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**ORAL MORPHOLOGY OF ANURAN LARVAE:
TERMINOLOGY AND GENERAL DESCRIPTION**

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This paper is an introduction to certain morphological features in the mouths of tadpoles. It was undertaken as part of a comparative investigation on the evolution of anuran larvae and the systematics of frogs.

The first use of larval morphology in anuran systematics was by Lataste (1879), who in 1888 proposed that frogs could be divided into two groups based on the spiracle position of their larvae. Many herpetologists since have used larval features in their systematic studies. The literature prior to mid-century has been ably reviewed by Orton (1944), whose own studies constitute a major contribution to our understanding of the superfamilial relationships of the Anura.

Orton (1953, 1957) proposed a classification of frog families based on four larval types. Her Type 1 includes the Pipidae and Rhinophrynidae, with tadpoles that have paired spiracles and lack keratinized mouth parts. Type 2 consists solely of the Microhylidae, with tadpoles lacking keratinized mouth parts and having a single, medial spiracle. Type 3 includes the families Ascaphidae and Discoglossidae, with keratinized larval mouth parts and a medial spiracle. Type 4 includes all the remaining families; their tadpoles have keratinized mouth parts and a sinistral spiracle. Although a few scientists object to use of any larval features in systematic studies (Griffiths and Carvalho, 1965), Orton's superfamilial groups have

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been accepted by most herpetologists. Starrett (1973) has gone so far as to replace Orton's numbers with names, giving formal taxonomic recognition to these groups. The value of this has been questioned by Sokol (1975), who objects to the phyletic implications of this move. For the purposes of this introductory study, I recognize Orton's groups without Starrett's names.

There is much disagreement among students of anuran systematics as to whether Orton's groups represent a linear evolutionary sequence (see Griffiths, 1963; Hecht, 1963; Tihen, 1965; Inger, 1967; Nevo, 1968; Starrett, 1968, 1973; Kluge and Farris, 1969; Spinar, 1972; Lynch, 1973; Savage, 1973; Sokol, 1975). The arguments all rest on the determination of primitive features in tadpoles and what weight can be given the two larval characters used in Orton's classification. With so few characters, the chance of convergence between the families is necessarily high. To determine whether certain families appear similar because of common ancestry or because of convergence is a major problem. One way to attack such a problem is to find additional diagnostic characters.

My study began with a search for new characters. For two reasons I chose to look at feeding structures. The first reason is one of convenience, in that a large proportion of tadpole tissue is involved in ingestion; consequently, feeding structures are relatively easy to examine. The second reason for studying feeding structures is that in nutrient acquisition an organism comes in direct contact with the environment. Thus, feeding structures are centers for evolutionary action that may be highly adaptive. The adaptive significance of the larval stage for anurans in general may be tied directly to the feeding mechanism of the tadpoles (Wassersug, 1975). The present study is limited to surface features in the oral cavity of tadpoles that are visible with a dissecting microscope; the emphasis here is on organs that are directly in contact with the water or with food in the water.

A preliminary examination of the inside of the oral cavity of a variety of tadpoles (Wassersug, 1973) revealed many morphological differences among tadpoles of various families, genera and species. A literature survey further demonstrated much diversity in the oral structures of anuran larvae. Descriptions or figures of structures in the oral cavity are available for the tadpoles of *Ascaphus truei* (Gradwell, 1971a, 1973), *Bombina igneus* (= *bombina*) (Goette, 1875), *Alytes obstetricans* (Magnin, 1959), *Rana pipiens* (Parker, 1881, Plate 1), *Rana agilis* (= *dalmatina*) (Kratochwill, 1933), *Rana temporaria* (Savage, 1952; DeJongh, 1968), *Rana catesbeiana* (Gradwell, 1970, 1972a), *Rana fuscigula* (Gradwell,

1972c), *Pelobates fuscus* (Schulze, 1870, 1892), *Bufo bufo* (Savage, 1952), *Phyllomedusa trinitatis* (Kenny, 1969a), *Hyla geographica* (Kenny, 1969b), *Pseudis paradoxa* (Parker, 1881), *Xenopus laevis* (Weisz, 1945; Sterba, 1950; Ueck, 1967; Gradwell, 1971, 1975), *Hymenochirus boettgeri* (Sokol, 1962; Ueck, 1967), *Pipa carvalhoi* (Sokol, in manuscript), *Calluella guttulata*, *Glyphoglossus molossus*, *Chaperina fusca* (Savage, 1952), *Hypopachus aguae* (Savage, 1955; Nelson and Cuellar, 1968), *Hypopachus variolosus*, *Gastrophryne olivacea*, *Gastrophryne usta* (Nelson and Cuellar, 1968) and *Phrynomerus annectens* (Gradwell, 1974). Unfortunately, the terminology used in these papers is inconsistent. Few of the descriptions or figures are complete, and many drawings tend to be stylized in a manner that does not inspire confidence in fine detail. Many oral structures have received two or three names; in some cases the names imply functions that are speculative at best. Other structures have been repeatedly ignored by anatomists. I have not referred to one major study (Severtzov, 1969) because the author claims a degree of morphological similarity in the larvae that he examined that I could not verify in my own material of the same genera and families.

