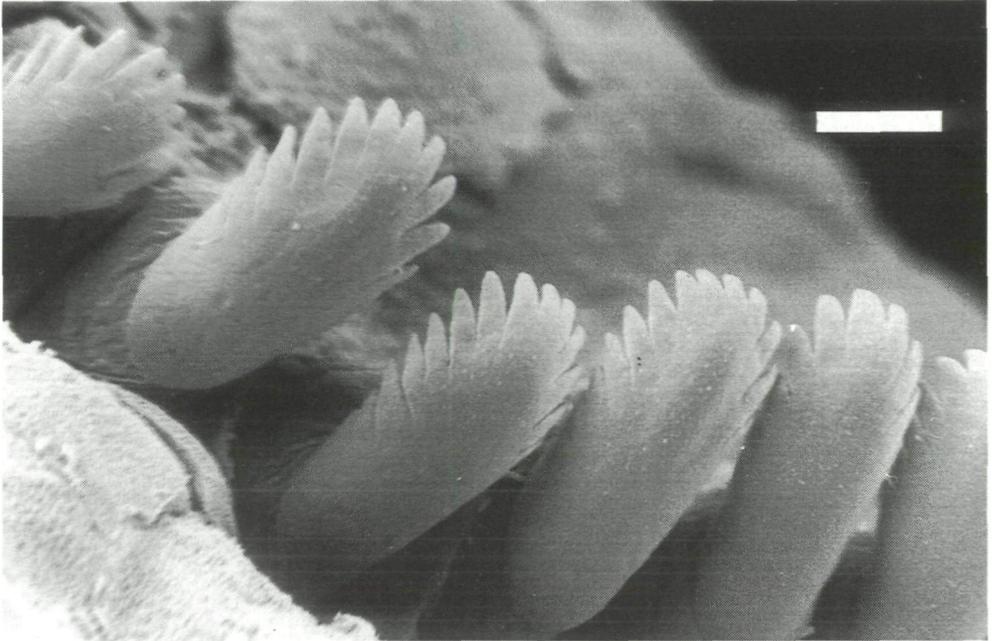


Fig. 2: Keratodonts of *Phrynohyas resinifictrix* (GOELDI, 1907) (stage 38; Panguana, Peru). Bar represents 10 μm .

Abb. 2: Lippenzähnen von *Phrynohyas resinifictrix* (GOELDI, 1907) (Stadium 38; Panguana, Peru). Balkenlänge entspricht 10 μm .

the lateral basis of the keratinized beak.

About halfway the longitudinal extension of the area, 2 symmetric, widely spaced pairs of infralabial papillae are distinct: the two major ones are elongate with 4 or 5 secondary broadly based marginal papillae (Fig. 4), and medially accompanied by one solitaire elongate cone each.

There are two medium-sized, typically shaped lingual papillae. The tongue anlage appears to be less distinct than in other ranoid tadpoles of comparative developmental stage. The buccal floor arena is elongate, comparable to a high trapezium, and in that resembles that of *H. dendroscarta* and *H. phlebodes* STEJNEGER, 1906 as figured in WASSERSUG (1980).

Not even traces of papillae do occur in the oral half of the arena. On a level with the apical margins of the buccal pockets there are 4 to 5 conspicuous, tall, tapering papillae per side. They are reduced in height towards the midline and arranged in an anteriorly concave semicir-

cular arc, seeming to protect the buccal pocket deepening and to guide food particles to the esophageal entrance. Except for these, papillae are scarce in the caudal portion of the buccal floor arena, mostly forming faint pustulations, rarely stout cones.

The buccal pockets are slightly longitudinally orientated, deep and narrow slits. The prepocket region proper completely lacks papillae.

The free surface of the ventral velum is slightly reduced compared to its normal extension in typical pond larvae and in that appears to be still a functional valve and quite similar to the ventral velum in *H. dendroscarta* (WASSERSUG 1980).

The velar margin is gently curved, concave posteriorly, corresponding to the filter cavities; slightly prominent marginal projections are reaching out caudally. No spicular support is evident. There is a thickened glandular zone of distinct secretory pits on the ventral margin of the velum.

