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Macroscopic and microscopic structure and age changes in the lingual papillae of the dog.

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MACROSCOPIC AND MICROSCOPIC STRUCTURE AND AGE CHANGES IN THE LINGUAL PAPILLAE OF THE DOG

by

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I. INTRODUCTION

There is a paucity of literature on the chemical senses in the canine. Nutritionists recognize the value of smell and taste in the palatability of foods. Food palatability is an important economic consideration for the manufacturer of commercial feeds for animals. Nutritionists have changed the diet of the dog from a strictly carnivorous to a partially omnivorous diet.

Scientists in the field of animal nutrition have recognized the significance of taste. Richter (1943) demonstrated that the sense of taste plays a critical role in nutrition and in maintaining a constant internal environment for the animal. He demonstrated that an adrenalectomized rat, when given a choice, drank enough salt water to maintain life and growth. If the parathyroid glands were removed, the rat showed an increased appetite for food containing calcium. Animals with a vitamin deficiency selected foods high in the deficient vitamin when allowed free choice. However, Richter (1943) pointed out that animals with resectioned peripheral taste nerves were no longer capable of regulating their diets to correct deficiencies and tended to eat indiscriminately.

Technically, age change studies are merely a study of the normal progressive variance in the tissues of an animal as they develop from the zygote to the time of death. Some investigators designate the period from the embryo to maturity as developmental changes. The chronological age of an individual is easy to obtain and classify, so the author prefers to use the term "age changes". The term, "normal age changes", is hard to define. A normal animal, if one ever exists in all respects, is one that conforms to the average of many apparently normal individuals. It is often difficult to distinguish between normal biological variation and a pathological condition.

These observations were performed on a limited number of individuals, so the author prefers to use the term "pattern" to designate average morphological conditions. These data are being collected as part of the overall problem connected with the sense of taste in the dog. The lingual papillae of the dog contain the end organs of the sense of taste, so their structure must be established before taste bud distribution on the tongue can be determined.

The objective of this investigation was to attempt to establish acceptable patterns for the structure of the lingual papillae, their distribution, their changes during aging and to investigate a new technique for resection of the chorda tympani nerve within the middle ear.

II. REVIEW OF LITERATURE

A. Embryology

A knowledge of embryological patterns can be very helpful in directing studies on adult morphology. There was a definite scarcity of literature on the embryology of the canine. Therefore, human embryological literature was drawn upon with the full realization that it may or may not have been fully applicable to the dog.

The tongue originated from the ventral ends of the branchial arches, Arey (1954), Patten (1953), Nelson (1953). The oral portion of the tongue was called the body and the pharyngeal portion the root. The body originated from the mandibular arches and was covered with ectodermal epithelium. Arey (1954) stated that the root originated primarily from the union of the second branchial arches, but received contributions from the third and fourth branchial arches. The root of the tongue was covered with entoderm. According to Arey (1954), the junction line between the ectoderm and entoderm was in front of the "V" shaped rows of vallate papillae. According to Johnston (1910) the taste buds of lower vertebrates originated entirely from entoderm. The dog did not have a visible foramen caecum to delimit this junction line as did the human tongue. However, the separating line between ectoderm and entoderm can be seen on the adult dog's tongue as an irregular, transverse line anterior to the vallate papillae.

Arey (1954) stated that at about the seventh week of fetal life the various papillae made their appearance. He further stated that in fetuses of nine and eleven weeks, the fungiform papillae may be distinguished grossly as elevations of the mucosa. The vallate papillae were entodermal in origin. In the tenth week, an epithelial ring developed around the vallate papillae and grew downward. This ring split by the fourth month, thus separating the vallate papillae from the rest of the mucous membrane, forming the typical trench around the papillae. At the same time epithelial outgrowth developed from the bottom of the trench; these were destined to become the glands of von Ebner, according to Arey (1954).

The foliate papillae of the human tongue were distinguishable as parallel folds during the third month of fetal life and the taste buds became distinguishable at about eight weeks, Arey (1954). He also stated that both the fungiform and vallate papillae in the human have dorsal taste buds. They disappeared from the top and were established on the sides of the vallate papillae before birth. Arey (1954) stated that the taste buds were entodermal in origin, but some taste buds were formed in ectodermal territory. He further stated that the taste buds start making their appearance at about the eighth week and that one taste bud preceded the appearance of each fungiform papilla on the dorsal surface. Several buds may be found on the dorsal surface of each vallate, but disappear before birth. Arey's account of the development of the human lingual papillae was interesting since this author found postnatal conditions in the dog that coincided with prenatal pictures in the human being.

According to Arey (1954), the chorda tympani branch of the facial nerve innervated the taste buds on the anterior two-thirds of the human tongue. The chorda tympani nerve was associated with the first branchial arches. The origin of the anterior two-thirds, or body of the tongue, was from the mandibular or first branchial arches. The glosso-pharyngeal nerve was associated with the third branchial arches and had sensory and motor components. The sensory components were derived from neuron bodies within the superior and petrosal ganglia (Nelsen, 1953). The portion of the glossopharyngeal nerve that supplied the taste buds on the posterior third of the tongue (from second, third and fourth branchial arches) was functionally classified as special visceral afferent. The vagus nerve was associated with the fourth and fifth visceral arches. The sensory components of the vagus nerve took their origin from neuroblasts of the neural crest which ultimately became incorporated in the jugular and nodosal ganglia. According to Nelsen (1953) the special visceral afferent fibers of the vagus nerve, whose cell bodies lie in the nodose ganglion, had their terminations in the taste buds of the pharyngeal area.

Embryological origins have not explained satisfactorily the innervation to the taste buds, especially in the area of the vallate and foliate papillae.

B. Structure of the Lingual Papillae

The terminology used in the literature to describe the lingual papillae was confusing. The author preferred to adopt the terminology of Bradley (1948) and Sisson and Grossman (1953) as it referred to the canine. Bradley (1948) referred to the filiform papillae as being the most numerous and occupying the dorsal portion of the tongue. He further stated that they were small anteriorly becoming increasingly larger posteriorly, finally blending with the conical papillae behind the "V" shaped rows of vallate papillae. He stated that the papillae were arranged in rows running backward toward the median groove. He noted that the conical papillae extended somewhat further back than the limits of the tongue.

Bradley (1948) described the location of the fungiform papillae as being similar to the distribution of the filiform papillae, but found none mixed with the conical papillae. He found the vallate papillae to be usually four in number; their position approximately limits the transition area between filiform and conical papillae.

Bradley (1948) described the foliate papillae as being two in number and located just anterior to the glossopalatine arch on the lateral edge of the mucosa of the tongue. He indicated that each papilla was crossed by six to eight ridge-like elevations.

According to Trautmann and Fiebiger (1952) the filiform papillae had merely a mechanical function and consisted of a connective tissue core derived from the lamina propria and covered with keratinized epithelium:

> In carnivores the connective tissue core extends above the surface epithelium and bears papillae of unequal sizes. The caudalmost of these is especially large (it is most distinct in the cat) and bears a thick caudally directed horny tooth. This primary papilla is braced by a rostral supporting papilla. Large conical papillae, whose core projects beyond the surface of the tongue, occur in all domestic mammals except the horse and donkey.

Thus, it seemed that the conical papillae were in conjunction with each filiform papilla. Such a classification was vague and leads to more confusion.

Trautmann and Fiebiger (1952) characterized the fungiform papillae as having soft epithelium and abundant taste buds.

Trautmann and Fiebiger (1952) described the vallate papillae as being surrounded by clefts lined with epithelium. The vallate papillae projected only slightly above the rest of the epithelium of the tongue. They described the glands of von Ebner as emptying into the moat or bottom of the cleft, and stated that in carnivores the gustatory field was restricted to the bottom of the moat and was therefore very small.

Trautmann and Fiebiger (1952) further stated that taste buds were usually absent in the surface epithelium of each papilla as well as in the peripheral wall of the moat.

Trautmann and Fiebiger (1952) described the foliate papillae as consisting of a series of parallel connective tissue ridges, bearing secondary papillae that projected into the covering squamous epithelium. The gustatory furrows separated the leaves or secondary papillae of the foliate papillae. The foliate papillae also had serous as well as mucous glands emptying into the moat at the bottom of each gustatory furrow.

Maximow and Bloom (1953), Greep (1954) and Smith and Copenhaver (1953) described the lingual papillae of the human. According to Maximow and Bloom (1953) the filiform papillae were 2 to 3 millimeters long and had a connective tissue core with secondary pointed papillae. They did not mention the conical papillae in their discussion. Smith and Copenhaver (1953) described the filiform papillae as being very numerous and evenly distributed over the anterior two-thirds of the tongue. It was apparent that there was some debate as to what constituted a filiform papilla and what was a conical papilla.

A fungiform papilla, according to Maximow and Bloom (1953) was characterized by having a short, slightly constricted stalk and a spherical, slightly flattened upper part. The connective tissue core formed numerous secondary papillae. The epithelium covering them, however, was thin and smooth. The taste buds may be found on the ends of those secondary dermal papillae. Smith and Copenhaver (1953) and Greep (1954) concurred with Maximow and Bloom (1953) in their description of the fungiform papillae.

The circumvallate or vallate papillae of the human were thus described by Maximow and Bloom (1953):

> The circumvallate papillae are sunk into the surface of the mucous membrane, and each is surrounded by a deep, circular furrow. The connective tissue core forms secondary papillae only on the upper surface. The covering epithelium is smooth, while that of the lateral surface of the papillae contains many taste buds...... In the outer wall of the groove surrounding the papillae a few taste buds may be present.

The glands of von Ebner secrete into the bottom of these furrows. Greep (1954) concluded that there were from six to twelve vallate papillae in the human, measuring 1 to 3 millimeters broad and 1 to 1.5 millimeters in height.

Maximow and Bloom (1953) located the foliate papillae of the human on the lateral surface of the posterior part of the tongue. They stated that these papillae were rudimentary.

Tuckerman (1889) described the gustatory organs of Vulpis vulgaris (fox). This was the only description of the dog's gustatory organs that was found in the literature. He related the following about the cone-shaped papillae of the dog's tongue:

> About the root and extreme posterior borders are thick, coarse, fleshy, recurved cone-shaped papillae. The rest of the dorsal surface is covered with small, closely-set cone or club-shaped mechanical papillae, having their apices directed backwards.
>
> Each papillae is seated upon one or two papillary upgrowths of the mucosa and has from one to three minute spines projecting from its upper surface.

Tuckerman's description of the vallate, foliate and fungiform papillae was similar to that of Maximow and Bloom (1953), Greep (1954), and Smith and Copenhaver (1953).

Miller (1952) described the conical or filiform papillae as being synonymous terms. He did, however, make a distinction between the large, unusually long filiform papillae on the root of the tongue, and the smaller filiform papillae on the body of the tongue. Miller (1952) stated that the fungiform papillae were scattered mostly over the tip and body of the tongue at 2 to 3 millimeter intervals. He further stated that the foliate papillae were very small in the dog, having occasionally two or three leaves that could be recognized along the lateral border near the junction of the body with the root. The vallate papillae were located by Miller (1952) on the dorsal surface of the root of the tongue; they numbered two to six and measured about 1 millimeter in diameter.

According to Sisson and Grossman (1953), the papillae back of the row of vallates were designated as conical papillae.

According to Hollingworth and Poffenberger (1917), the filiform papillae were conical or cylindrical in form and varied in height from 1.5 to 2.5 millimeter. They further stated that sometimes these papillae were covered with tiny secondary papillae which were not apparent to the unaided eye.

Sonntag (1923) described the morphology of the tongue of the carnivora, and was in agreement with the above workers' descriptions. He failed to make a distinction between the so-called conical and the filiform papillae.

Kutuzow (1951) described the filiform and conical papillae of white rats, but the morphology of the rat's tongue was different from that of the dog. She categorized conical papillae as having simple and giant forms. However, they had the same general distribution over the dorsum of the tongue as did the filiform papillae. It is interesting to note that Kutuzow's conical papilla had only one prominence and rested on one dermal papilla.

Huber and Eggerth (1917) described the foliate papillae of the rabbit from a morphogenic viewpoint. They were very prominent in the rabbit, but again the morphology of the rabbit's lingual papillae did not coincide with that found in the dog.

Review of the literature indicated the need for coordination and definition of terms used to describe the lingual papillae of the dog. In addition, the lingual papillae of the canine were not adequately described in all respects.

C. Innervation of the Taste Buds of the Dog and Man

The nerves to the sense of taste most often referred to in the literature included: the chorda tympani, glossopharyngeal, vagus and the lingual nerves. There was some debate as to the role each nerve played in innervating the taste buds.

Arey (1954) used the branchial derivatives to link the various cranial nerves with their areas of innervation. This may have been significant in some cases, but the area of conflict, namely around the vallate and foliate papillae, was still inaccurately mapped in the dog.

Parker (1922) stated that there may be four sources of innervation to the taste buds, namely: vagus, glossopharyngeal, facial and trigeminal nerves. He stated that the vagus was distributed to the larynx and epiglottis as well as to the posterior part of the tongue itself. He further stated that the glossopharyngeal nerve supplied the posterior third of the tongue including the foliate and vallate papillae. The latter statement was first recorded by Vintschgau and Honigschmied (1876). These latter two men cut the glossopharyngeal nerve and noted the disappearance of the taste buds on the vallate and foliate papillae. Parker (1922) explained that there was some decussation in the case of the innervation to the central vallate papillae in the human. Whiteside (1927) noted in the rat that there was nerve overlap, or a gustatory chiasma, along the center of the tongue. The overlap was greatest just in front of the vallate papillae and again on the very tip of the tongue. The single vallate papilla of the rat was dually innervated according to Whiteside (1947). The foliate papillae of the rat were also found to have a dual innervation since all of them did not degenerate upon resection of the glossopharyngeal nerve.