As a prelude to a comparative study of tadpole oral structures (Wassersug, in manuscript) I present here a general description of the oral features of tadpoles. Old terms are redefined and some new ones are introduced. I have selected terminology that is most applicable to Orton's Type 4 tadpoles because these are the most common type of larvae. The description is relevant to tadpoles between stages 26-39 (Gosner, 1960). Ontogenetic variation is treated in a separate work (Wassersug, 1976). In most cases I follow Kratochwill's terminology (1933) with English translations. All terms pertaining to the inside of the oral cavity are printed in bold-face capitals as they are introduced. Major features are illustrated in Figs. 1 to 3. Appended is an outline for the description of tadpole oral surface features.

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MATERIALS AND METHODS

The description presented here is based on a review of the literature, the detailed study of 26 species from six families (Ascaphidae, Discoglossidae, Rhinophrynidae, Microhylidae, Hylidae and Pelobatidae; Wassersug, 1973), and a cursory examination of an assortment of species from three additional families (Bufonidae, Ranidae, Leptodactylidae). Figs. 1 and 2 were made with a camera lucida from a *Hyla regilla* tadpole. This species was the most extensively studied and its larval oral structures are described in fuller detail elsewhere (Wassersug, 1976).

The tadpoles that I dissected were washed briefly in tap water to remove superficial preservatives. All dissections were made with assistance of a stereoscopic microscope. Observations and measurements were taken on tadpoles pinned under water in a depression carved in a black-stained paraffin block. Dissections were made by carefully inserting the blade of a scissors into the left corner of the mouth between the upper and lower beaks and cutting back to the posterodorsal corner of the pharynx. The scissors were then gently worked transversely and the mouth cut to the opposite, posterodorsal corner. Oral surface could then be exposed by simply opening the mouth from the side. As the mouth was opened, the intermeshing nature of dorsal and ventral features could be assessed. A longitudinal cut was made along the side of the mouth, freeing the

roof from the floor. This cut separated the ceratohyal on the right side from the palatoquadrate bar. Externally it was not always possible to determine exactly the position of the posterodorsal corner of the pharynx; in such cases the initial cut was made relatively high. This procedure assured the retention of intact gill filters but at the expense of damage to the pressure cushions and ciliary groove.

In tadpoles lacking extensive pigmentation of the buccal and pharyngeal epithelia, surface features are transparent and difficult to discern. Therefore, these tadpoles were stained with either a methyl blue or crystal violet solution after they had been dissected. Because of the mucin specificity of methyl blue, secretory tissues were specifically accentuated.

GROSS FEATURES

In tadpoles the forelimbs and gills are covered by a flap of skin, the operculum. The elongate intestine is tightly coiled. The oral orifice is small due to the short Meckel's cartilage. Structures peculiar to tadpoles, infralabial and supralabial cartilages, serve as the functional jaws. The most remarkable feature of tadpoles in comparison to other tetrapods is the greatly elongate palatoquadrate, which is rotated anteriorly so that it parallels the trabeculae cranii. At metamorphosis this suspension is largely rebuilt. The quadrate rotates down and backwards into a more typically vertical position and Meckel's cartilage elongates. The forelimbs emerge, and the tail and gills are absorbed.

Free-swimming Type 3 and 4 larvae have externally visible keratinized mouth parts surrounding the mouth opening. The major elements are the upper and lower beaks, which sheath the supralabial and infralabial cartilages. Rows of keratinized denticles or teeth ("odontoids" of Sokol, 1975) are arranged in characteristic patterns above and below the beaks on the oral disc. The denticle rows may be continuous or medially divided. Denticle patterns have been much used in diagnosis of tadpoles; the notational schemes for denticle patterns have been reviewed by Lynch (1971). By the simplest scheme, that of giving the upper and lower row counts divided by a slash, the 2/3 pattern is the commonest. The margins of the oral disc are lined with various pustulations and short, blunt papillae. Their form and pattern have also been used extensively in tadpole identification (Altig, 1970; Duellman, 1970; van Dijk, 1966). By definition, Orton's Type 1 and 2 tadpoles lack keratinized mouth parts, but may have elaborate structures on the

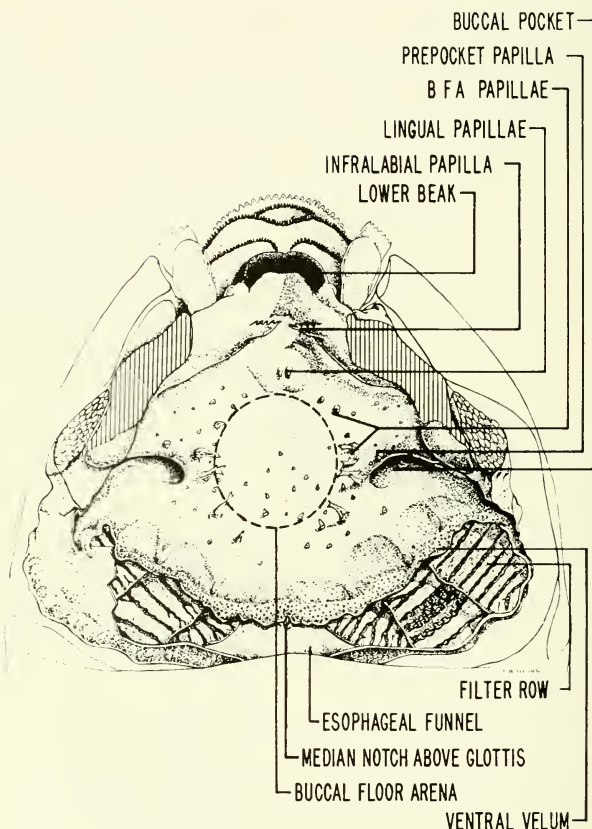


FIG. 1.—The floor of the mouth of a typical Type 4 tadpole (Orton, 1953, 1957). The illustration is based on a stage 37 *Hyla regilla* larvae (max. width of pharynx = 6.1 mm). The filter folds are schematically drawn.

oral disc or lips. Examples include the “funnel mouth” in certain microhylids such as *Microhyla heymsi* (Parker, 1934) and the tentacles in *Xenopus* and *Rhinophrynus*.