The median notch is conspicuously

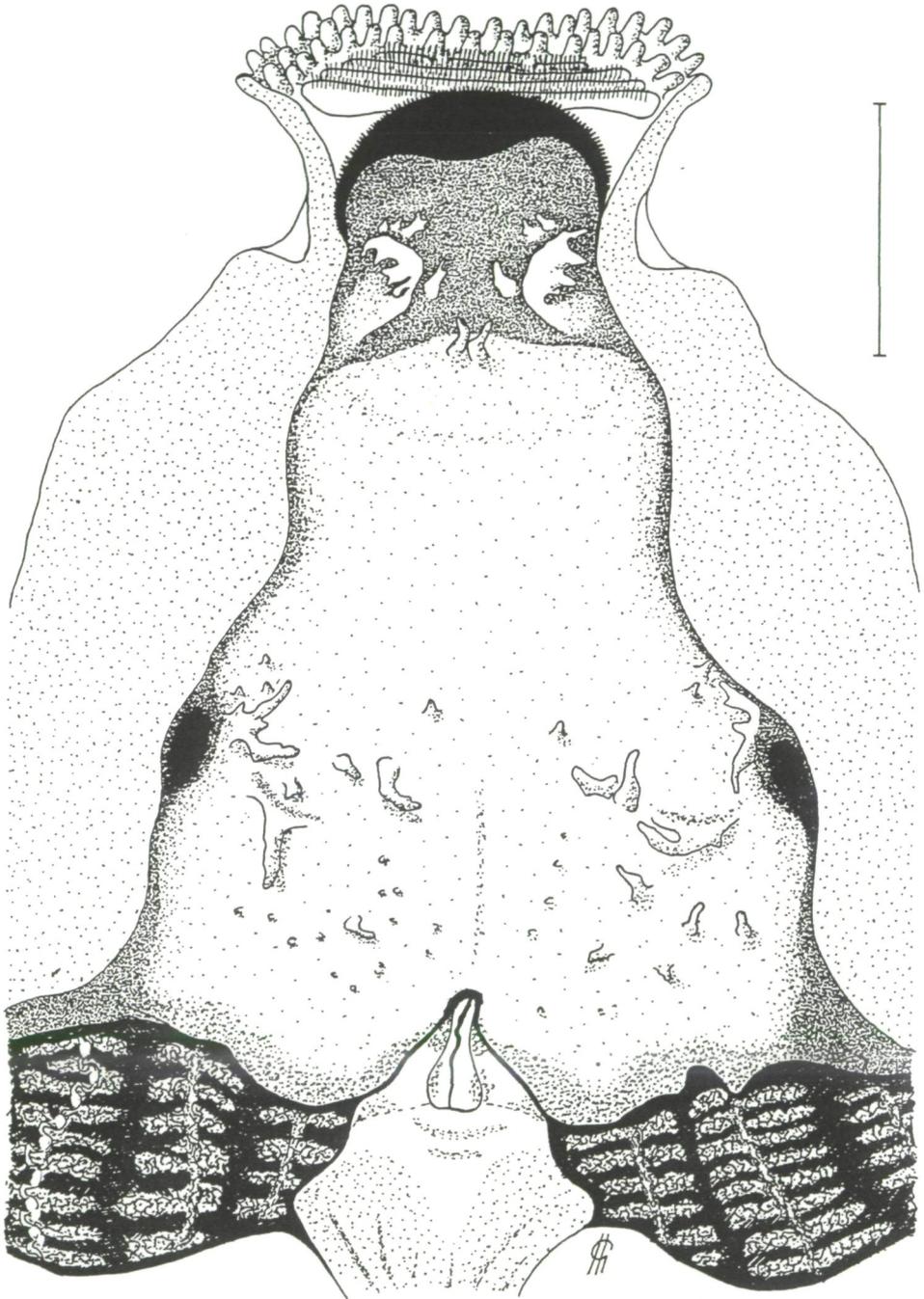


Fig. 3: Floor of the buccopharyngeal cavity of *Phrynohyas resinifictrix* (GOELDI, 1907) (stage 38; Panguana, Peru) drawn from SEM micrographs. Bar represents 1 mm.

Abb. 3: Boden der Buccopharyngealhöhle von *Phrynohyas resinifictrix* (GOELDI, 1907) (Stadium 38; Panguana, Peru) gezeichnet nach REM-Photos. Balkenlänge entspricht 1 mm.

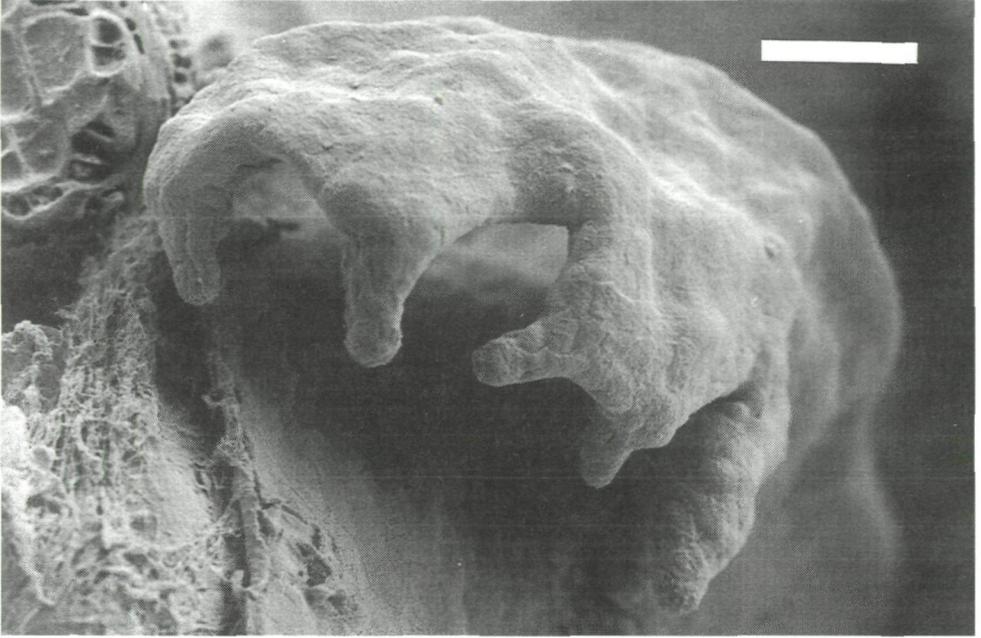


Fig. 4: Infralabial palp of *Phrynohyas resinifictrix* (GOELDI, 1907) (stage 38; Panguana, Peru). Bar represents 50 μ m.

Abb. 4: Infralabial-Palpus von *Phrynohyas resinifictrix* (GOELDI, 1907) (Stadium 38; Panguana, Peru). Balkenlänge entspricht 50 μ m.