Parker (1922) had some doubts as to the complete innervation of the anterior two-thirds of the tongue; he mentioned the trigeminal, facial and glossopharyngeal nerves. He felt that all of these nerves communicated through a plexus of fine branches near their roots.

Cushing (1903) concluded that when the Gasserian ganglion was extirpated in the human, the sensation of taste returned to the anterior two-thirds of the tongue after some time. He assumed that the chorda tympani nerve was left intact. He also believed that the degenerating trigeminal fibers had an adverse effect on the chorda tympani fibers, and thus caused a temporary loss of taste impulses over the chorda tympani nerve.

Hollingworth and Poffenberger (1917) stated that the lingual nerve conveyed the taste fibers from the anterior two-thirds of the tongue, that the glossopharyngeal nerve carried fibers from the posterior third of the tongue, including the base of the tongue, soft palate and foliate papillae, and that the vagus carried fibers from the epiglottis and larynx. They also believed that the chorda tympani nerve was the connecting link between the facial nerve and the lingual branch of the fifth cranial nerve. They mentioned the fact that the chorda tympani traveled across the cavity of the middle ear before joining the facial nerve.

Gowers (1902) concluded that upon extirpation of the Gasserian ganglion (semilunar ganglion) of the human, there was a complete loss of taste both anterior and posterior to the vallate papillae. Cushing (1903) concluded that upon extirpation of the Gasserian ganglion there was a temporary loss of taste on the affected side anterior to the vallate papillae. He attributed this to mechanical or toxic interference with the conduction within the chorda tympani nerve, due to the degeneration of the lingual nerve.

Harris (1953) believed that tactile sensibility (including pain and thermal fibers) in the tongue and palate had, in the great majority of persons, an important share in the recognition of taste sensations. He believed, therefore, that loss of the fifth nerve will impair the acuity of taste for most persons. This may explain partial recoveries after extirpation of the fifth nerve ganglion.

Dixon (1897) supported the idea that the chorda tympani, branch of the facial nerve, and the nerve of Jacobsen from the glossopharyngeal nerve, carried the sensations of taste to the higher center.

Ferguson (1890) declared that the fifth nerve received all of the impulses of taste. Impulses traveled over the chorda tympani to the vidian nerve and then to the fifth nerve via the otic ganglion. Impulses traveled over the glossopharyngeal nerve to the mandibular nerve via the tympanic plexus and geniculate ganglion, and over the lesser petrosal nerve to the otic ganglion and hence to the fifth nerve, according to Ferguson (1890).

Wirtanen and Olmstead (1934) devised two experiments to determine whether the nerves of taste traveled back to the brain via the fifth cranial nerve. They cut the vidian nerve in the cat and severance of this nerve failed to cause any degeneration of the taste buds. They also had some surgeons remove the semilunar (Gasserian) ganglion in the dog and this also failed to cause the degeneration of the taste buds on the anterior two-thirds of the tongue.

Olmstead (1921) cut the lingual nerve in the dog and concluded that the taste buds disappeared from the fungiform papillae on the anterior two-thirds of the tongue. He further stated that only the taste buds on the operated side were affected. The taste buds degenerated and were phagocytized by leucocytes. Cells resulting from mitosis in the germinative layer filled in the vacancy left by the degenerated taste buds.

Olmstead (1922) severed the chorda tympani branch of the facial nerve in two dogs just cranial to its junction with the lingual. This was difficult to accomplish and a great deal of trauma was produced in the area. There were a number of failures before two specimens survived. All papillae which were examined from the operated side, were lacking in taste buds. Taste buds were present on an equal number of papillae on the unoperated side. Olmstead (1922) declared that it was almost impossible in brachiopcephalic breeds to expose the chorda tympani nerve using this technique. He also cut the mandibular nerve just cranial to the junction of the chorda tympani nerve with the lingual nerve, but it had no effect on the appearance of the taste buds on the operated side. He stated that this particular dog had great difficulty in drinking and the left side on the tongue was paralyzed.

Schwartz and Wendell (1938) observed human patients operated on for tic doulaureux, and postulated two possible routes for the taste fibers coming from the anterior two-thirds of the tongue. The classical route via the chorda tympani nerve to the geniculate ganglion and then through the intermediate nerve to the brain, was their most often encountered route. The second route was over the chorda tympani nerve through the otic ganglion to the greater superficial petrosal nerve, and hence to the geniculate ganglion and the intermediate nerve. Schwartz and Wendell (1938) stated that the greater superficial petrosal nerve was much the lesser of the two routes. Other authors (previously referred to) stated that the course of taste impulses was from the geniculate ganglion over the greater superficial petrosal nerve to the semilunar ganglion. This is the reverse of the direction described by Schwartz and Wendell (1938).

Lewis and Dandy (1930) compiled an extensive foreign bibliography and were of the opinion that there was but one course from the chorda tympani nerve to the geniculate ganglion through the intermediate nerve.

Sabotky (1918) believed that the route of taste impulses from the anterior two-thirds of the tongue was via the chorda tympani branch of the facial nerve.

Harris (1953) believed that in a small minority of cases, taste was permanently lost or much diminished in intensity after fifth nerve lesions. He believed that the vast majority lost taste perception immediately after extirpation of the Gasserian ganglion, but regained it after varying periods of time. Many workers failed to determine the taste threshold before the operations, so they had no control by which to accurately judge the acuity of taste perception after the operations. Some clinicians that tested the acuity of taste before the operations, found some patients to be taste blind or partially deficient.

Olmstead and Pinger (1936) severed the lingual nerve with its chorda tympani nerve component, and anastomosed the distal cut end of the lingual nerve with the proximal cut end of the hypoglossal nerve. They concluded that the hypoglossal nerve can initiate regeneration of the taste buds which have disappeared from the fungiform papillae on the operated side. The hypoglossal nerve is a motor nerve primarily, but it may carry a few afferent proprioceptive fibers. It was difficult to understand how a motor nerve could cause the regeneration of sensory endings.

According to May (1925), regeneration of taste cells was brought about when the regenerating neurofibrils entered the places where taste buds had formerly existed. However, it is not the scope of this review to explain or test the facts and theories of taste bud regeneration.

III. MATERIALS AND METHODS

A. Age Groups Studied and Collection Procedures

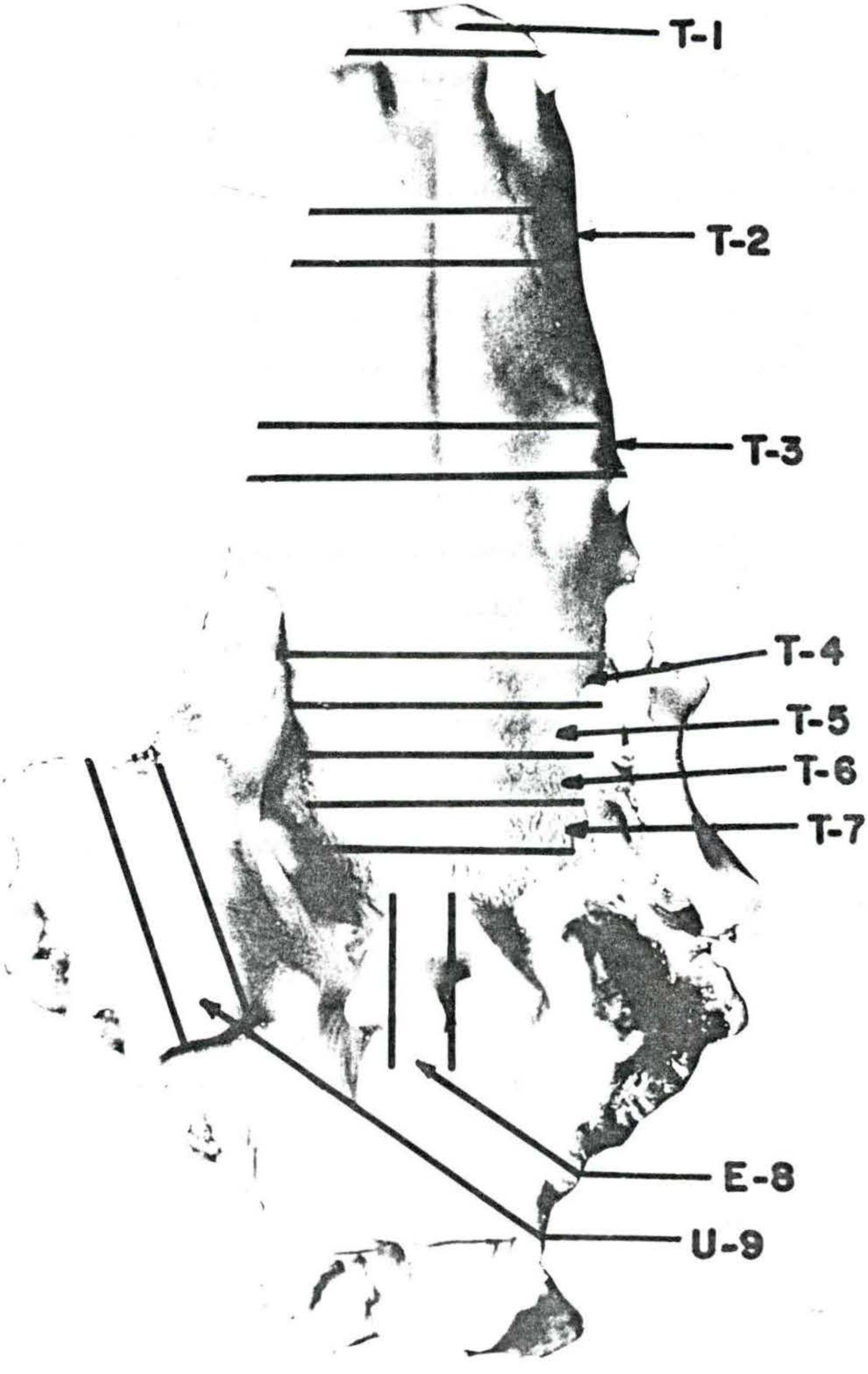
Any problem involving age change studies in dogs must allow for the sampling of dogs of a known age group. A dog colony was started by the writer for this expressed purpose. It was expedient to use mongrel dogs in the beginning, Fig. 9, and to supplement these numbers with two purebred dogs at the end of the experiment.

The diet for the dog colony was furnished by Gaines Dog Foods, General Foods Corporation, Kankakee, Illinois. The nutritional analysis of Gaines Meal was furnished by Gaines Research and Development Laboratory (1953). One-half of the protein of Gaines dog food was from animal sources, one-third from special vegetable sources and one-sixth from cereals. The ration contained 1500 to 1600 calories per pound of feed. This analysis compared favorably with the analysis given in the booklet "Nutrient Requirements for Dogs" published by the National Research Council (1953). The ration was fed dry, in self feeders, from weaning to the termination of the experiment. The dogs had access to fresh tempered water at all times. No symptoms of nutritional deficiency were in evidence throughout the experiment.

Internal parasites were controlled by careful sanitation and regular fecal examinations. When worming was necessary, either N-Butyl Chloride or Vermiplex capsules were used according to the dose schedule and directions furnished by the manufacturer. Fleas and lice were controlled with a commercial benzene hexachloride mixture.

A total of thirty-two dogs were used in this study. The following age groups were represented: one dog at birth, one dog at 12 hours, two dogs at 30 hours, two dogs at three days, two dogs at one week, two dogs at two weeks, two dogs at three weeks, three dogs at four weeks, two dogs dogs at six weeks, two dogs at eight weeks, two dogs at ten weeks, two dogs at 12 weeks, two dogs at 16 weeks, two dogs at 20 weeks, two dogs at 24 weeks, two dogs at 28 weeks and one dog at four years of age. The dogs were destroyed by electrocution, which was found to be instantaneous and humane. Nine tissue blocks were taken from each dog according to the areas shown on Fig. 1. .Seven areas were taken from the tongue proper, one from the epiglottis and one from the uvula. A series of tissue baskets were devised by the writer (Appendix, Fig. 33) made of stainless steel tubing and screen. This allowed very accurate control of the tissues from fixation into the paraffin block. A raw data sheet (Appendix, Fig. 34) was used to record the various procedures employed. The paraffin tissue blocks were accu-

Fig. 1. The tongue, epiglottis and uvula of the dog, indicating where the various blocks of tissue were taken. T-1 through T-7 are blocks from the tongue. Block E-8 represents the section taken from the epiglottis and Block U-9 the block taken from the uvula.


T-1
T-2
T-3
T-4
T-5
T-6
T-7
E-8
U-9

rately identified in long blocks representing the nine areas to be studied. The pieces of tissue taken were approximately six to eight millimeters thick. They were fixed in approximately 40 times their volume of a ten percent solution of commercial formaldehyde for 24 to 48 hours. The tissues were dehydrated in a series of ethyl alcohols from 70 percent up through two changes of absolute alcohol, cleared in cedar oil for 24 hours, and the cedar oil removed in three changes of benzene for an hour each and infiltrated in three changes of 54 degree centigrade paraffin for one to one and one-half hours each. The tissues were embedded in long trays (Appendix, Fig. 33) which enabled accurate records to be kept of each series of tissues.

The nine blocks were sectioned at eight microns on a Spencer Rotary Microtome. Five to 20 slides were made of each block of tissue. The sections were taken at various places in the long ribbons of tissue. There were from five to 18 serial sections on each slide.

Six hundred slides were prepared in the above mentioned fashion for the microscopic study of the structure of the lingual papillae. In this study the individual papillae were taken instead of a whole transverse section of tongue. The five types of lingual papillae were cut in three different planes: frontal (horizontal), transverse (cross), and sagittal or (longitudinal). The blocks were cut serially to facilitate a complete study of the lingual papillae.