The oral orifice opens anteriorly or anteroventrally. The orifice is usually less than a quarter the width of the mouth, rarely larger. Internally, the mouth or oral cavity widens posteriorly and then abruptly constricts along the posterior walls of the pharynx into the

esophagus. The oral cavity thus is roughly triangular in shape in the horizontal plane and dorsoventrally compressed (Figs. 1 and 2). The oral cavity can be divided into two major regions: an anterior, **BUCCAL CAVITY** and a posterior, **PHARYNGEAL CAVITY**. These cavities are separated on both structural and functional grounds by a distinctive, movable but non-muscular flap, which is essentially continuous across the floor and roof of the mouth. It should be noted that by using this prominent ring of tissue as the boundary between the two regions, the first gill pouch resides in the buccal, rather than the pharyngeal, cavity. The terms buccal and pharyngeal are therefore not strictly homologous to the same terms used for other vertebrates. The ventral portion of the dividing flap is supported by posteriorly projecting, cartilaginous spicules on the posterodorsal margin of the hypobranchial plate. In the few tadpoles (*viz.* Pipidae) that lack this flap there is a common buccopharyngeal cavity. Viewed from above, the ventral portion of the flap is a continuation of the buccal floor. Its posterior margin, grossly a posteriorly directed "U" or "V", is free and unsupported. This trailing edge may be slightly thickened and bears large, paired crenulations or short caudad projections on each side of the midline. These projections often appear in one to one association with the individual gill pouches that they partially cover. A **MEDIAN NOTCH** lies in the middle of the ventral portion of the flap. The lower surface of the ventral portion of the flap opposes the gill filters and the anterior portion of the pharyngeal cavity.

The ventral portion of the flap has been called either the **VENTRAL VELUM** or the **ANTERIOR FILTER VALVE** (Kenny, 1969a; Sokol, 1975) in the literature of the last forty years (reviewed by Gradwell, 1970). While convincingly demonstrating a valvular function for the organ in *Rana catesbeiana*, Gradwell chose to use the term "velum", with the realization that the structure may, in part, serve an auxiliary role of redirecting water currents. He also followed Savage in claiming historical priority for the term "velum", credited to Goette (1875). In fact, Schulze in 1870, first named this structure the "gill cover plate" (*Kiemendeckplatte*), but for brevity, I will use the shortest accurate term, ventral velum. The lower surface of the ventral velum has some unique histological features, which will be discussed in more detail below.

The continuation of the velum on the roof of the mouth is more posterior than the trailing edge of the ventral portion. It has been called both the **DORSAL VELUM** and the **POSTERIOR FILTER VALVE**. Both Gradwell (1970, 1973, 1974) and DeJongh (1968)

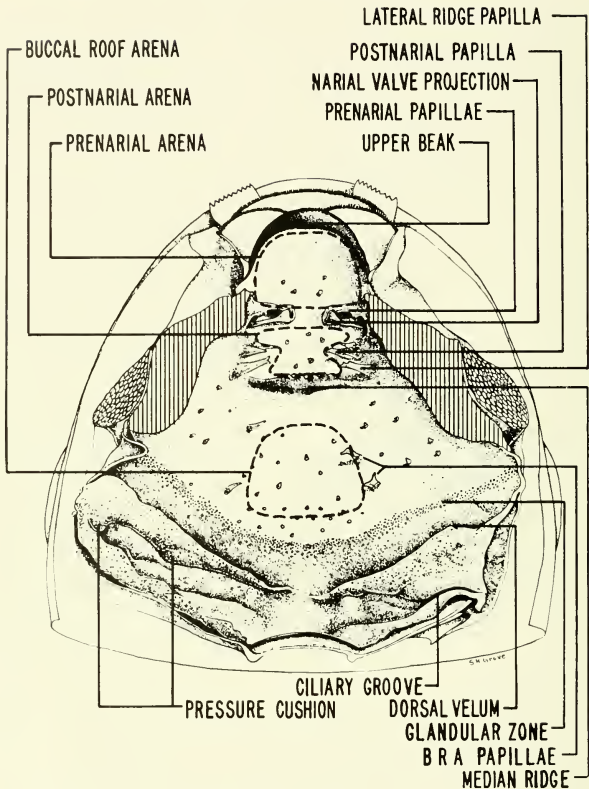


FIG. 2.—The roof of the mouth of a typical Type 4 tadpole (Orton, 1953, 1957). The illustration is based on the same stage 37 *Hyla regilla* larvae seen in Fig. 1.

and, to a certain extent, Kratochwill (1933) have suggested a true velar function for this structure. The dorsal velum is deepest directly above the second and third ceratobranchials and shallowest or absent on the midline in front of the esophagus. Thus, it has sometimes been considered a paired structure symmetrical about the midline. The dorsal velum is a finer, more delicate epithelial fold lacking both the cartilaginous spicules and the extensive connective tissue support of the ventral velum. It does not project directly ventrad but tends to curl forward in fixed specimens.