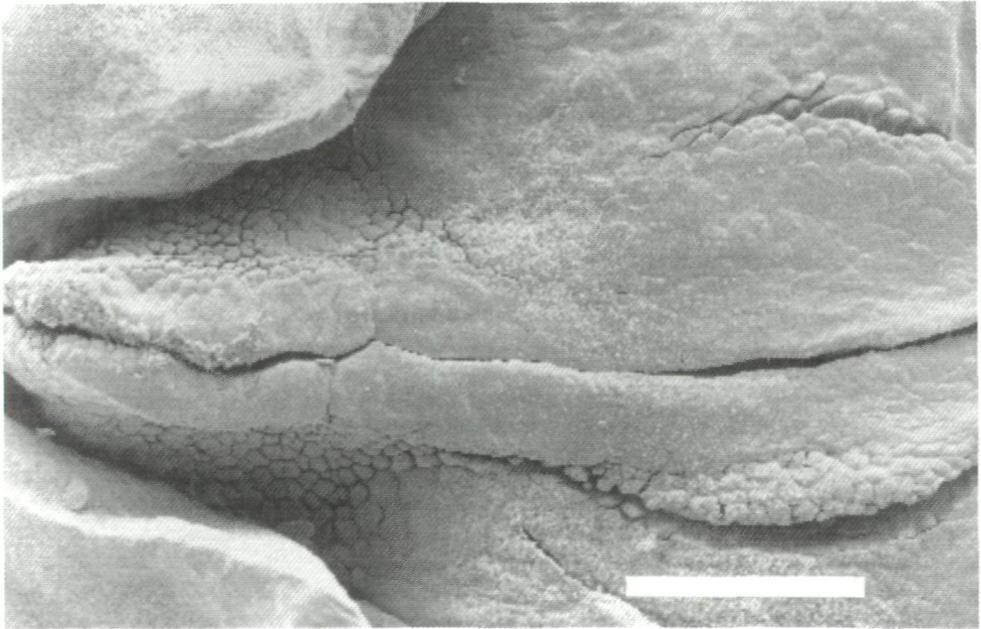


Fig. 5: Glottis and median notch of ventral velum of *Phrynohyas resinifictrix* (GOELDI, 1907) (stage 38; Panguana, Peru). Bar represents 100 μ m.

Abb. 5: Glottis und Medianbucht des ventralen Velums von *Phrynohyas resinifictrix* (GOELDI, 1907) (Stadium 38; Panguana, Peru). Balkenlänge entspricht 100 μ m.

smoothedged and V-shaped; its cranial indentation, is completely giving space to the exceptionally large, anteriorly directed glottis (Fig. 5) and almost seems to divide the ventral velum into two separate symmetrical portions. The total extension of the median notch occupies about one third of the velar marginal length. The cranial dilatation of the median notch is unimportant and leaves the laryngeal disk fully exposed.

The glottal slit is markedly long, measuring about 1/6 of the total sagittal length of the buccal floor arena, a ratio which is almost attained by *O. brunneus* only (micrographs in LANNOO & al. 1987). Further corresponding values on species with a more or less exposed glottis were taken from figures in WASSERSUG (1980), and do not exceed 1/9, even in its extremes seen in Discoglossidae, *A. spinosa*, and *H. phlebodes*.

The glottal lips are well developed. The laryngeal disk appears slightly elevated.

Lung sacs are especially large, their terminal apices reaching as far as the most caudal gut spiral curvature.

The lumen of the esophageal funnel is remarkably extended, suited to lead rather large food particles to the gastrointestinal tract; its width somewhat equals that of the internal buccal opening.

Buccal roof (Fig. 6)

In the buccal roof the prenarial arena appears spacious; its length almost equals its width. There is a peculiar, pustulate, anteriorly directed, V-shaped prenarial ridge (Fig. 7). Its both legs rise immediately in front of the anterior choanal edges, converge in continuation of the the main choanal axes, join each other at about half the distance between the median basis of the beak and the most oral part of the median ridge, and there form a distinct, knoblike, blunt elevation, which in stereomicroscopic examination appears to be a dark pigmented, keratinized, rounded spot.

The internal nares form elongate

slits, directed postero-laterally. The anterior narial walls are slender, with two tiny pustulations on the anterolateral margin, one or two pustulate papillae at the lateral corners, and a slightly elevated, stout projection rising from the anterior edge of the opening on each side. The posterior walls of the nares are distinct and apparently suitable to act as valves. No narial wall projections could be ascertained.

The postnarial arena shows one or two slightly elongate papillae, and 5 to 6 minor pustulations per side. Lateral to the median ridge there are two symmetrical, broadly based, palp-like lateral ridge papillae bearing two or three conical secondary pustulations.

The palps are almost as large as the average sized median ridge, and dissimilar to the corresponding attenuate structures in *A. spinosa* and *H. dendroscarta* (WASSERSUG 1980). In *O. brunneus* they are completely absent.

The median ridge is an anteriorly directed trapezoid flap with one median and two lateral pustulations on the anterior edge and one tiny cusp in the middle of its lateral margins on each side.

Corresponding to the comparatively poor papillation of the buccal floor arena, the central buccal roof arena is bare and the adjacent area is scattered with very weak lateral roof pustulations only. A glandular zone is indistinct.

The dorsal velum is distinct which is the usual situation. There is only one species known (*A. spinosa*) that lacks a dorsal velum (WASSERSUG 1980).