B. Staining Procedures

Castroviejo's (1932) trichromic stain was used on the majority of the slides studied. Only a slight modification was found to be necessary. The acetic-fuchsin-formalin mixture had to be prepared fresh every day. The picro-indigo-carmine mixture was good indefinitely.

The slides were stained with acetic-fuchsin-formalin mixture for five minutes, washed briefly in water and stained in picro-indigo-carmine for five minutes. The slides were hurried up the alcohol series to absolute alcohol and then into carbol-xylol (75 percent xylene, 25 percent phenol crystals) for three minutes. They were rinsed in xylol and the cover glass was mounted.

The results of this stain were very brilliant. The epithelium was red; connective tissue, blue; nuclei, dark red; erythrocytes, yellow; and muscle, yellow green.

Harris' hematoxylin was used, Guyer (1936). The tissue sections were stained for five minutes in hematoxylin. The sections were then decolorized in a one percent acid alcohol and intensified in one percent alkaline alcohol. The eosin stain was prepared according to the technique of Pearson (1942). The sections were stained for 30 seconds in this eosin preparation. The slides were cleared in two changes of xylol and coverslips were mounted, using Technicon mounting medium.

C. Procedures for Subgross and Gross Observations

1. Subgross procedures

Ths lingual papillae of the dog were studied using a Spencer Stereoscopic Microscope on an adjustable arm. The eye pieces were 15X magnification, while the objectives were 1X, 3X, and 6X respectively. An alcoholic solution of crystal violet was used as contrast medium to stain the gross structure of the lingual papillae. Subgross pictures were taken through one eye piece receptacle of this microscope using the Leitz Micro Ibso attachment and the Leica camera.

2. Gross procedures

The gross procedures were concerned with the methods and techniques employed for the dissection and operative techniques concerned in a new approach to the specific nerves of the sense of taste.

Any experimental surgical procedure should be preceded by a thorough anatomical study of the area involved. A total of six embalmed dogs were used for this phase of the problem, and numerous fresh heads were dissected. The embalming mixture was composed of a solution of isopropyl alcohol, formaldehyde, phenol, glycerine and water. The arteries were injected with red latex in the left carotid artery near the thoracic inlet. The veins were injected with blue latex through the angularis oculi vein on the right side.

The gross anatomy of the entire area from the manubrium sterni to the symphysis of the mandible was carefully dissected, but only that anatomy closely associated with the operative field was described.

Eighteen mongrel dogs ranging in age from six weeks to maturity were used in this phase of the experiment. Surgical anesthesia was accomplished by the administration of pentobarbital sodium.

IV. INVESTIGATION AND FINDINGS

A. Macroscopic Anatomy

1. Submacroscopic structure of the lingual papillae

a. Filiform. The filiform papillae were located on the anterior two-thirds of the tongue. Their most posterior extent coincided with the uneven line in front of the vallate papillae, Fig. 2. The terminal line began at the anterior extent of the group of foliate papillae, crossed toward the mid-line to the anterior laterally located vallate papilla, and passed backward along the anterior edge of the vallate papillae to the mid-line. There was no central vallate papilla in the canine, so the filiform papillae blended with the conical papillae just caudal to the posterior medially located vallate papillae.

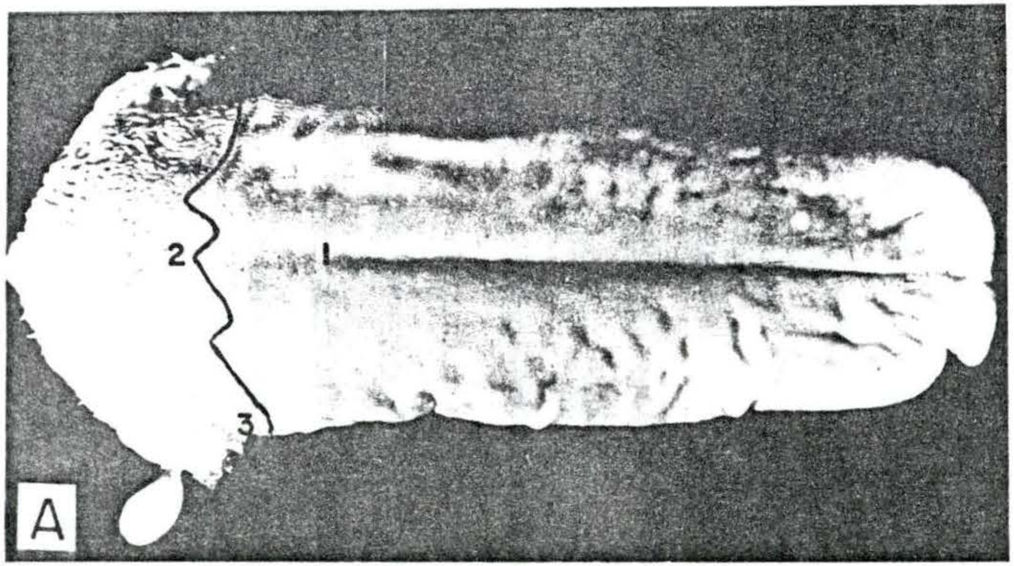
The filiform papillae were greatly modified on the lateral edge of the tongue of the puppy up to six weeks of age, Fig. 7D. This fringe of modified filiform papillae disappeared from the puppy's tongue at six to eight weeks of age. This fringe of papillae on the lateral edge of the tongue was used extensively by the suckling pup to increase

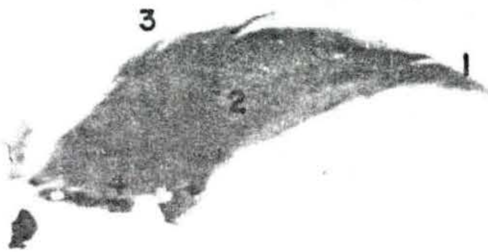
Fig. 2. The location and subgross structure of the filiform papillae

A. The dorsal view of the tongue of the dog
   1. Termination of the mid-dorsal groove of the tongue
   2. Medial junction of the conical and filiform papillae
   3. Area of foliate papillae

B. Subgross structure of filiform papilla, 240X
   1. Primary filiform
   2. Secondary filiform
   3. Tertiary filiform
   4. Basal papilla

C. Schematic drawing of filiform papilla
   1. Primary filiform
   2. Secondary filiform
   3. Tertiary filiform
   4. Basal portion of filiform papilla





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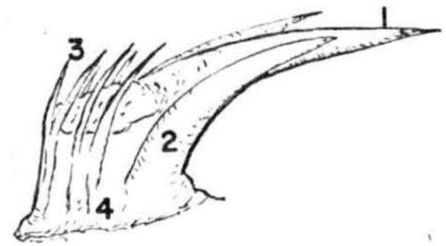


C

the area of contact with the nipple of the bitch. The anterior portion of the tongue of the pup had a natural dorsal concavity until after weaning when it became convex as the function of the tongue changed from sucking to lapping.

The filiform papillae were regularly arranged on the tongue of the dog. The rows were parallel to the "V" formed by the two rows of vallate papillae. Grossly they appeared as overlapping scales, with the free border of the scale directed caudally. The rows of filiform papillae from each side converged on the mid-line in a median groove. This groove was visible grossly from the tip of the tongue approximately three-fourths of the way back to the base of the tongue, Fig. 3A. It did not pass behind the apex of the "V" formed by the vallate papillae.

The gross structure of the filiform papilla is shown in Fig. 2. The term filiform means thread-like. It was not appropriate for the description of the entire papilla. The base of the filiform papilla was broad and tapered dorsally into many different sized filiforms, Fig. 2. The largest or primary filiform was located on the mid-caudal portion of the basal papilla. It had a large tooth-like projection that was curved posteriorly and overlapped the caudally adjacent one to form the scaly appearance. There were two secondary filiforms located laterally and slightly anterior to the primary filiform. There were five to seven filiforms, located on the

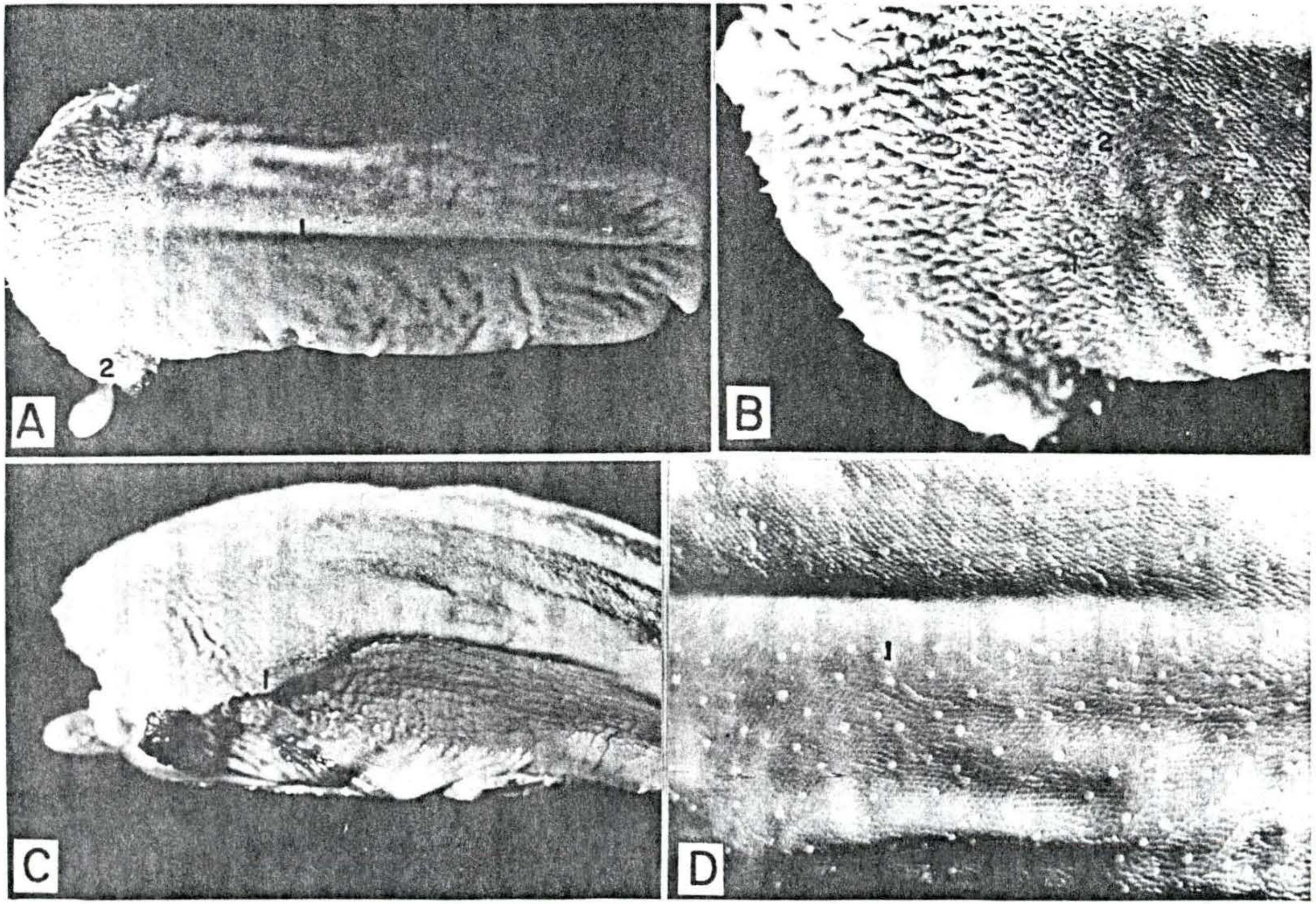
Fig. 3. The subgross structure of the surface of the tongue

A. Dorsal aspect of the whole canine tongue
   1. Median groove
   2. Anterior pillar attachment

B. Close up of the junction of filiform and conical papillae
   1. Vallate papillae
   2. Area of blending of the filiform and conical papillae

C. Lateral view of the tongue, indicating the junction of the papillated mucous membrane and the smooth ventral mucous membrane
   1. Area of foliate papillae

D. Dorsal aspect of canine tongue, higher magnification
   1. Fungiform papilla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anterior basilar portion of the parent papilla, which were called the tertiary filiforms. Fig. 2 indicates the location and relative size of these horny projections. The human description did not suffice for the canine filiform papillae as they were morphologically much different. Maximow and Bloom (1953) indicated that the filiform papillae were not keratinized in the human, as they had been found to be in the canine in this investigation. On the human tongue, the scales of the filiform papillae continually slough during health, but were retained during illness. Coating probably did not occur on the canine tongue because the morphology of the papillae was very different from that of the human. There was an inter filiform portion of the filiform papillae that resembled the surface of the fungiform papilla. However, the primary, secondary and tertiary filiforms so modified the shape of the basal papilla as to make the comparison difficult without the aid of a high power dissecting microscope.

b. Fungiform. The fungiform papillae were, in general, located from the tip of the tongue caudally to the anterior border of the "V" formed by the vallate papillae. However, contrary to many histology and anatomy texts, fungiform papillae were often observed back of the rows of vallate papillae. The fungiform papillae were not arranged in a regular fashion as were the filiform papillae, Fig. 4. They occurred indiscriminately over the surface of the tongue at 0.1 to 1.0 millimeter intervals. They were even so close in apposition as to coalesce occasionally, especially in the area of the vallate papillae. Fungiform papillae were found abundantly on the tip of the tongue and along the sides where the dorsal papillated lingual mucosa joins the smooth ventral lingual mucosa. There were no lingual papillae located within the ventral mucosa of the tongue. This last statement referred only to the epithelial papillae, as there were an abundance of dermal papillae in the ventral lingual mucosa.