FEATURES OF THE BUCCAL CAVITY

The floor of the buccal cavity has several distinctive topographic features, though from the posterior margin of the short Meckel's cartilage to the margin of the velum it is generally flat. The most anterior projections of the epithelium within the buccal cavity are called **INFRALABIAL PAPILLAE**, because they lie over the infralabial cartilage and its articulation with Meckel's cartilage. The infralabial papillae, as with other major papillae in the oral cavity, may be single, multiple, attenuate, blunt, bifurcate, multiple-branching, compressed, pointed, conical, pustulate, curved, recurved, finger-like, etc. **PAPILLAE** are here defined simply as any projection with a circular or elliptical base and a height twice the diameter of the base. Smaller projections are called **PUSTULATIONS**.

In all glossal frogs the **TONGUE** develops medially, just behind the infralabial cartilages at the front of the ceratohyals. It is an anteriorly convex, raised ridge in the beginning of its ontogeny. Later it expands posteriorly into a roundish pad. Its development has been reviewed most recently by Hammerman (1969). Premetamorphic lingual papillae, which degenerate with development of the tongue, have been studied by Rieck (1932), Hammerman (1964, 1965), Helff and Mellicker (1941), and Schulze (1870). Kenny (1969a) calls these sensory papillae. They arise medially near the anterior base of the tongue and are normally paired, being symmetrically arranged about the midline. I call these structures **LINGUAL PAPILLAE** restricting the term to premetamorphic structures.

Most papillae on the buccal floor posterior to the tongue anlage are arranged with the larger ones more or less evenly spaced and forming two rows aligned from front to back. At the edge of the hypobranchial plate these papillate rows begin to converge toward the midline and may parallel the edge of the ventral velum. The papillae, if large enough, often curve anteromesiad and circumscribe the area in the center of the buccal floor. This area is called the **BUCCAL FLOOR ARENA (BFA)**. The papillae which define this area are therefore **BUCCAL FLOOR ARENA PAPILLAE** or **BFA PAPILLAE**. Various minor papillae and pustulations may occur within or about the arena.

The epithelium of the buccal floor descends into the lateral spaces between the posterolateral margin of the ceratohyals and the anterior margins of the first ceratobranchials, forming deep pockets on each side. These pockets may be visibly perforated in certain tadpoles, thus forming the first true gill slits which lead to

the **ATRIAL (OPERCULAR) CHAMBER**. These slits serve as independent connections from the buccal cavity to the atrial chamber and a functional bypass of the pharynx (at least in *Rana catesbeiana*; Gradwell and Pasztor, 1968—"gill cleft #1"="pharyngeal by-pass"). There is no filter epithelium lining these pockets. For convenience they can be called **BUCCAL POCKETS** or **BUCCAL SLITS** for their topographic position, anterior to the edge of the velum and independent of the remaining gill slits in the pharynx. Papillae and pustulations are often present in front of the buccal pockets on the buccal floor above the lateral arms of the ceratohyal. Large and distinctive papillae arranged in a line along the edge of the pocket are called **PREPOCKET PAPILLAE**.

In general the buccal roof is level. The rostral area, however, may curve sharply ventrad. Topographic features allow a convenient division of most of the buccal roof into three major sections. The most anterior section is the **PRENARIAL ARENA**. It is enclosed by the supralabial cartilages anteriorly and internal nares posteriorly. Pustulations, papillae, or ridges are often present in the prenarial arena; when present, these structures generally show symmetry about the midline. The second section, the **POST-NARIAL ARENA**, is a small, but structurally complex area between the nares anteriorly and a transverse median ridge or flap posteriorly. The transverse flap, here called the **MEDIAN RIDGE** (the "*Gaumenquerklappe*" = "palatal transverse flap" of Schulze, 1870; "transverse fold" of DeJongh, 1968; "sensory papillae" of Kenny, 1969b), is an important landmark usually about halfway back on the buccal roof. The last section of the buccal roof is the **BUCCAL ROOF ARENA (BRA)**, a faintly defined area which corresponds to the buccal floor arena ventrally. The buccal roof arena begins behind the median ridge and is bound laterally by papillae. The prenarial and postnarial arenas are generally smaller than the BRA and together make up a third or less of the total surface area on the buccal roof.

The **INTERNAL NARES** or choanae are a major feature on the buccal roof. They project down from the rostral surface, and are slit-like, with an oblique to transverse orientation. The fold of mucosa that makes up the narial wall on each side starts at the anterolateral corner of the nares, where the nare does not project noticeably because of the natural curvature of the rostrum. Small, sometimes paired, posteriorly directed papillae occur in certain species at this anterolateral corner and project over a portion of the narial opening. While these are not properly shaped or positioned to act as valves, they were originally called "*vordere Choanenklap-*

pen" by Schulze (1870). I will refer to them as **ANTERIOR NARIAL PAPILLAE** or **PRENARIAL PAPILLAE**. Posteriorly, the flap of mucosa which constitutes the narial wall tucks into a lateral pocket on each side rather than abutting directly on the rostral surface. The posterior narial wall thus forms an extensive free flap, the **NARIAL VALVES**. As is consistent with an undisputed valvular function for this posterior wall (e.g., Gradwell and Pasztor, 1968), the posterior narial rim is always thinner and more freely movable than the anterior narial wall. Single, tall tongues of the narial valves are called **NARIAL VALVE PROJECTIONS**. When present, they are usually on the medial end of the narial valve.