The branchial baskets show average size and configuration, but the filter mesh is clearly reduced (Fig. 8). On each filter plate the filter rows number 6 to 9 which is quite usual. But, they are comparatively wide spaced, reduced in height, and partially shortened in length. The filter canals are completely open and at least as wide as the filter rows which almost show no tertiary folds. The diameter of the filter niches is about 25 μm . The size of the internal gills is about half of that in average pond-type larvae.

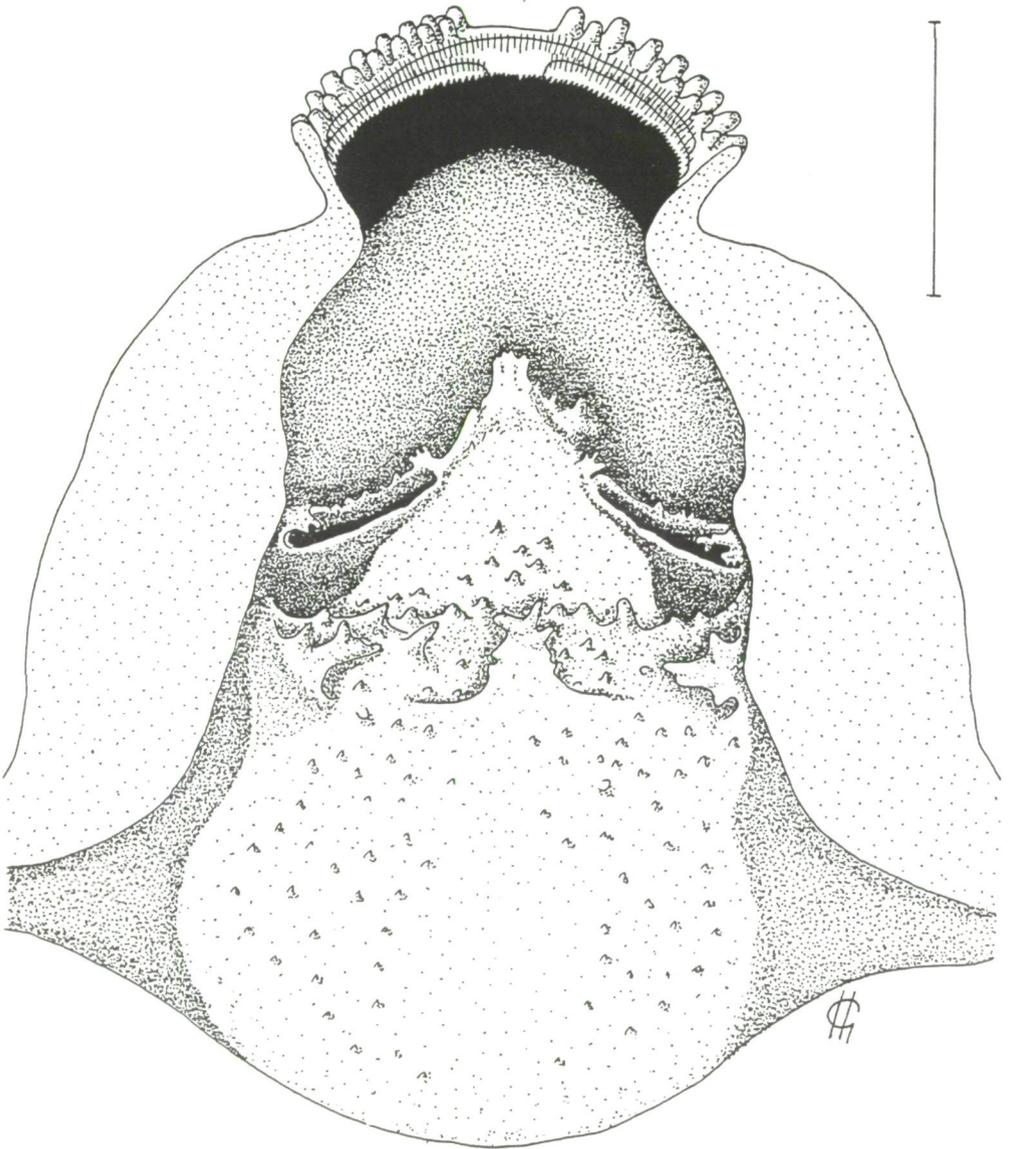


Fig. 6: Roof of the buccopharyngeal cavity of *Phrynohyas resinifictrix* (GOELDI, 1907) (stage 38; Panguana, Peru) drawn from SEM micrographs. Bar represents 1 mm.

Abb. 6: Dach der Buccopharyngealhöhle von *Phrynohyas resinifictrix* (GOELDI, 1907) (Stadium 38; Panguana, Peru) gezeichnet nach REM-Photos. Balkenlänge entspricht 1 mm.