In appearance, the fungiform papilla, Fig. 4, was mushroom-shaped. This was less evident in the canine than in the human fungiform papillae. The base of the fungiform papillae of the canine was only slightly constricted. The dorsal surface was rounded and smooth in the canine. Gross measurements varied from 0.2 millimeter to 0.75 millimeter in diameter. In an adult animal, the fungiform papillae may measure as much as 1.0 millimeter in diameter. These papillae were few in number and were located in the area of the vallate papillae. The diameter is smallest, 0.2 millimeter on the tip of the tongue and largest 0.5 to 0.75 millimeter on the caudal portion of the tongue. Fig. 4 shows the gross structure of the fungiform papillae.

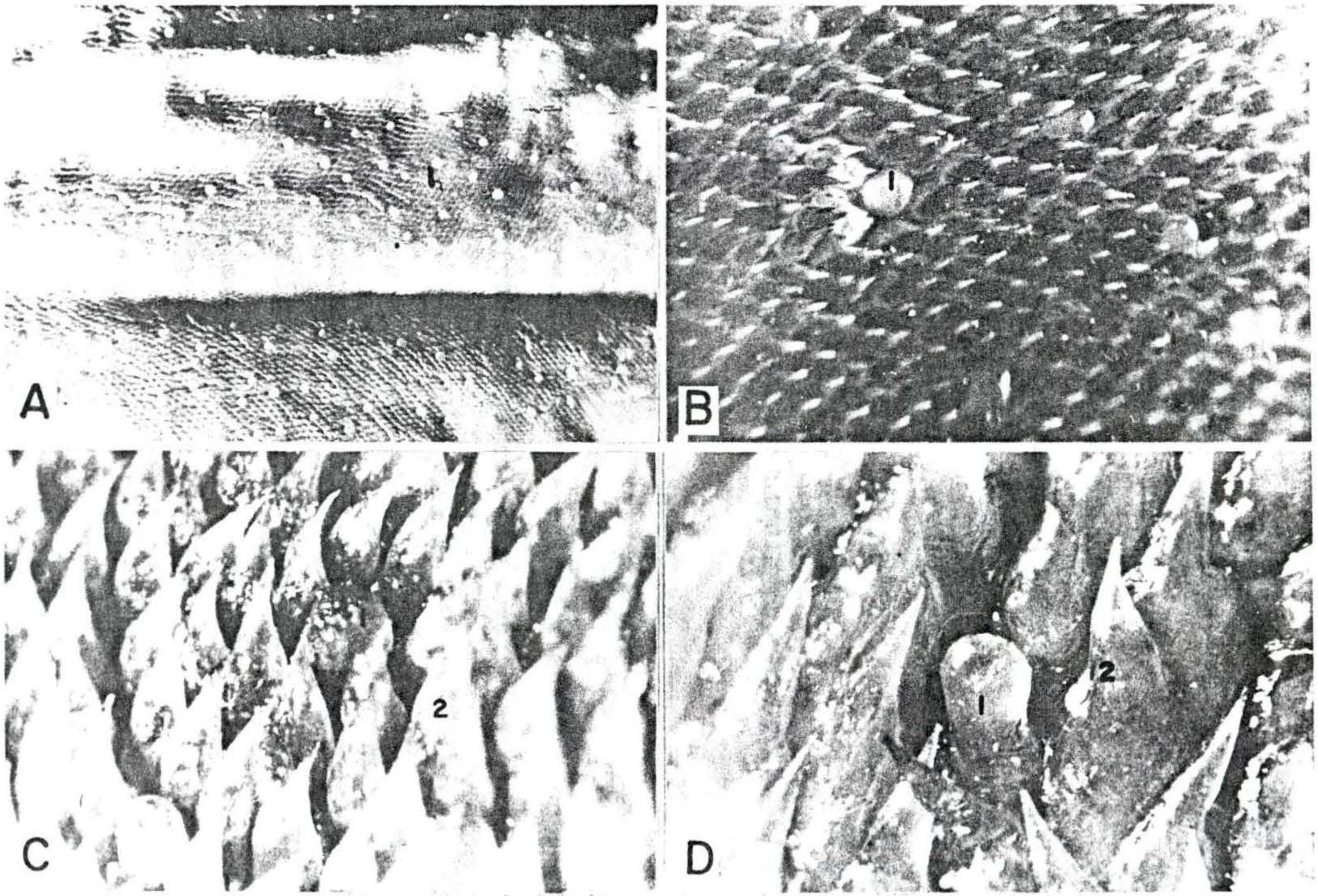
Fig. 4. Subgross structure of the fungiform papilla

A. Dorsal aspect of the tongue, approximately six magnifications
   1. Fungiform papillae

B. Isolated fungiform papillae among the filiform papillae, approximately 20X
   1. Dorsal view of fungiform papilla

C. Fungiform papillae among the conical papillae, approximately 40X
   1. Fungiform papilla. There is another papilla in the lower left hand corner of this view
   2. Conical papilla

D. Isolated fungiform papilla among the conical papillae
   1. Fungiform papilla, showing only a slight constriction at the base of the papilla
   2. Conical papilla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c. Vallate. The vallate papillae usually numbered four to six and were located at the junction of the anterior two-thirds and the posterior one-third of the tongue. The vallate papillae were arranged in the form of a "V" with the apex of the "V" directed posteriorly. The dog did not have a medial vallate papilla as did the human. The vallate papillae delineated the area of junction of the filiform and conical papillae in the canine. As many as five vallate papillae were seen on one side, and three on the other side of the tongue. However, one vallate papilla was located 0.5 millimeter caudal to the middle papilla in among the conical papillae.

The vallate papillae had a deep moat or trench around the papilla proper, Fig. 5. The wall of the moat was covered with stratified squamous epithelium and on the surface it was formed into swirls of modified conical papillae, Fig 5, whose apices were directed caudally.

The dorsal surface of the vallate papilla did not have epithelial projections as it did in the human, but there was a depression in the middle of the papilla proper that varied in depth and size as the papilla changed its shape, Fig. 5.

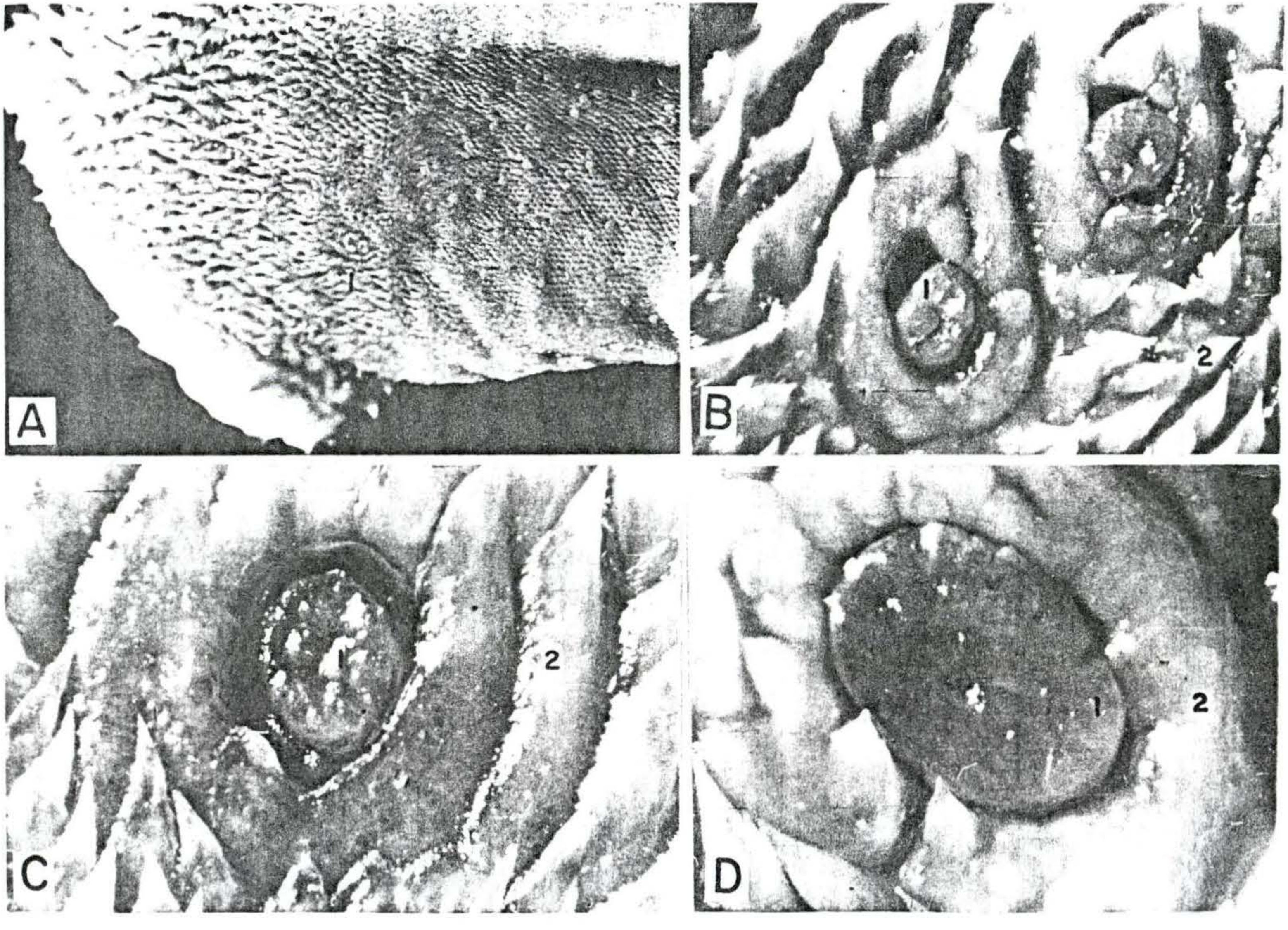
Average measurements of the vallate papillae of the canine varied from 1.5 to 2.5 millimeter in diameter, but this measurement did not include the ring around the papilla.

Fig. 5. A. Posterior half of tongue, approximately 6X
1. Just above this figure on the picture are located the vallate papillae

B. Close up of two vallate papillae, approximately 20X
1. Vallate papilla proper. Note the depression in its center. Also note the swirls of modified conical papillae forming the ring around the papilla proper
2. Transitional form of filiform papillae. This area has characteristics of both filiform and conical papillae

C. Vallate papilla, approximately 25X
1. Vallate papilla proper
2. Modified conical papilla contributing to swirl around papilla proper

D. Vallate papilla, approximately 50X
1. Vallate papilla proper, showing the depression in the dorsal surface
2. Ring around vallate papilla. Note the moat between number 1 and number 2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In a few instances, much larger papillae were observed, but they were not included in the "average". The entire vallate papilla, including the ring, measures 3.5 to 5.0 millimeters in diameter.

d. Foliate. The foliate papillae were described as two distinct papillae on each side of the root of the tongue. They were located just anterior to the anterior pillar of the fauces. Miller (1952) described two papillae composed of two or three leaves each, as the foliate papillae of the dog. Bradley (1948) counted two papillae crossed transversely by six to eight ridge-like elevations. In the human, histologists distinguished only two papillae which were oval bulgings in the mucous membrane containing parallel ridges. In order to clarify the terminology, the author distinguished the oval bulging as the area of the foliate papillae and each bulge as consisting of eight to 12 foliate papillae. According to Dorland's Medical Dictionary, foliate meant "having leaves", "leaf-shaped"; papilla, "any small, nipple-like process of connective tissue". The author observed that each leaf-like projection of the so-called foliate papilla was similar in structure, both macroscopically and microscopically, to either the fungiform or vallate papillae. The taste buds were located on the sides of these papillae as well as the dorsal surfaces, similar to the locations on the fungiform or vallate papillae.

Grossly, Fig. 6, the leaves, or papillae were not arranged in parallel rows as they were reported to be in the human, Maximow and Bloom (1953). The leaves or primary papillae were arranged like the petals of a flower. They had a definite point toward which the basal portion of each papillae converged, Fig. 7. The papillae in the middle of the series were more parallel than those anteriorly or posteriorly located. The author observed from eight to 14 of these primary foliate papillae or leaves on each side of the tongue. At the bottom of the furrow between each papilla was a blind crypt or pocket that penetrated into the subepithelial connective tissue of the tongue. Dorsally, these papillae were continuous with the conical papillae back of the rows of vallate papillae.

e. Conical. There was a transition area just anterior to the vallate papillae, Fig. 2, between the filiform and the conical papillae. The filiform papillae became reduced in size until only the primary filiform remained.

The conical papillae progressively increased in size as the area of the epiglottis was approached. They became the largest on the posterior portion of the root of the tongue, Fig. 8.

The structure was similar to the filiform papilla.