Within the narial arena, between the internal nares and the median ridge, there may be short, distinct rows of papillae. When present, these rows are usually oriented obliquely, anteromedial to posterodorsad. These papillae are usually positioned directly behind each narial valve and will be called posterior narial papillae or **POSTNARIAL PAPILLAE**. These postnarial papillae do not structurally parallel the prenarial papillae (that is, they are not associated with the narial walls); nevertheless, I accept the term because of its simplicity. In certain species there are **POSTERIOR NARIAL RIDGES** instead of papillae within the narial arena.

At about the middle of the buccal roof, the median ridge arises as a transverse fold. It is a free, thin epithelial flap, the edge of which points anteroventrad and may be papillate and have a medial notch. Subsidiary **LATERAL RIDGE PAPILLAE** ("sensory papillae," Kenny, 1969b), usually one on each side of the median ridge, may be present. In certain species the lateral ridge papillae are the most conspicuous feature on the buccal roof. A secondary papillary zone or fringe may develop on the anterior surface of the median ridge. Secondary papillae, likewise, can occur on the anterior surface of lateral ridge papillae.

Papillae are common on the buccal roof proper, posterior to the median ridge. They are never as numerous as on the corresponding central region of the buccal floor. Papillae of the buccal roof proper are arranged into two symmetrical regions. Larger papillae form rows aligned in an approximately anterior to posterior direction, roughly halfway between the lateral margins of the mouth and the midline. These are the **BRA PAPILLAE** that serve to define the lateral limits of the buccal roof arena. **LATERAL ROOF PAPILLAE**, always smaller in size and usually fewer in number, sometimes occur in clusters or short rows far lateral on the buccal roof.

The posterior limit of the buccal roof behind the buccal roof

arena is lined with a transverse crescentic band, which was first identified as a mucous membrane ("*Schleimhaut*") by Schulze (1870). Under low magnification this tissue has a buffed texture and was called the glandular zone ("*Drüsenzzone*") by Kratochwill (1933). In most species definite **SECRETORY PITS** can be seen with 50X or higher magnification. While Kenny (1969a) felt that this was a major region of food collection, and referred to the zone as the "dorsal food traps," I am not convinced of the function implied in this term and choose to retain DeJongh's simple, descriptive term **GLANDULAR ZONE**. This secretory zone often extends posteriorly and laterally onto the dorsum velum. Identical secretory pits line the posterior edge of the ventral velum in many species.

FEATURES OF THE PHARYNGEAL CAVITY

Surfaces exposed behind the dorsal and ventral vela, but in front of the esophagus and internal to the gill slits, are pharyngeal. Viewed from above, the major and most conspicuous features in the pharynx are the **GILL FILTERS**. These are ruffled epithelial organs associated with the posterior surfaces of ceratobranchial 1 (cb. 1), the anterior surface of ceratobranchial 4 (cb. 4), and both the anterior and posterior surfaces of ceratobranchials 2 (cb. 2) and 3 (cb. 3). They project outward from dorsomesad projecting plates of connective tissue, the **FILTER PLATES**.

The filter plates are oriented parallel to the gill slits in an anteromeso-posterolateral direction surrounding the **FILTER CHAMBERS**. The plates originate anteriorly, from the posterior margin of the hypobranchial plate, where the ceratobranchials begin. The ventral velum also originates here, and for a short distance posteriorly, the velum is attached to the dorsal edge of the filter plate, before it becomes a completely free flap. The filter plates are rarely perpendicular to the buccal floor, but are usually imbricated to varying degrees, with their dorsal edges posterior and medial to their ventral supporting ceratobranchial cartilages. The plates are not necessarily fixed in this position in life; they are rather flexible and could become more erect with depression of the branchial basket during the regular oral pumping cycle. The height of the filter plate reflects the size and depth of the branchial baskets. The filter chambers or cavities are spaces in the pharyngeal cavity above the gill slits, between whole filter plates on opposing arches. There are three filter cavities on each side. The first is between the filter plates of cb. 1 and 2, the second between cb. 2 and 3, and the last between cb. 3 and 4. The second filter cavity is the largest.

The gill filters arise as epithelial folds on the filter plates. The filters have been termed "gills", "internal gills", and "gill rakers" in the older literature, but should not be confused with the true gills that arise from the distal edges of the interbranchial septa. The essential structure of the filters was described by Naue (1870), who reported no major differences between the filters of *Pelobates fuscus*, *Rana temporaria*, and *Rana esculenta*. Kratochwill (1933) made a detailed description of the filter apparatus in *Rana agilis* (= *dalmatina*) and Kenny (1969a) described the filters of *Phyllomedusa trinitatis*. Gradwell (1972a) described the filters of *Rana catesbeiana*. The filter epithelium is convoluted into **FILTER RUFFLES** ("Filterkrause," Kratochwill, 1933) or **FILTER FOLDS** (Kenny, 1969a), that run in parallel rows down the filter plates from dorso-posteromedial to ventroanterolateral. Full filter rows run the length of the filter plates and are usually a bit wider near their ventral margin on the plates than near their dorsal margin. In species with dense filter surfaces, partial folds form triangular wedges that project down the filter plate. These partial rows fill spaces between full rows along the dorsal margins of the filter plates. These features of filter anatomy are illustrated in Fig. 3.