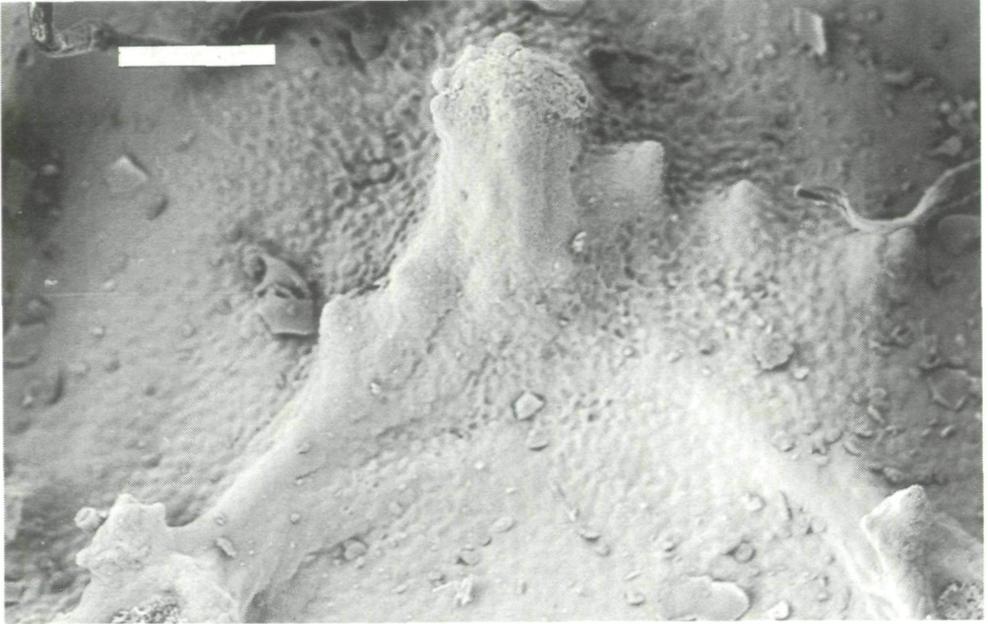


Fig. 7: Prenarial ridge of *Phrynohyas resinifictrix* (GOELDI, 1907) (stage 38; Panguana, Peru). Bar represents 100 μm .

Abb. 7: Prächoanaler Kamm von *Phrynohyas resinifictrix* (GOELDI, 1907) (Stadium 38; Panguana, Peru). Balkenlänge entspricht 100 μm .

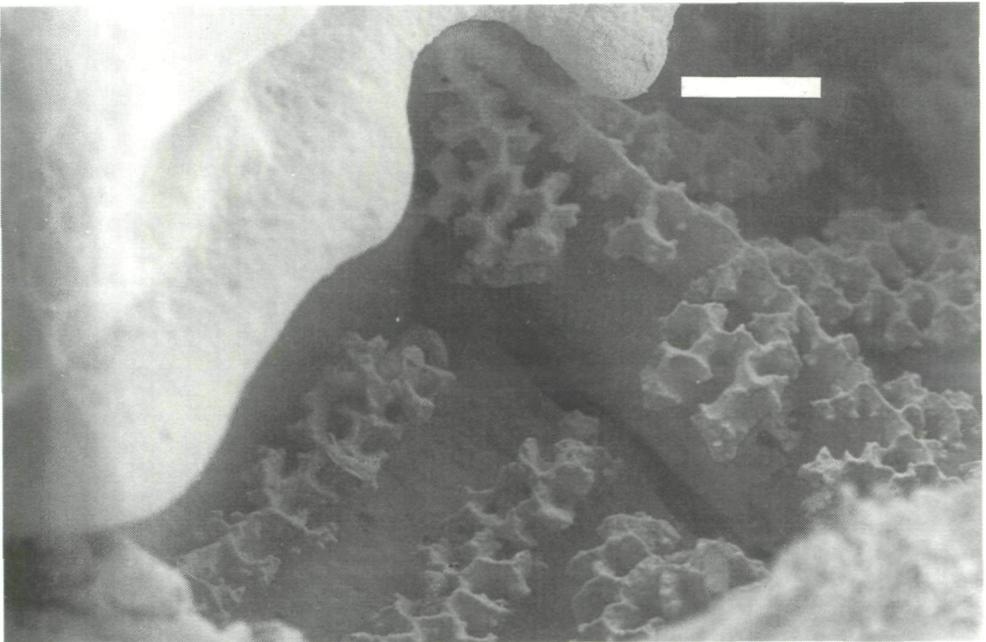


Fig. 8: Gill filter of *Phrynohyas resinifictrix* (GOELDI, 1907) (stage 38; Panguana, Peru). Bar represents 100 μm .

Abb. 8: Kiemenfilter von *Phrynohyas resinifictrix* (GOELDI, 1907) (Stadium 38; Panguana, Peru). Balkenlänge entspricht 100 μm .

Gut contents

Gut contents consisted predominantly of flat-spread or voluminous plant fragments, up to a length of 0.55 mm and a width of 0.25 mm, but mostly 1/5 to 1/10

of that size; thready particles even can be clearly longer; the amount of wooden material equals that of leaves and other macrophytal matter. Frequently fungous hyphes, and rarely nematodes (0.6 to 1.0 mm long) were found.