Fig. 6. A. Lateral view of tongue showing the location of the foliate papillae
1. Foliate papillae, approximately actual size

B. Close up of foliate papillae
1. Gustatory furrow between two foliate papillae
2. Dorsal blending of the tops of the foliate papillae with the conical

C. Close up of foliate papillae, approximately 10X
1. Foliate papilla

D. Another group of foliate papillae
1. A foliate papilla. Note the two gustatory furrows on each side of this papilla

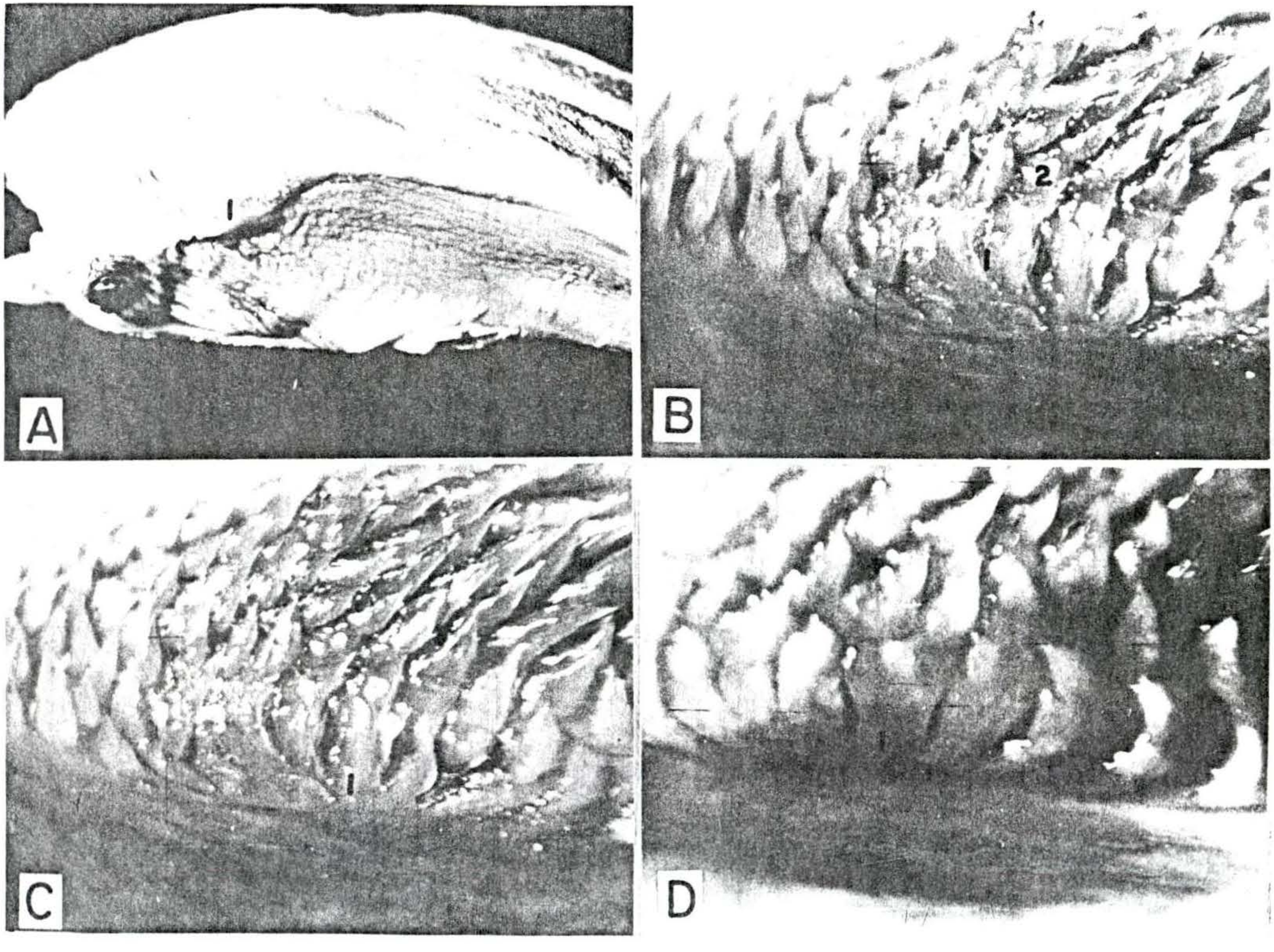
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Fig. 7. A. Lateral view of another group of foliate papillae
1. Vertical foliate papilla in center of group
2. Caudal-most foliate papilla of the group. Note the convergence toward a more central point of the base of this papilla

B. Another group of foliate papillae
1. Central, vertical foliate papilla
2. Gustatory furrow between papillae

C. Another group of foliate papillae
1. Central, vertical foliate papilla

D. Modified filiform papillae on the anterior lateral edge of the tongue of the puppy. This fringe is lost between six and eight weeks
1. A modified filiform papilla
2. Dorsal, papillated mucous membrane

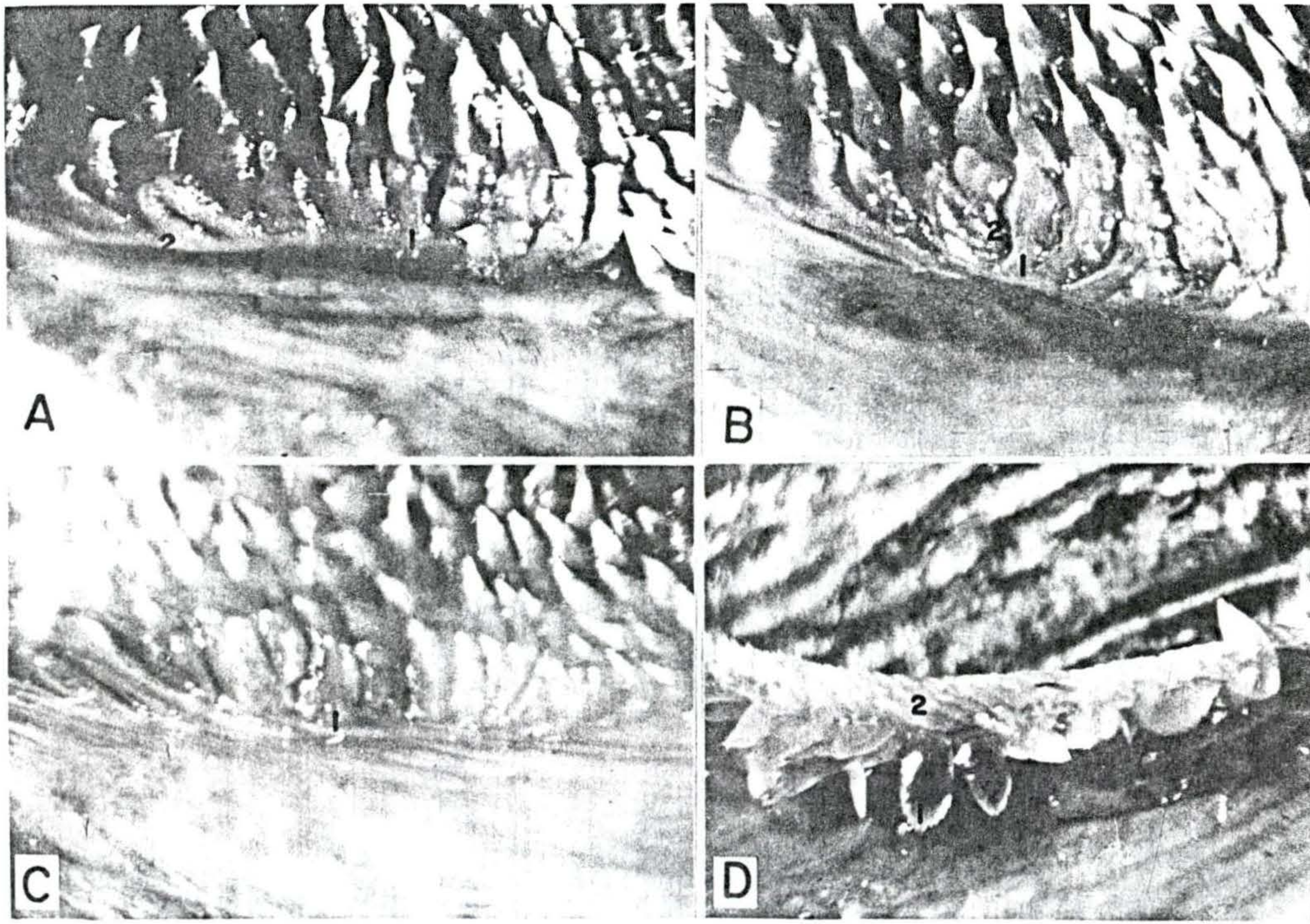
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Fig. 8. A. Low power of the posterior half of the tongue of the canine, approximately 6X

1. Fungiform papilla just anterior to the junction line of the filiform and conical papillae. Note the increase in size of the conical papillae as the posterior portion of the tongue is reached

B. Close up of conical papillae posterior to the vallate papillae, approximately 10X

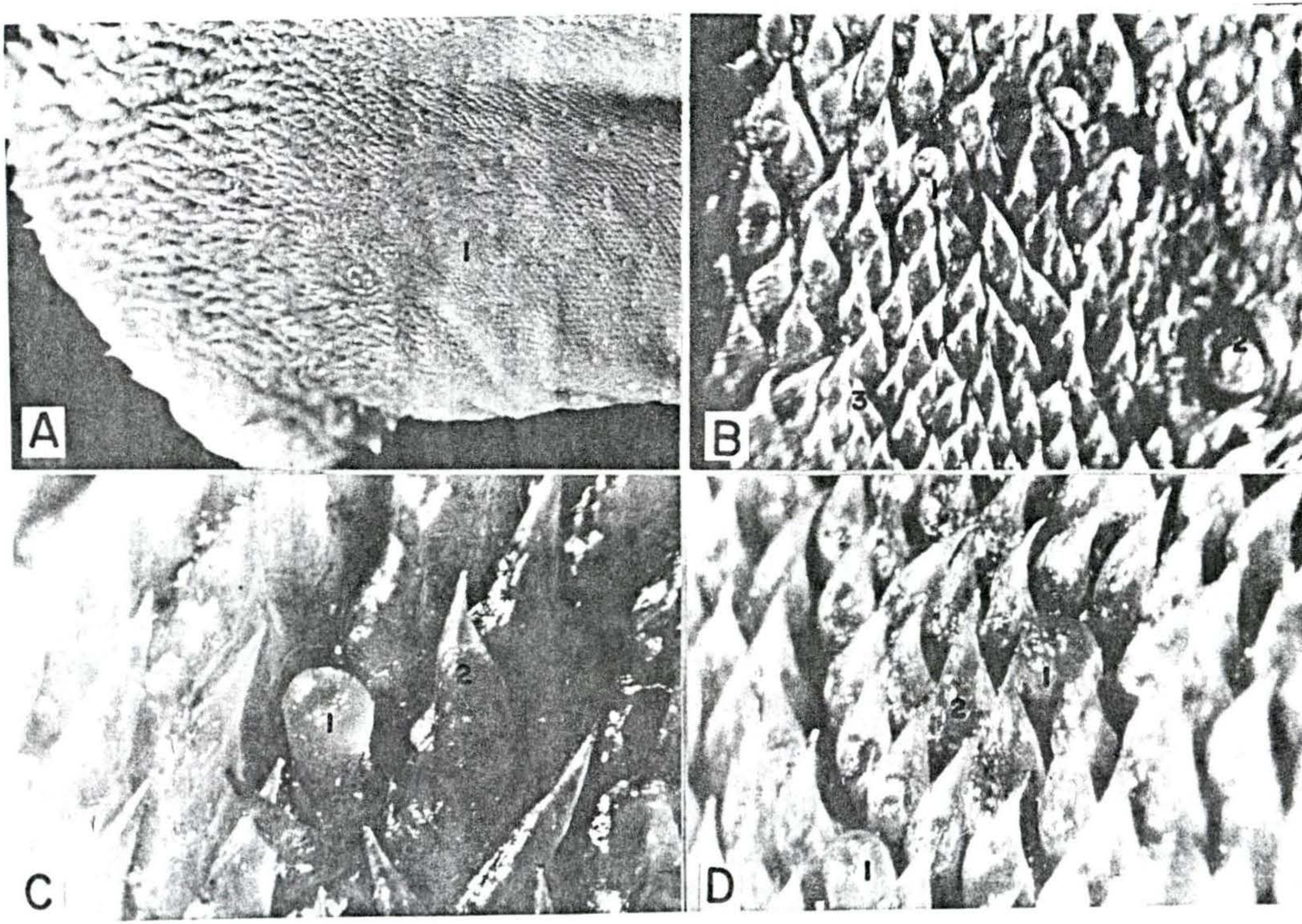
1. Fungiform papillae located behind the row of vallate papillae in among the conical papillae
2. Vallate papilla
3. Conical papilla with its apex directed caudally

C. Close up of conical and fungiform papillae, approximately 40X

1. Structure of fungiform papilla located among the conical papillae. Note the slightly constricted base and the smooth dorsal surface
2. Conical papilla. Note the large base tapering to the sharp pointed apex

D. High power of conical papillae, approximately 40X. Note the scale-like appearance of the overlapping conical papillae

1. Fungiform papillae located back of the vallate papillae among the conical
2. Conical papilla undisturbed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However, the conical papilla had only one large caudally directed pointed filiform or cone, Fig. 8. The basal portion of the papilla was very large and tapered very quickly to a soft point. As the area of the epiglottis was approached, the conical papillae not only became larger, but also became further apart. The gross measurements of the conical papilla varied from 3.0 to 9.0 millimeters in length, depending on the size of the tongue. The size of the tongue, either from differences in breed or age, was the more important factor in determining average measurements.

2. Distribution of lingual papillae

Distribution studies were difficult to make on mongrel dogs, especially because of the differences in size. It possibly would be much more accurate on purebred dogs and taken as a developmental problem. The lingual papillae counts are recorded in Fig. 9.