Unlike the true gill filaments, which are often elongate, the filter ruffles appear short and truncate in section. In some ways they resemble abutting, overly trimmed garden hedges in that they are widest away from their substrate attachment, in this case, the surface of the filter plate. This results in the formation of partially to fully covered passages between neighboring folds called **FILTER CANALS**. The short and stout ruffled appearance of the filters is caused by the sequence of folding on each ruffle. The **MAIN FOLD** (=middle fold of Kratochwill, 1933 and Kenny, 1969a) of each ruffle is low and broad. The **SECONDARY**, **TERTIARY** and occasionally higher order **SIDE FOLDS** that follow are increasingly shorter. The spaces between any two neighboring branches of one filter ruffle are **FILTER CREVICES** (Kenny, 1969a). The open, multi-sided spaces that form between the secondary and tertiary filter folds have been called the **FILTER NICHES** by Kratochwill and by Kenny.

The **GLOTTIS** lies on the midline between the anterior portions of the fourth ceratobranchials. It is a simple longitudinal slit in the middle of a circle that indicates the presence of the trachea below. It may have distinct lips. The circular outline of the trachea is identifiable as a **LARYNGEAL DISC**. The laryngeal disc, the glottis, or both, are often slightly elevated on an elliptical dome. The glottis increases in prominence with metamorphosis. Before meta-

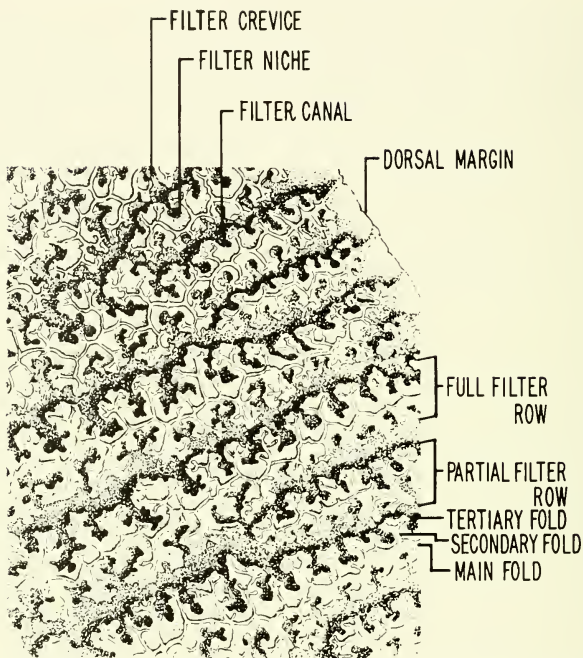


FIG. 3.—Greatly enlarged segment of a single filter plate showing details of the filter folds. This drawing was based on a low magnification scanning electron micrograph of the second filter plate in a *Rana pipiens* larva. Because of drying artifacts the filter density is not quite as great as it may have been in life.

morphosis it is most distinct in the species whose larvae have lungs that begin to function earliest (Wassersug and Seibert, 1975). Viewed from above, the trailing edge of the ventral velum partially or fully obscures the glottis.

A short distance behind the glottis is the **ESOPHAGEAL FUNNEL**, where the pharynx narrows into the esophagus. The profile of the funnel is determined by both the width of the esophagus and the width of the pharynx. If the pharynx is narrow and the esophagus slender, the tadpole will appear to have a small, narrow funnel. With a broad esophagus and wide pharynx the funnel may appear both larger and broader.

Essentially the esophagus is an extension of the **CILIARY**

GROOVE, the most posterior and lateral feature on each side of the pharynx. The ciliary groove runs in the horizontal plane at the margin of the roof of the pharynx. It starts on each side at the anterolateral corner of the ventral velum, where the velum is abruptly reflected dorsally and posteriorly. The groove continues behind the dorsal velum around the wall of the pharynx, first posteriorly, then more medially, and finally directly into the esophageal funnel. The ciliary groove varies from being open and rather shallow posteriorly to being more inset and trough-like laterally. The groove ("*Flimmerrinne*") was first identified by Kratochwill (1933) and seems to be an invariant feature of all microphagous larvae. Obviously, cilia are not visible in gross dissection of the ciliary groove. Food particles however compacted in mucous cords, often mark the ciliary groove in specimens that were eating extensively before they were fixed.

The anterior limit of the ciliary groove is in the immediate vicinity of the lateral limit of the **SECRETORY RIDGES**. These secretory ridges are on the ventral surface of the ventral velum and appear as fine parallel striations when stained with methyl blue. Near the margin of the velum the ridges parallel the velar edge. More anteriorly the ridges tend to follow the posteriorly concave arches formed by the adjoining filter plates and the hypobranchial plate. The ridges maintain an orientation at right angles to the long axis of the filter plates. The collection of ridges between each arch have been called **BRANCHIAL FOOD TRAPS** by Kenny (1969a) and have been numbered to correspond with each filter chamber. Anteriorly, in each filter chamber the food traps may extend ventrad from the velar surface proper. Posteriorly, the secretory ridges are often continuous from one filter cavity to the next under the free margin of the velum. In certain species the ridges cover the whole ventral surface of the velum and, consequently, the branchial food traps are not as disjunct as Kenny's coding would imply. Kenny homologized his branchial food traps with the structures termed "crescentic organs" and "collecting organs" by Savage (1952 and 1955). Others, such as Kratochwill, Gradwell, and DeJongh, have preferred to leave this tissue unnamed or simply refer to it descriptively as the secretory or glandular tissue of the ventral surface of the ventral velum.