DISCUSSION

The oral disks of both *P. resinifictrix* and *P. venulosa* have more tooth rows developed in the posterior than in the anterior labium (negatively imbalanced according to ALTIG & JOHNSTON 1989) with unusual balance values of -2. In both species the basal general pattern of two anterior and three posterior labial tooth rows is still evident by the retarded ontogenetic appearance and the variable manifestation of outermost tooth rows (additional to 3) in the lower lip (for *P. venulosa* see oral disks figured in ZWEIFEL 1964, PYBURN 1967 and DUELLMAN 1970, and for several other hylids the descriptions and figures in DUELLMAN 1970). These facts might prove the additional rows phylogenetically young if there was a typical lentic-nectonic common ancestor - or might indicate a tendency of reduction if derived from stream adapted forms, which WASSERSUG (1980) supposes for the *H. bromeliacea* group. The latter case would not need a specific functional interpretation since increased numbers of tooth rows are known to be correlated with lotic environment; secondary invasion (presumably tertiary reinvasion) of lentic habitats simply could remove adaptive force on the maintenance of the additional rows. The former case would ask for ecomorphological explanation; this could be seen in an advantage of supernumerous tooth rows to the larvae when adhering to macrophytal material during mastication, but a definite answer to this question cannot be given yet. Labial tooth row formulae of 2/4 are most common within Middle and South American hylid larvae, and there are assigned to arboreal types (e. g. *H. bromeliacea*, *H. dendroscarta*) which feed on plant matter and detritus. Like *P. resinifictrix*,

they are less extremely macrophagous than for instance *A. spinosa*, *H. zetekii* or *O. brunneus*, mainly oophages, with the number of tooth rows decreased to 2/2, 1/1, and 1/0 respectively.

Large hand-like infralabial papillae in the buccal floor like in *P. resinifictrix* have been especially seen in stream-adapted bottom-feeding tadpoles (e. g. *H. smaragdina* TAYLOR, 1940 - DUELLMAN 1970; *H. mixe* DUELLMAN, 1965 - WASSERSUG 1980; *Rana ibanorum* INGER, 1964 - INGER 1985). These papillae can protrude out of the mouth, and, according to WASSERSUG (1980), thus, might perform taste or pressure receptive functions when the tadpoles contact a hard surface. One extreme is shown by the bromeliad, predominantly oophagous *O. brunneus* in complete absence of these structures (LANNOO & al. 1987). Within the arboreal hylid larvae examined and discussed by WASSERSUG (1980) *H. dendroscarta* shows simple unbranched infralabial papillae, whereas in *A. spinosa* there are 4 to 5 stubby secondary terminal projections which, as compared to the drawing in WASSERSUG, except for their somewhat smaller size, appear quite similar to the very structures observed in *P. resinifictrix*. *H. dendroscarta* develops in the leaf axils of Bromeliaceae and is supposed to be macrophagous herbivorous, detritivorous; *A. spinosa* lives in tree holes and is known to feed on mosquito larvae, other arthropods, and frog eggs (WASSERSUG 1980; LANNOO & al. 1987). So there might be a correlation between a facultatively macrophagous zoophagous nutrition in tadpoles ingesting small, moving prey as a whole and the possession of palp-like infralabial papillae, as it is

seen in *P. resinifictrix* and *A. spinosa*. A tactile receptive function connected with rapid mouth closure may be hypothesized.

Even more than *H. dendroscarta* (comp. WASSERSUG 1980), *P. resinifictrix* matches with the known correlation between macrophagous nutrition and reduction of papillae in the buccal floor arena as do *A. spinosa* or *O. brunneus* among others.

As to the extent of the craniad dilatation of the median notch which leaves the laryngeal disk fully exposed, *P. resinifictrix* is unique among anuran larvae known in this respect; *O. brunneus* comes closest to this (LANNOO & al. 1987). Size and degree of exposition is positively correlated with aeral respiration, and early development of functioning lungs (WASSERSUG 1980). An even broader but very shallow median notch is only known in *A. spinosa* (WASSERSUG 1980).

A large diameter of the esophageal funnel (as in *P. resinifictrix* larvae) is closely related to large prey. This has been reported from *A. spinosa* (which exhibits the largest esophageal entrance among the tadpoles examined by WASSERSUG 1980), and from *O. brunneus* (as to the micrographs in LANNOO & al. 1979).

Elevated prenarial ridges in the buccal roof which continuously connect the internal nares have been described for *A. spinosa* by WASSERSUG (1980). This author supposes "a mechanical function related to maintaining beak occlusion or positioning and anchoring macroscopic food items during mastication" in anteriorly curved prenarial crests. As to the figures in WASSERSUG (1980) and INGER (1985) the keratinized knob in the center of the prenarial arena in *Scaphiopus bombifrons* is the corresponding structure, most similar to that found in *P. resinifictrix*; it is said to serve in macrophagous herbivorous nutrition (WASSERSUG 1980).

According to its fully developed postnarial buccopharyngeal structures, *P. resinifictrix* is peculiar within the arboreal species hitherto known. In *A. spinosa*,

among others, the median ridge is reduced to a tall papilla (WASSERSUG 1980). In *H. dendroscarta* there also seems to be a tendency of reduction of this structure which again is completely absent in *O. brunneus*.

The poor papillation of the buccal roof in *P. resinifictrix* is correlated with macrophagous nutrition (WASSERSUG 1980) and evolved convergent to *A. spinosa*, and *O. brunneus* respectively.

Reduction of the filter mesh is associated to macrophagous, carnivorous or herbivorous nutrition, and is most extreme in *H. phlebodes* and *A. spinosa* (WASSERSUG 1980). In this *P. resinifictrix* mostly resembles the species with so-called slight filter reduction (e. g. *H. sarayacensis* SHREVE, 1935, a macrophagous herbivore - WASSERSUG 1980); the degree of filter mesh reduction in *P. resinifictrix* noticeably exceeds that in *O. brunneus*. The internal gills of *P. resinifictrix* show about half of the extension compared to average pond-larvae, whereas gill filaments are absent in *O. brunneus* (LANNOO & al. 1987). Thus, even in its extremes, predominance of aeral respiration (as in *P. resinifictrix*), expressed by the presence of large lungs, and a completely exposed glottis, can, but needs not be connected with maximum gill reduction.