The vallate papillae of the canine were relatively constant in location and number. They were located at the junction of the body and root of the tongue, just opposite the anterior pillar of the fauces. The papillae were arranged in two converging rows forming a "V" whose apex was directed caudally. No central vallate papilla was found in

Fig. 9. The lingual papillae counts on the tongues of 18 dogs of mixed breeding and ages

Breed	Age	Vallate Pap. Side Rt.	Vallate Pap. Side Lt.	Foliate Pap. Side Rt.	Foliate Pap. Side Lt.	Fungiform Papillae Per Sq. Cm. Area No's 1	2	3	4	5	Filiform Papillae Per Sq. mm. Area No's 1	2	3	4	5	Conical Pap. Per Sq. mm. Area No's 6
Laborador X	4W	3	2	12	11	43	39	52	62	64	25	22	22	20	17	6
Border Collie X	2M	2	2	13	11	27	30	31	33	32	29	19	15	13	10	3
Border Collie X	2M	2	2	14	13	30	24	25	25	32	28	19	11	12	12	5
Wierhaired X	3M	2	3	8	9	14	20	37	38	31	25	19	10	9	8	2
Collie X	3M	2	2	6	5	16	24	29	29	31	21	16	9	9	8	2
Fox Terrier X	4M	2	1	6	9	22	22	31	40	36	25	15	12	10	11	3
Fox Terrier X	6M	2	3	8	10	23	17	13	21	115	16	14	9	10	7	4
Border Collie X	1Y	2	3	7	5	11	16	20	14	21	18	12	9	8	8	2
Collie X	1½Y	3	2	8	10	12	19	11	28	15	17	12	10	8	7	2
Collie X	1½Y	2	3	10	6	11	15	15	22	17	14	7	7	5	5	2
Collie X	1½Y	2	2	10	12	10	9	13	22	16	25	13	9	9	8	3
Beagle	1½Y	3	2	0	4	5	19	16	10	15	20	14	9	6	8	2
Terrier X	1½Y	2	2	5	8	9	22	31	21	13	23	13	12	7	5	3
Cocker X	2Y	3	3	4	5	13	20	24	23	17	14	12	8	8	7	1
Collie X	2½Y	3	3	9	5	4	11	10	10	26	18	14	9	8	10	2
Pointer X	2½Y	2	3	9	11	13	13	12	12	11	21	9	8	5	8	2
Laborador X	2½Y	3	3	8	9	15	16	13	16	14	14	7	6	5	3	1
S. Spaniel X	6Y	2	1	5	7	2	3	9	11	17	16	12	9	6	5	1

the dog.

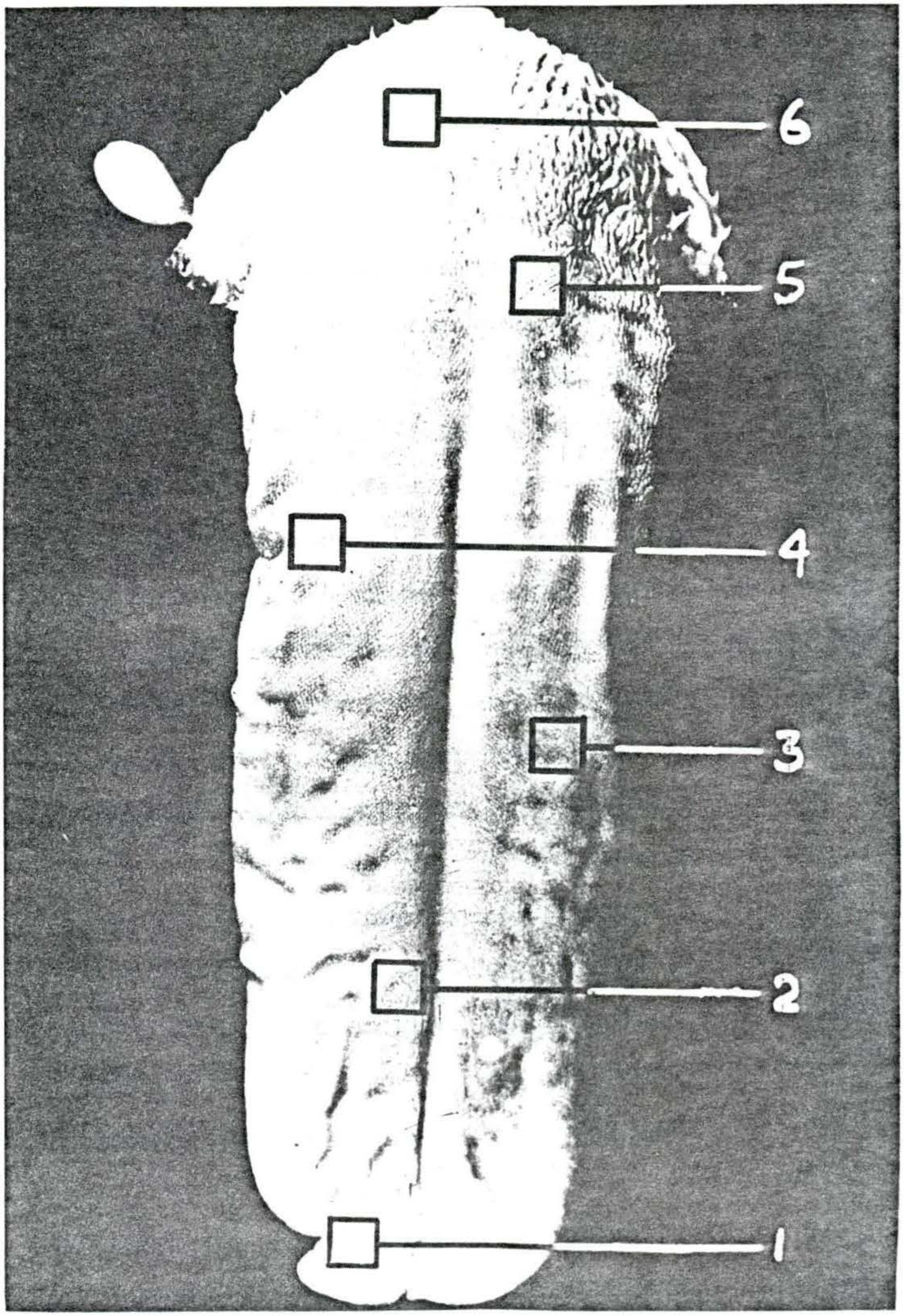
The right side of the tongue had an average of 2.3 vallate papillae. The left side also had an average of 2.3, making the average for 18 dogs, ranging in age from four weeks to six years, to be 4.6 vallate papillae per tongue.

The foliate papillae were located on each side of the tongue just anterior to the anterior pillar of the fauces; at the junction of the papillated dorsal lingual mucosa. The foliate papillae had two or three parallel papillae in the center of the group and the anterior and posterior papillae converged toward the base of the central foliate papillae. There was an average of 7.9 foliate papillae on the right side of the tongue, and an average of 8.3 on the left side of the tongue. The average figures come from Fig. 9 and represent 18 dogs ranging in age from four weeks to six years. Breed differences seemed to make more difference in the total numbers of papillae than the age of the individual animal, Fig. 9.

Fig. 10 indicates the areas counted in determining the numbers of filiform papillae per square millimeter, fungiform papillae per square centimeter, and conical per square millimeter.

Fig. 9 represents the data as they are taken from the tongues of 18 dogs ranging in age from four weeks to six years. The areas mapped out in Fig. 10 are used to determine

Fig. 10. The approximate areas represented in the last three columns of Fig. 9. Areas 1 to 5 were counted twice, using a one square centimeter frame to count the fungiform papillae and a four square millimeter frame to record the number of filiform papillae. A 16 square millimeter frame was used to count the conical papillae represented by number 6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a possible difference in the concentrations of the fungiform and filiform papillae.

There was an inverse relationship between filiform and fungiform papillae concentrations on the tongue. The anterior portion of the tongue contained the highest number of filiform papillae, 20.5 per square millimeter. The papillae became larger and more sparse as the area of the vallate papillae was approached.

Table 1 shows the average fungiform papillae and filiform papillae counts determined from Fig. 9. The fungiform papillae increased in number per square centimeter as the vallate papillae area was approached. Also, the size of the fungiform papillae increased in size from anterior to posterior. For comparison, the areas where fungiform papillae were counted can be changed from square centimeter to square millimeter by counting off two places from the right and adding a decimal point.

The author found fungiform papillae behind the rows of vallate papillae in among the conical papillae, Fig. 4. Research workers quoted in the review of literature indicated that fungiform papillae were not distributed behind the vallates, but the present work indicated their presence in this area.

The conical papillae were counted in only one area. There was an average of 2.5 per square millimeter. However,

Table 1. Average papillae counts taken from Fig. 9

Average filiform papillae per square millimeter				
Area numbers				
1	2	3	4	5
20.5	13.7	10.2	8.7	8.2

Average fungiform papillae per square centimeter				
Area numbers				
1	2	3	4	5
15.5	18.8	21.7	24.3	29.0

the conical papillae were smallest just behind the vallates and largest at the epiglottis. The conical papillae were distributed beyond the confines of the tongue proper. They were found on the ventral position of the wall of the pharynx and on the ventral side of the epiglottis. The apices of the conical papillae were directed backward, and medially.

B. Microscopic Anatomy

1. Microscopic structures of the lingual papillae

a. Filiform. The five types of lingual papillae were studied from three different planes: sagittal (longitudinal), frontal (horizontal) and transverse (cross). The tongues of dogs 20 weeks of age were used for this portion of the problem since it was ascertained that 20 weeks was the developmental peak of the lingual papillae.

The filiform papilla, Fig. 2, had three sizes of filiforms associated with a large basal papilla. The three types of filiforms were namely: primary, secondary and tertiary. The primary filiform was situated on the caudal most portion of the basal papilla. The epithelium conformed in layers to this long pointed projection. The surface layers of epithelial cells were keratinized, giving the papilla a horny structure, Figs. 11 and 13. The secondary filiforms were located lateral and anterior on each side of the primary projection. They also were keratinized and served to brace the primary filiform. The tertiary filiforms, five to seven in number, situated on the anterior portion of the basal papilla, were short keratinized projections.

The dermal papilla, upon which the stratum germinativum

Fig. 11. Sagittal (longitudinal) sections of the filiform papillae

A. High power, approximately 95X
   1. The stratified squamous epithelial covering of the primary filiform. Note the dark staining layer on its dorsal surface, this is the keratinized layer
   2. Keratinized projection of the center tertiary filiform
   3. Dermal core of the primary filiform
   4. Basal dermal papilla. Note just anterior to No. 4 the dermal projections for the tertiary filiform

B. High power, approximately 95X
   1. Primary filiform
   2. Dermal core for primary filiform. Note the dark layer covering these papillae, the cornified layer

C. Low power, approximately 57X, of Fig. 11 A
   1. Intrinsic striated lingual muscle

D. Low power of Fig. 11 B
   1. Intrinsic striated lingual muscle

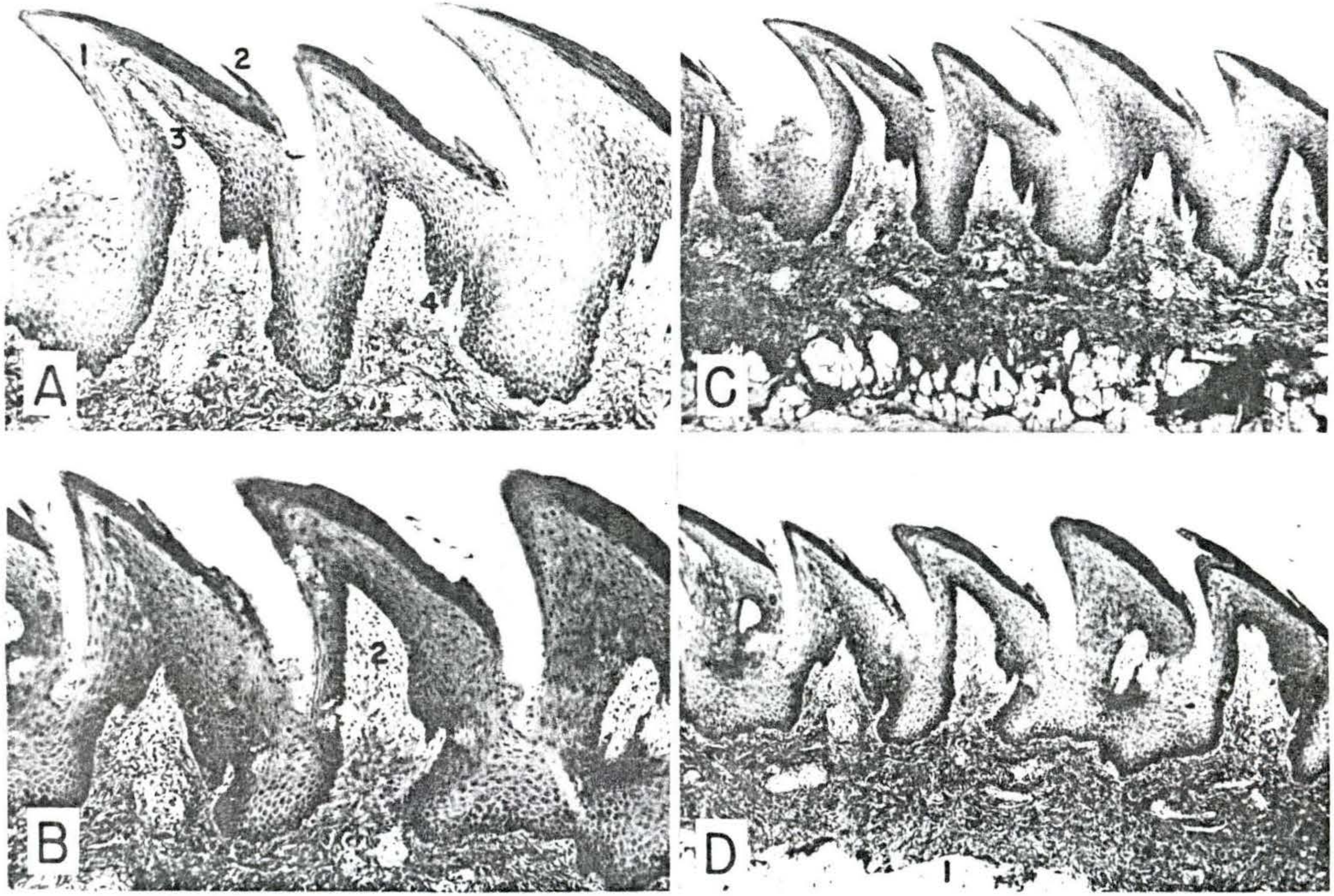
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Fig. 12. Frontal (horizontal) sections of the filiform papillae