Kenny has given much attention to the comparative histology of this secretory tissue. The secretory ridges may vary in their size, density and uniformity. In certain species the secretory tissue in the branchial food traps is not well organized into ridges. Kenny

notes generic as well as possible familial differences in the microscopic patterns of these ridges.

In *Xenopus* the floor of the buccopharyngeal cavity is covered with secretory ridges forming what Weisz (1945) called the pharyngobranchial tract. Savage (1952) suggested the "pharyngobranchial tract" (Savage's modification) is identical to his ventral velum. This homology has been accepted by most authors. According to Sokol (1975) the "pharyngobranchial tract" (Sokol's modification) in *Xenopus* is a remnant of the ventral velum of non-pipid larvae, while to Gradwell (1975) the ventral velum of non-pipids is derived from the pipid configuration (specifically by a contralateral proliferation and spreading of squamous epithelium on the floor of the buccopharyngeal cavity). Without entering this controversy, I accept the homology of the secretory ridges of the pharyngobranchial tract with the secretory ridges of other tadpoles, but consider the Pipidae as lacking a true ventral velum. I am here restricting the term velum to a freely suspended epithelial flap and use the descriptive term, "secretory ridges," to refer to such ridges whether they occur under the velum or elsewhere in the oral cavity.

The only remaining major oral features are the **PRESSURE CUSHIONS** or pads of Kenny (1969a). These have also been called "*Druckpolster*" (Kratochwill, 1933), "dorso-pharyngeal fold" (Weisz, 1945), "velar pads" (Gradwell, 1975, 1972a and earlier) and "lymph sacs" (Witschi, 1959). The pressure cushions are oblong bulges of epithelium that descend, two on each side, from the roof of the pharynx posterior to the dorsal velum. They are oriented with their long axes perpendicular to the margin of the dorsal velum and parallel to the filter cavities. The **LATERAL PRESSURE CUSHIONS** fill the dorsal and posterior portions of the first filter cavities in undisturbed specimens. The **MEDIAL PRESSURE CUSHIONS** are aligned above the second filter cavities. There is only loose areolar tissue in association with the cushions, and, as noted by Kenny, they are often shrunken and distorted in fixed material. The lateral sides of the lateral pressure cushions make up the medial edge of the ciliary groove. Posterior portions of the medial pressure cushions contribute to the formation of the ciliary groove along the back of the pharynx.

SUMMARY

A general description is presented of oral surface features in the mouths of tadpoles. Past terminology is reviewed and several previously undescribed structures are identified and named.

Except for the Pipidae, which have a common buccopharyngeal cavity, all tadpoles have their mouths partitioned into distinct anterior, buccal, and posterior, pharyngeal, cavities. Epithelial flaps known as dorsal and ventral vela are the partitioning structures. By this separation the first pharyngeal gill clefts (the buccal pockets) technically lie in the buccal rather than pharyngeal cavity. The ventral velum is a functional valve.

Typical features of the buccal floor include: anterior paired infralabial papillae; lingual papillae on the tongue anlage; pre-pocket papillae in front of the buccal pockets; a central field on the buccal floor termed the buccal floor arena (BFA) circumscribed by paired longitudinal rows of papillae, the BFA papillae.

The buccal roof is characterized by: an anterior prenarial arena between the upper beak and the internal nares; a postnarial arena between the internal nares and a medial transverse fold called the median ridge; a buccal roof arena (BRA) dorsal to the BFA. Collections of papillae, termed the postnarial papillae and the BRA papillae, define the lateral boundaries of the postnarial and buccal roof arenas respectively. Other papillae on the buccal roof occur lateral to the median ridge (lateral ridge papillae) and in association with the narial valves (narial valve projections and prenarial papillae). The posterior margin of the buccal roof is lined by a secretory mucosa called the glandular zone.

The shape of the buccal cavity and the number and arrangement of all major papillae and projections may differ among species. The number and shape of papillae and pustulations in the buccal cavity of tadpoles also varies intraspecifically. Patterns of pigmentation are extremely variable within any species. The ventral velum varies in its amount of attachment to the underlying filter plates and the extent of crenulation along its posterior margin. Dorsal and ventral vela vary in their integrity on the midline.

The gill filters are the most conspicuous feature of the floor of the pharynx in tadpoles. They cover the filter plates on the 1st through 4th ceratobranchials.

The posterior lateral margin of the pharynx is defined by a ciliary groove which runs posteriorly into the esophageal funnel. Anterior to the esophageal funnel lies the glottis on the laryngeal disc. These structures are partially or fully obscured from dorsal view by the free trailing edge of the dorsal velum in most tadpoles (Orton type 4).

On the ventral surface of the ventral velum lies secretory tissue. This tissue is usually organized into distinct ridges. The collection of secretory tissue in each filter cavity is called branchial food traps.