Little is known about embryogenesis in arboreal hyloid species. Early larval stages of the pond-breeding hyloid *P. venulosa* are known to have markedly well-developed external gills. These structures were regarded as adaptations to low amount of dissolved oxygen in warm, standing water (ZWEIFEL 1964). Early stages of *P. resinifictrix* larvae may be expected to show even bigger respiratory structures.

Compared to the rather pond-type larva of *P. venulosa*, *P. resinifictrix* clearly shows modifications of the body proportions which could be interpreted as adaptations to a life in tree holes: the smaller size, the somewhat shorter and less deep tail, and the smaller diameter of the eye bulb.

CONCLUSIONS

Larval habitats in water filled phytothelms can be characterized by several physical, chemical and biological features: limited quantities of water, confined space; relatively hypoxic and aphotic conditions; almost no primary production, food source limited to detritus, heterotrophic organisms, (and spawn); comparatively little predatory pressure, and potentially high inter- and intraspecific competition.

In general these characteristics can be correlated with certain physiological, morphological and phenological modifications in the anuran inhabitants of the phytothelms: a small number of offspring per water body; alterations in larval body proportions; increase of respiratory surface area in embryos; reduction of aqueous respiration and buccal pumping activity, predominance of aeral respiration, reduction of microphagous suspension-feeding, and predominance of macrophagy in larvae. Furthermore, evidence from study of *O. brunneus* (LANNOO & al. 1987) indicates increased photosensitivity, reduction of neuromasts, and peculiarities in larval swimming behavior. Special mating and spawning behavior and several forms of parental care might be added to this list. The present study clearly indicates that several of these arboreal adaptations are present in *P. resinifictrix*.

None of the tendencies listed above needs to be extremely manifest to indicate an arboreal larval existence. Not one of these traits is found exclusively in arboreal or a subtype of arboreal larvae, and each may be found more or less distinctly developed in larvae of other extreme habitats. But certain combinations of external morphological, buccopharyngeal, and etho-physiological characteristics have resulted in ecomorphological clustering of phenotypes of arboreal larvae (DUELLMAN 1970; WASSERSUG 1980; ALTIG & JOHNSTON 1986, 1989; LANNOO & al. 1987).

Buccopharyngeal features of *P. resinifictrix* in general show clear reductions of structures associated with microphagous

filter-feeding (papillation, filter mesh density) and aqueous gas exchange (internal gills); marked development of glottis and lungs is correlated with increased aeral respiration; special modifications (heavy prenarial ridge, keratinized prenarial knob, large esophageal entrance) are associated with macrophagous nutrition. The functional relevance of the large prelingual palps, the well developed median ridge, and the lateral ridge papillae, remains uncertain.

According to the larval gut contents *P. resinifictrix* is a detritivorous (necrophagous), facultatively carnivorous (zoophagous) form, apparently a macrophagous generalist. The larva seems to feed on allochthonous plant material and decaying ligneous matter, fungus hyphae, and bacteria. Nematodes in the gut presumably were parasitic or ingested by chance, as might be other animals of appropriate size. Frog eggs have not been found in the gut contents or even associated to the tadpoles in the tree holes.

In *P. resinifictrix* larvae no structural characteristics associated with extreme modes of nutrition are found in the peribuccal area, and no marked adaptive alterations in body proportions do occur. In summary, the larva of this species is a characteristic omnivorous and generalized type with certain special adaptations associated with macrophagous nutrition and aeral respiration.

LANNOO & al. (1987) recognized several groups of arboreal tadpoles. Larvae representative of their "group 4", a category adopted by ALTIG & JOHNSTON (1989) (section II, type 4), were defined as "shorter tadpoles with stout bodies; tail/body ratios < 2 ; denticle formula greater than $2/3$ (typically with two to four extra rows superiorly); little or no reduction of internal oral features associated with macrophagy; gill filters and gill filaments normal to greater than normal density; darkly pigmented. Tadpoles included in this group are rhacophorids in the genera *Rhacophorus*, *Theloderma*, and *Nyctixalus* as well as the hyperoliid

Acanthixalus. This is primarily an Old World group, but not strictly so, since *Phrynohyas resinifictrix* evidently also belongs here. These larvae retain the internal oral morphology of tadpoles with generalized diets and aquatic, buccopharyngeal respiration. As such, they appear restricted to larger aquatic bodies, which are more likely to occur in tree holes than leaf axils."

P. resinifictrix with its tail/body ratio of almost 2, but with its tooth row formula of 2/3-5, its partly reduced, partly well developed buccopharyngeal structures, its reduced filter mesh, and the comparably light coloration does not fit well into "group 4".

There are some good reasons to place

P. resinifictrix larvae into LANNOO & al. (1987) - "group 3 - subgroup 1" (also adopted by ALTIG & JOHNSTON 1979 - "section II, type 3") which is defined as follows:

"Elongate tadpoles with attenuate bodies; tail/body ratio >1.7; denticle formula greater than 2/3; little or no reduction of the internal oral features associated with microphagous feeding in pond larvae (e. g. well-developed gill filters); no specialisation of the cranial musculoskeletal system for macrophagy." "There may be two different types of tadpoles here. First there are those, such as hylids, that increase their denticle formula above the 2/3 common for pond larvae by adding one or two lower rows."