A. High power of frontal sectioned filiform papillae, approximately 95X
   1. Dermal core of primary filiform

B. High power, approximately 95X
   1. Dermal core of primary filiform which is continuous with the dermal cores of the secondary filiforms
   2. The epithelial cores can be seen to the right of number 2. It is possible to distinguish six on some of these papillae
   3. The common basal dermal papilla. At the right, it is possible to see some of the dermal cores of the tertiary filiforms

C. Low power, approximately 57X, of Fig. 12 A
   1. Filiform papilla showing the dermal core for the primary filiform and the epithelial cores for the secondary filiforms
   2. Space between the filiform papillae

D. Low power, approximately 57X, of Fig. 12 B

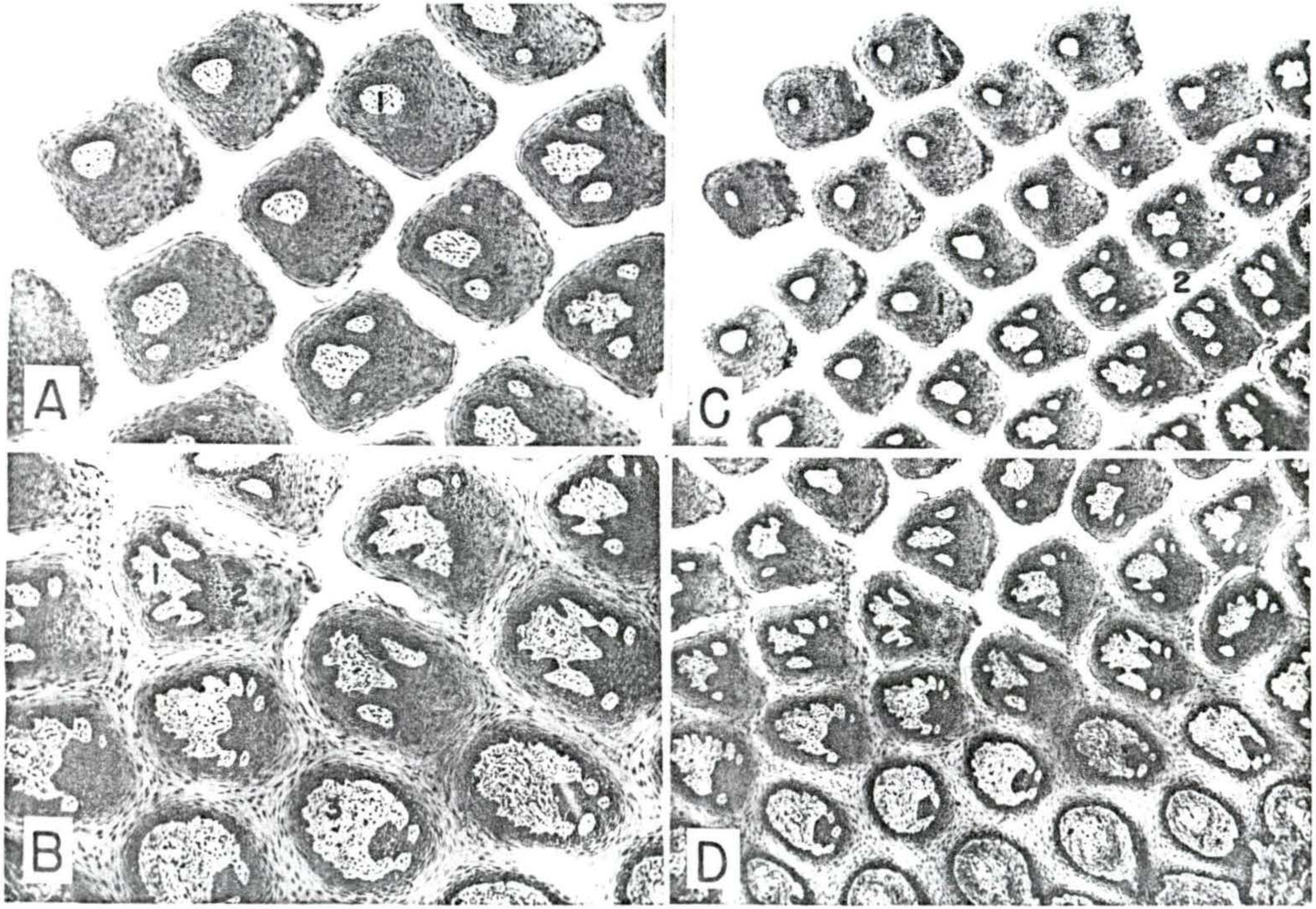
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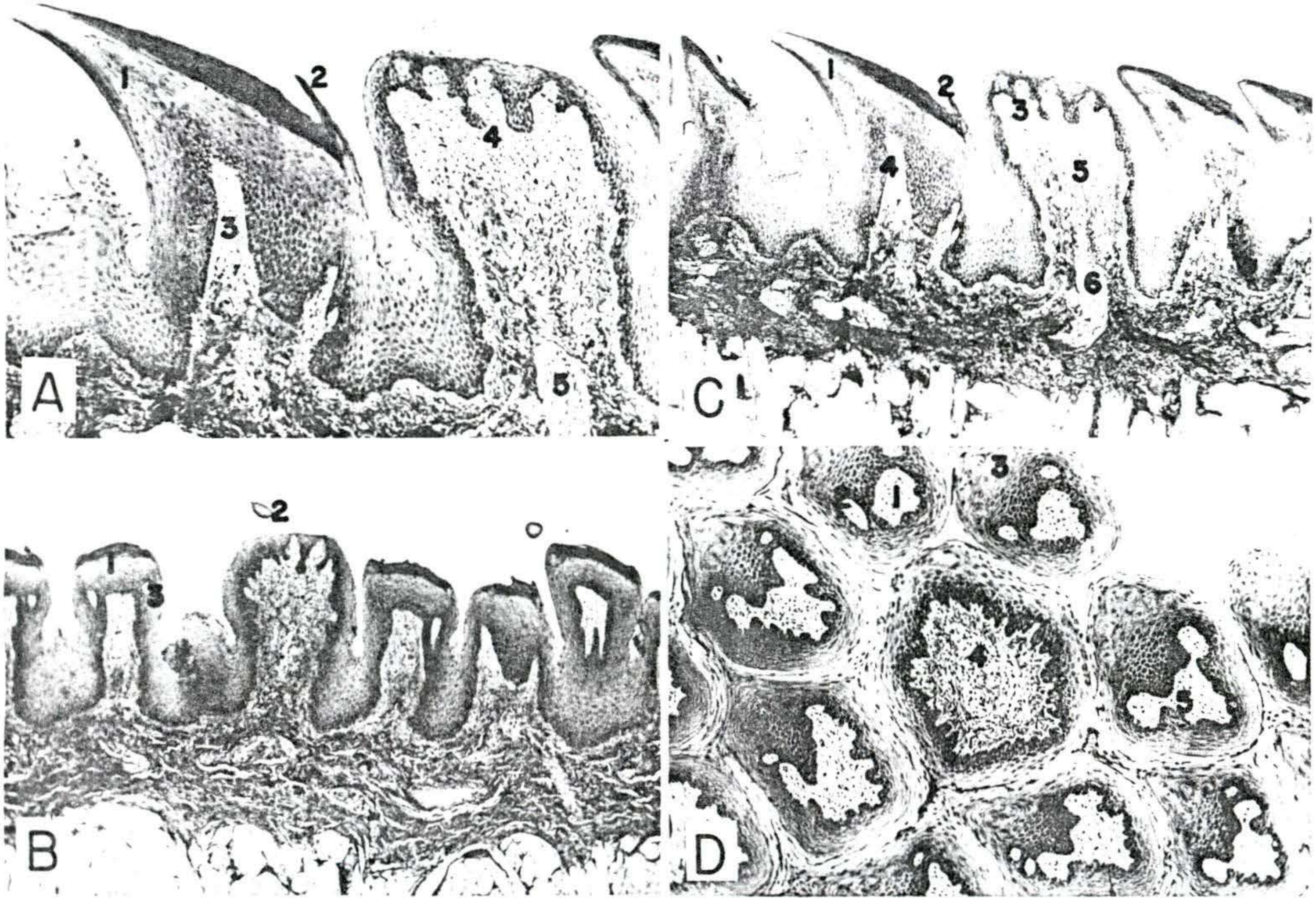
Fig. 13. Fungiform and filiform papillae cut sagittaly, transversely and frontally

A. High power, approximately 95X, fungiform and filiform papillae
   1. Primary filiform with keratinized outer layer
   2. Tertiary filiform
   3. Dermal core for the primary filiform
   4. Secondary dermal papilla with a taste bud on its summit
   5. Nerve plexus entering the fungiform papilla

B. Low power, approximately 57X, transverse fungiform and filiform papillae
   1. Epithelium of filiform papilla
   2. Cross section of the very tip of the primary filiform
   3. Dermal core of a secondary filiform

C. Low power, approximately 57X, sagittal section
   1. Primary filiform
   2. Tertiary filiform
   3. Secondary dermal papilla of fungiform papilla
   4. Dermal papilla of primary filiform
   5. Secondary dermal papilla of fungiform papilla
   6. Nerve plexus entering fungiform papilla

D. High power, approximately 95X, of frontal section of filiform and fungiform papillae
   1. Dermal core of primary filiform
   2. Dermal core of secondary filiform
   3. Anterior portion of basal papilla, showing the epithelial cores of the tertiary papillae
   4. Primary dermal papilla of the fungiform papilla. Note the convolutions of the stratum germinativum
   5. Confluence of the primary and secondary dermal papillae of the filiform papilla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rests, was the most extensive in the primary papilla, Figs. 11 and 13. The dermal core for the secondary filiform was less extensive and did not project above the basal portion of the papilla proper. The dermal cores were very small and projected only a short distance into the tertiary filiforms, which were mostly keratinized.

It was easy to distinguish the filiform papillae from the fungiform papillae by the thickness of the epithelial portion of the papilla. The epithelium of the filiform was two to three times thicker than that of the fungiform papilla and carried a thick layer of keratin on its dorsal surface. Also, the kerato hyaline granules were very prominent in the surface epithelial layers of the filiform papilla and were rarely seen in the epithelial layers of the fungiform papilla.

On the transverse section, Fig. 14, the secondary epithelial projections stood out on the dorsolateral portion of the basal papilla-like ears. These projections, Fig. 14A, might be confused with taste buds, but the thickness of the epithelium, the presence of keratohyaline granules, and a thick keratinized layer of epithelial cells distinguished this as a filiform papilla. The author had never observed taste buds associated with filiform papillae in this investigation. The transverse section, Figs. 13B and 14A, illustrated the ears or cores of the secondary filiforms.

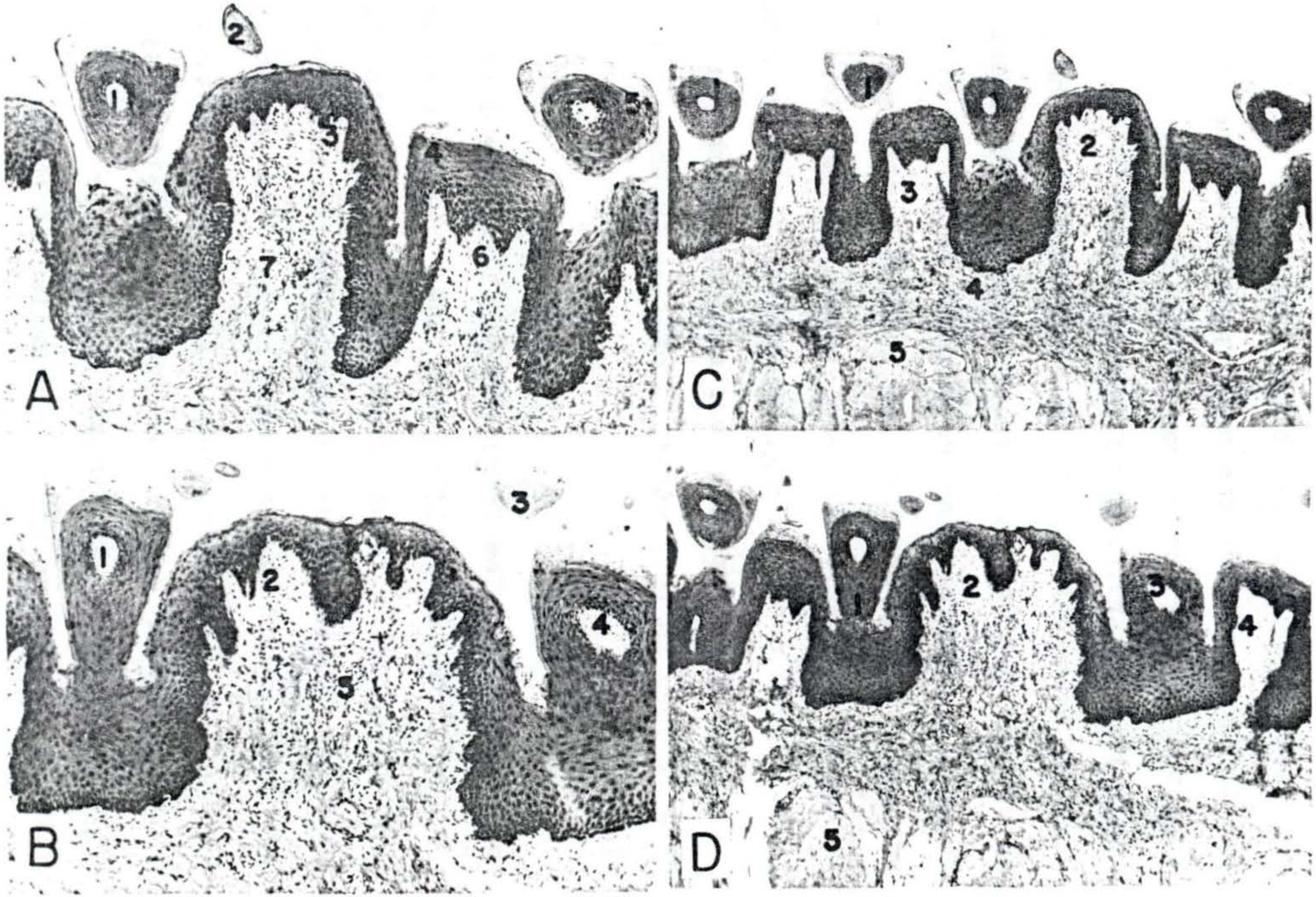
Fig. 14. Transverse sections of fungiform and filiform papillae