Two oblong bulges of epithelium descend from dorsal velum into the filter cavities on each side of the pharynx. These are termed the medial and lateral pressure cushions and are the only major features of the typically small dorsal pharynx of tadpoles.

There is much intraspecific variation in the size and shape of the pharynx in anuran larvae. Tadpoles differ in the folding pattern of their gill filters, the density of their filters, and the height and length of their filter plates. The premetamorphic size of the glottis, the distinctness of secretory ridges and the size of branchial food traps also show much variation among species.

This study adds to our knowledge of the anatomical complexity of tadpoles. The structures described here all come in direct contact with the feeding currents of tadpoles. Interspecific variation in these structures is thus likely to reflect differences in the feeding ecology of tadpoles.

All of the newly described features are relatively easy to examine and may be applicable to studies of anuran systematics. An outline for description of oral surface features in tadpoles has been included as an appendix.

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APPENDIX

Outline for Description of Tadpole Oral Surface Features

The following outline is used by Wassersug (1973, 1976 and in manuscript) for a comparative study of the oral features in the larvae of 26 species from six families. It emphasizes the features that are of most comparative value. The outline presents features in the order of ventral, anterior to posterior, then dorsal, anterior to posterior. This is a convenient sequence for examination, but it contrasts with the functional organization (all buccal features followed by all pharyngeal features) used in the preceding description. Not all features listed in this outline will be applicable to every species.

I. General shape of floor of mouth; length to width ratio

II. Ventral Buccal

A. Infralabial papillae

1. Number

2. Position

3. Relative size

4. Presence and number of secondary projections or pustulations on papillae

B. Lingual papillae

1. Number

2. Shape

3. Relative size

C. Buccal floor arena (BFA)

1. General shape

2. BFA papillae

a. number

b. size—position of largest; uniformity in size

c. number of bifurcations

D. Prepocket papillae—number, general size

E. Papillae and pustulations elsewhere on buccal floor

1. Numbers

2. Region of concentration

F. Buccal pockets

1. Size; length to width ratio

2. Angle from transverse plane

3. Perforated or not perforated

G. Free velar surface

1. Relative extent; area compared to rest of buccal floor

2. Spicules

a. length

b. stiffness

3. Posterior margin
 - a. shape
 - b. size of peaks over filter cavities
 - c. extent of emargination of middle portion; number of projections
 - d. median notch; size
 4. Secretory pits
 - a. conspicuousness
 - b. density
 - c. distribution on posterior velar margin
- III. Ventral Pharynx
- A. Branchial baskets
 1. Length to width ratio; general shape
 2. Size compared to buccal area; depth
 3. Relative size of filter cavities; prevalent orientation from midline
 - B. Filter plates
 1. Shape of dorsal edge
 2. Length to height ratios; amount of imbrication
 3. Number of filter rows on each plate
 - C. Filter mesh
 1. General density
 2. Folding pattern of filter rows (e.g., presence of 3° folds, length of 2° folds, etc.)
 3. Width of rows
 4. Abutment of rows
 5. Filter canals
 - a. general size compared to filter rows
 - b. covered or open
 - D. Branchial food traps (collecting organs)
 1. Relative area
 2. Secretory ridges
 - a. conspicuousness
 - b. size
 - c. uniformity
 - E. Glottis
 1. % visible as viewed from above
 2. Relative size
 3. Thickness and height of lips
 4. Size and conspicuousness of laryngeal disc
 - F. Esophageal funnel
 1. Profile
 2. Size
- IV. General shape of roof of mouth; length to width ratio; relative position of nares and median ridge
- V. Dorsal Buccal
- A. Prenarial arena
 1. Pustulations
 - a. pattern
 - b. numbers
 2. Projections and other features
 - a. shape
 - b. size
 - B. Nares
 1. Relative size and internarial distance
 2. Angle of orientation from transverse plane
 3. Anterior wall
 - a. height; thickness

- b. prenarial papillae
 - 1) number
 - 2) size, position
- 4. Posterior wall (narial valve)
 - a. relative height to length
 - b. narial valve projection—distinctiveness, height
- C. Postnarial arena
 - 1. Postnarial papillae
 - a. number
 - b. size, shape
 - c. position
 - 2. Median ridge
 - a. general shape
 - b. presence and number of serrations or secondary papillae on ventral margin
 - c. presence and size of pustulations or secondary ridge on anterior surface
 - 3. Lateral ridge papillae
 - a. size
 - b. shape
 - c. presence of secondary bifurcations
- D. Buccal roof arena (BRA)
 - 1. General shape
 - 2. BRA papillae
 - a. number
 - b. size—position of largest, uniformity in size
 - c. number bifurcated
- E. Pustulations and papillae elsewhere on buccal roof
 - 1. Numbers
 - 2. Region of concentration
- F. Glandular zone
 - 1. Secretory pits
 - a. distinctiveness, size
 - b. density
 - 2. Conspicuousness of anterior margin
 - 3. Relative length and uniformity of length
- G. Dorsal velum
 - 1. Length—maximum fully extended
 - 2. Presence on the midline
 - 3. Marginal papillation
- VI. Dorsal Pharynx
 - A. Pressure cushions
 - 1. Distinctiveness
 - 2. Size
 - 3. Shape of lateral cushion
 - 4. Shape of median cushion
 - B. Ciliary groove
 - 1. Depth
 - 2. Width

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