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LITERATURE

- ALTIG, R. & JOHNSTON, G. F. (1986): Major characteristics of free-living anuran tadpoles.- *Smithsonian Herpetol. Inform. Serv.*; 67: 1-75.
- ALTIG, R. & JOHNSTON, G. F. (1989): Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats.- *Herpetol. Monogr.*; 3: 81-109.
- BOULENGER, G. A. (1891): A synopsis of the tadpoles of the European batrachians.- *Proc. Zool. Soc.*; 1891: 593-627.
- CEI, J. M. (1980): Amphibians of Argentina.- *Monit. Zool. Italiano; (N. S. Monogr.)* 2: 1-609.
- DUELLMAN, W. E. (1956): The frogs of the hylid genus *Phrynohyas* FITZINGER, 1843.- *Misc. Publ. Mus. Zool. Univ. Michigan*; 96: 1-47.
- DUELLMAN, W. E. (1970): The hylid frogs of Middle America.- *Monogr. Mus. Nat. Hist. Univ. Kansas*; 1: 1-753.
- DUELLMAN, W. E. (1971): A taxonomic review of South American hylid frogs, genus *Phrynohyas*.- *Occ. Pap. Mus. Nat. Hist. Univ. Kansas*; 4: 1-21.
- DUELLMAN, W. E. (1977): Liste der rezenten Amphibien und Reptilien. Hylidae, Centrolenidae, Pseudidae.- *Das Tierreich*; 95: 1-225.
- GOELDI, E. A. (1907): Description of *Hyla resinifictrix* GOELDI, a new Amazonian treefrog peculiar for its breeding-habits.- *Proc. Zool. Soc. London*; 1907: 135-140.
- GOSNER, K. L. (1960): A simplified table for staging anuran embryos and larvae with notes on their identification.- *Herpetologica*; 16: 183-190.
- GRILLITSCH, B. (1984): Zur Eidonomie und Differentialdiagnose der Larven von *Bufo b. bufo*, *B. calamita* und *B. viridis* im Verlaufe ihrer Entwicklung von der Schlupfreife bis zum Einsetzen der Schwanzreduktion; Ph. D. Thesis, Univ. Vienna.
- HERO, J. M. (1990): An illustrated key to the tadpoles occurring in the central Amazon rainforest, Manaus, Amazonas, Brazil.- *Amazoniana*; 11(2): 201-262.
- HÖDL, W. (1991): *Phrynohyas resinifictrix* (Hylidae, Anura) - Calling behaviour.- *Wiss. Film, Wien*; 42: 63-70.
- INGER, R. F. (1985): Tadpoles of the forested regions of Borneo.- *Fieldiana Zool.*; (N. S.) 26: 1-89.
- LANNOO, M. J. & TOWNSEND, D. S. & WASSERSUG, R. J. (1987): Larval life in the leaves: arboreal tadpole types, with special attention to the morphology, ecology, and behavior of the oophagous *Osteopilus brunneus* (Hylidae) larva.- *Fieldiana zool.*; 38: 1-31.
- LESCURE, J. (1976): Contribution à l'étude des amphibiens de Guyane française. VI. Liste préliminaire des anoures.- *Bull. Mus Nat. Hist. Nat. Paris*; (3. Ser.) 377 (Zool.) 265: 475-525.
- LUTZ, B. (1973): Brazilian species of *Hyla*; Austin, London (Univ. Texas Press).
- MERTENS, R. (1957): Das Märchen vom harznestbauenden Laubfrosch.- *Natur und Volk, Frankfurt/M.*; 87(3): 100-103.
- MIRANDA-RIBEIRO, A. de (1926): Notas para servirem ao estudo dos Gymnobatrachios (Anura) Brasileiros.- *Arch. Mus. Nac.*; 27: 1-227.
- MÜLLER, L. (1912): Zoologische Ergebnisse einer Reise in das Mündungsgebiet des Amazonas. I. Allgemeine Bemerkungen über Fauna und Flora des bereiten Gebietes.- *Abh. bayerischen Akad. Wiss., math. physik. Kl.*; 26: 1-42.
- PYBURN, W. F. (1967): Breeding and larval development of the hylid frog *Phrynohyas spilomma* in southern Veracruz, Mexico.- *Herpetologica*; 23(3): 184-194.

VIERTEL, B. 1982. The oral cavities of central European anuran larvae (Amphibia). Morphology, ontogenesis and generic diagnosis.- *Amphibia-Reptilia*; 4: 327-360.

WASSERSUG, R. (1976): Oral morphology of anuran larvae.- *Occ. Pap. Mus. Nat. Hist. Univ. Kansas*; 48: 1-23.

WASSERSUG, R. (1980): Internal oral features of larvae from eight anuran families: Functional, systematic, evolutionary and ecological considerations.- *Misc. Publ. Univ. Kansas Mus. Nat. Hist.*; 68: 1-146.

WUNDER, W. (1932): Nestbau und Brutpflege bei Amphibien.- *Ergebnisse Biol.*; 8: 180-220.

ZIMMERMANN, B. & HÖDL, W. (1983): Distinction of *Phrynohyas resinifictrix* (GOELDI, 1907) from *Phrynohyas venulosa* (LAURENTI, 1786) based on acoustical and behavioural parameters (Amphibia, Anura, Hylidae).- *Zool. Anz., Jena*; 211: 341-352.

ZWEIFEL, R. G. (1964): Life history of *Phrynohyas venulosa* (Salientia: Hylidae) in Panama.- *Copeia*; 1964: 201-208.

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