A. High power, 95X, of fungiform and filiform papillae
   1. Dermal core of primary filiform
   2. Cornified tip of the primary filiform
   3. Secondary dermal papilla of fungiform papilla
   4. Ear-like projections of the epithelial core of secondary filiform
   5. Epithelium of primary filiform
   6. Confluence of the primary and secondary dermal cores
   7. Primary dermal papilla of the fungiform papilla

B. Fungiform and filiform papillae, 95X
   1. Dermal core of primary filiform
   2. Secondary dermal papilla of fungiform
   3. Cornified tip of primary filiform
   4. Dermal core of primary filiform
   5. Dermal core of primary fungiform papilla

C. Fungiform and filiform papillae, 57X, transverse section
   1. Primary filiforms
   2. Primary dermal papilla of a fungiform papilla
   3. Basal dermal papilla of a filiform papilla
   4. Lamina propria mucosa
   5. Intrinsic, striated lingual muscle

D. Double fungiform and filiform papillae, 57X
   1. Caudal epithelial stalk of the filiform papilla
   2. Secondary dermal papilla of a fungiform papilla
   3. Dermal core of a primary filiform
   4. Basal portion of dermal core of filiform papilla
   5. Intrinsic, striated lingual muscle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In these figures, the secondary dermal papillae could be distinguished. The primary dermal papilla of Fig. 14A can be seen to project above the basal portion of the papilla out into the core of the primary epithelial filiform.

Fig. 12 illustrates the frontal (horizontal) section of the filiform papillae. In this figure all of the transition stages from the basal dermal core to the dermal core of the primary filiform can be distinguished. In Fig. 12C, the secondary dermal cores of the secondary filiforms can be distinguished anterior-lateral to the primary dermal core. It can be noted in Fig. 13D that the stratum germinativum of filiform papillae does not have as many convolutions as it does in the fungiform papilla in the center of the field.

b. Fungiform. The fungiform papillae were different in structure from the filiform papillae. The epithelium covering the dermal core was much thinner than in the filiform papillae. Because the epithelium was so thin, the red color from the blood in the capillaries caused them to take on a reddish color in life. The epithelium was covered by a very thin layer of keratinized epithelial cells. No keratohyaline granules were found in the upper layers of epithelium as they were in the epithelium of the filiform papillae. On most of the fungiform papillae, taste buds were seen penetrating the entire thickness of the epithelium.

The dermal core was divided into primary and secondary connective tissue papillae of the proper mucosa. In this study, the taste buds were always found on the tops of the secondary dermal papillae, Fig. 13A.

The primary dermal core was abundantly supplied with nerves, blood vessels and lymphatics. Fig. 13A, number 5, illustrates the large plexus of unmyelinated and myelinated nerves entering and leaving a fungiform papilla. There was no difference noted in the structure of the fungiform papilla cut sagittaly from those cut transversely. Fig. 13D, illustrates the frontally cut fungiform papillae; the stratum germinativum is thrown into folds and many secondary dermal papillae may be noted.

Fig. 14B, illustrates a double fungiform papilla. This was found to be quite common in the area just anterior to the rows of vallate papillae.

The fungoid shape of the fungiform papillae may be seen in Fig. 13, although it is much more noticeable in the dermal cores than in the epithelial covering.

c. Vallate. Figs. 15, 16, and 17 illustrate different levels through a vallate papilla sectioned through the frontal plane. There was an extremely large nervous plexus in the center of the dermal core. In the basal portion of

Fig. 15. Frontal sections through vallate papilla, 57X

A. Basal portion of papilla before epithelium appears
   1. A portion of the nerve plexus
   2. A section of the serous glands of von Ebner

B. Basal portion of papilla with epithelium and a moat
   1. Central nerve plexus
   2. Moat

C. Basal portion of papilla, the moat is not complete
   1. Large nerve plexus starting to be distributed
   2. Moat

D. Vallate papilla. Note that the taste buds are now appearing on both papilla and moat walls
   1. Nerve plexus
   2. Moat
   3. Moat or trench wall

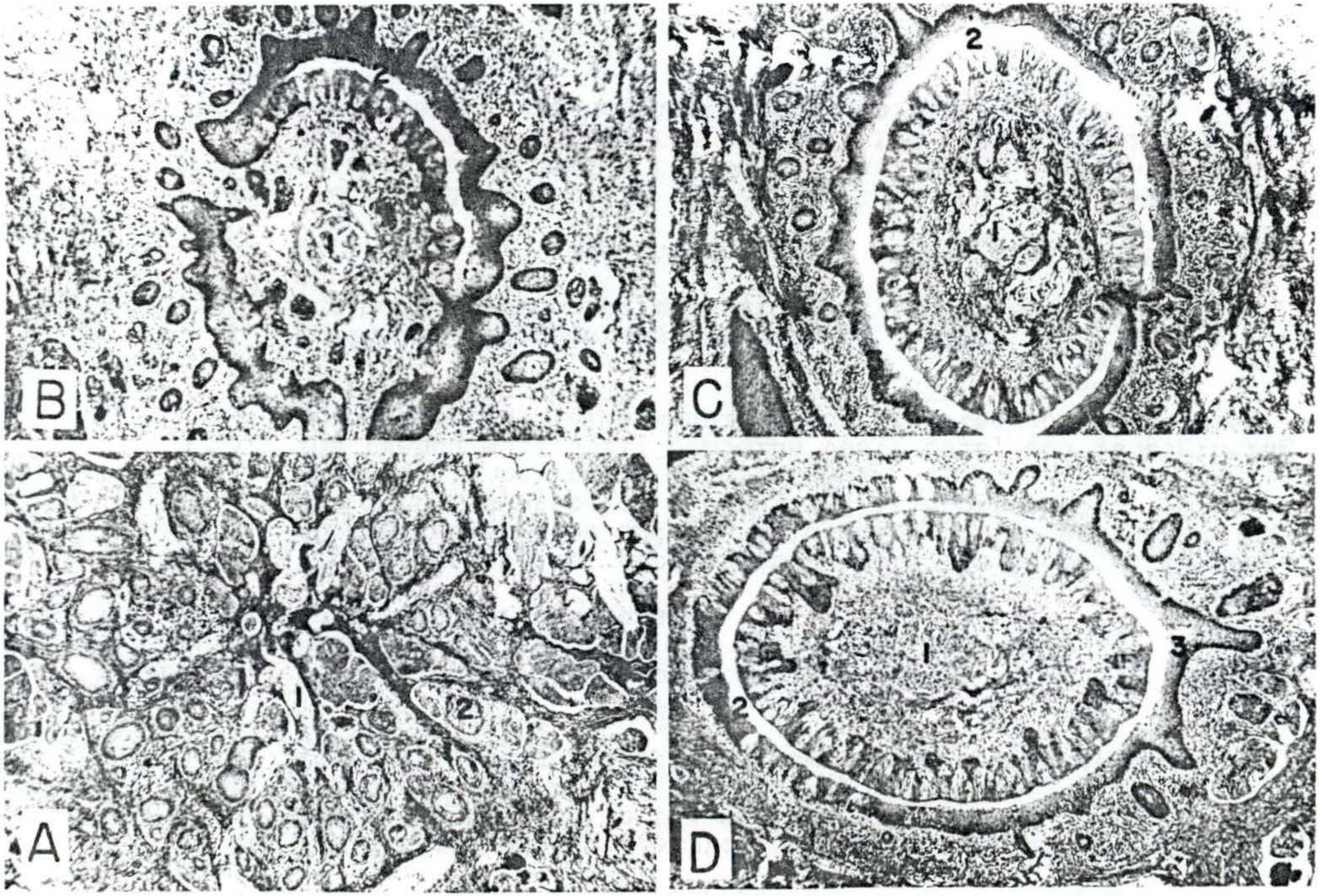
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Fig. 16. Frontal section of the vallate papilla midway up the papilla

A. 1. The ventral most projection of the epithelium from the dorsal depression in the vallate papilla
   2. Moat of trench
   3. The epithelial projections between the secondary dermal papillae

B. 1. Ventral epithelial projection
   2. Moat
   3. Epithelial projections

C. 1. Ventral epithelial projections. Note the decrease in size of the dermal core and the thickening of the epithelium as the dorsal surface of the papilla is approached
   2. The moat is beginning to widen out
   3. The trench wall still contains taste buds, and is beginning to have epithelial communications with the dorsal portion of the trench wall

D. 1. Epithelial depressions starting to coalace
   2. The moat is becoming much wider as the dorsal surface is approached
   3. Papilla wall. Note the shrinking of the size of the dermal core
   4. Trench wall. Note to the right, that the trench wall epithelium is coming together. There is a dermal portion which forms the base for the modified conical papillae that form a swirl around the vallate papilla

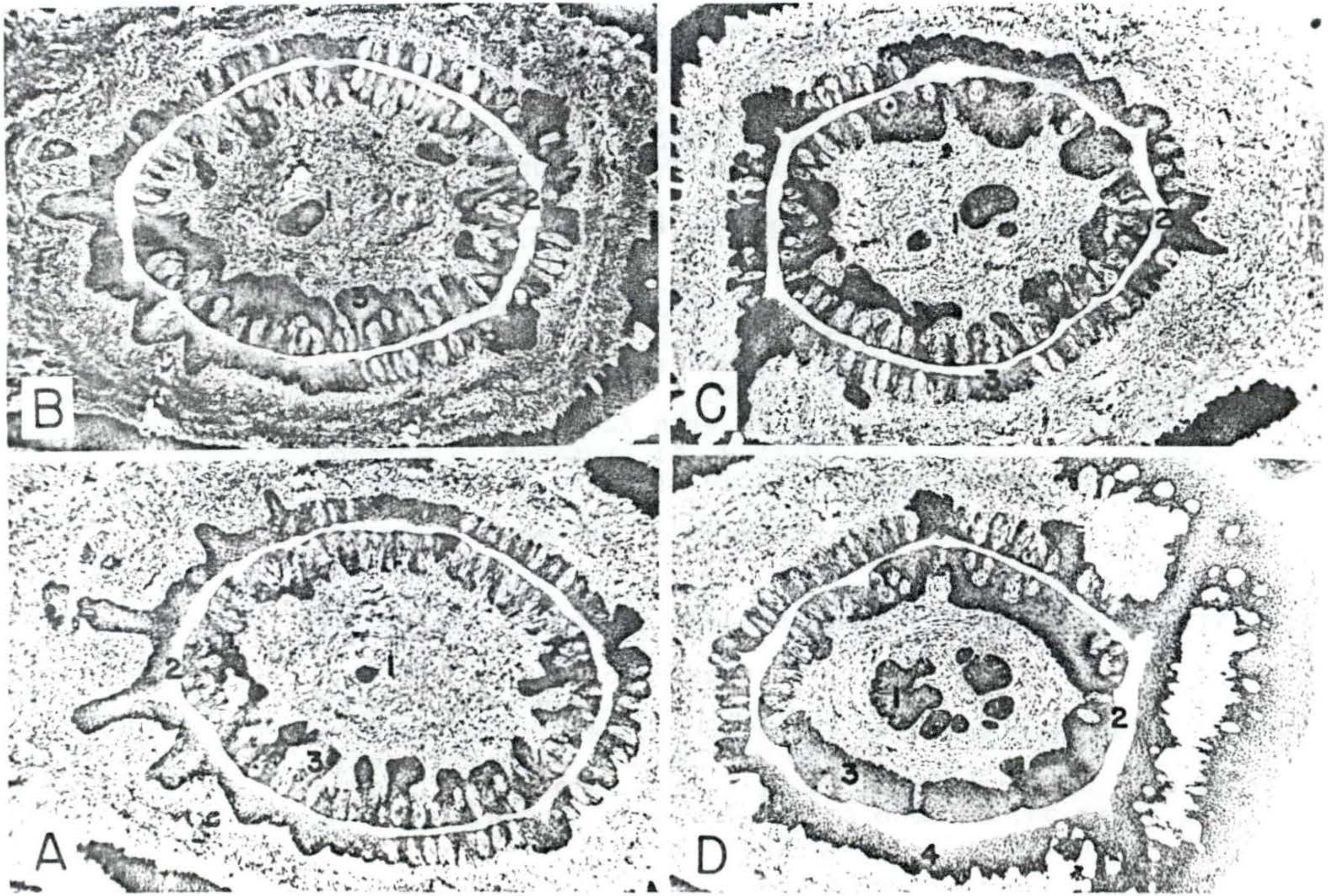
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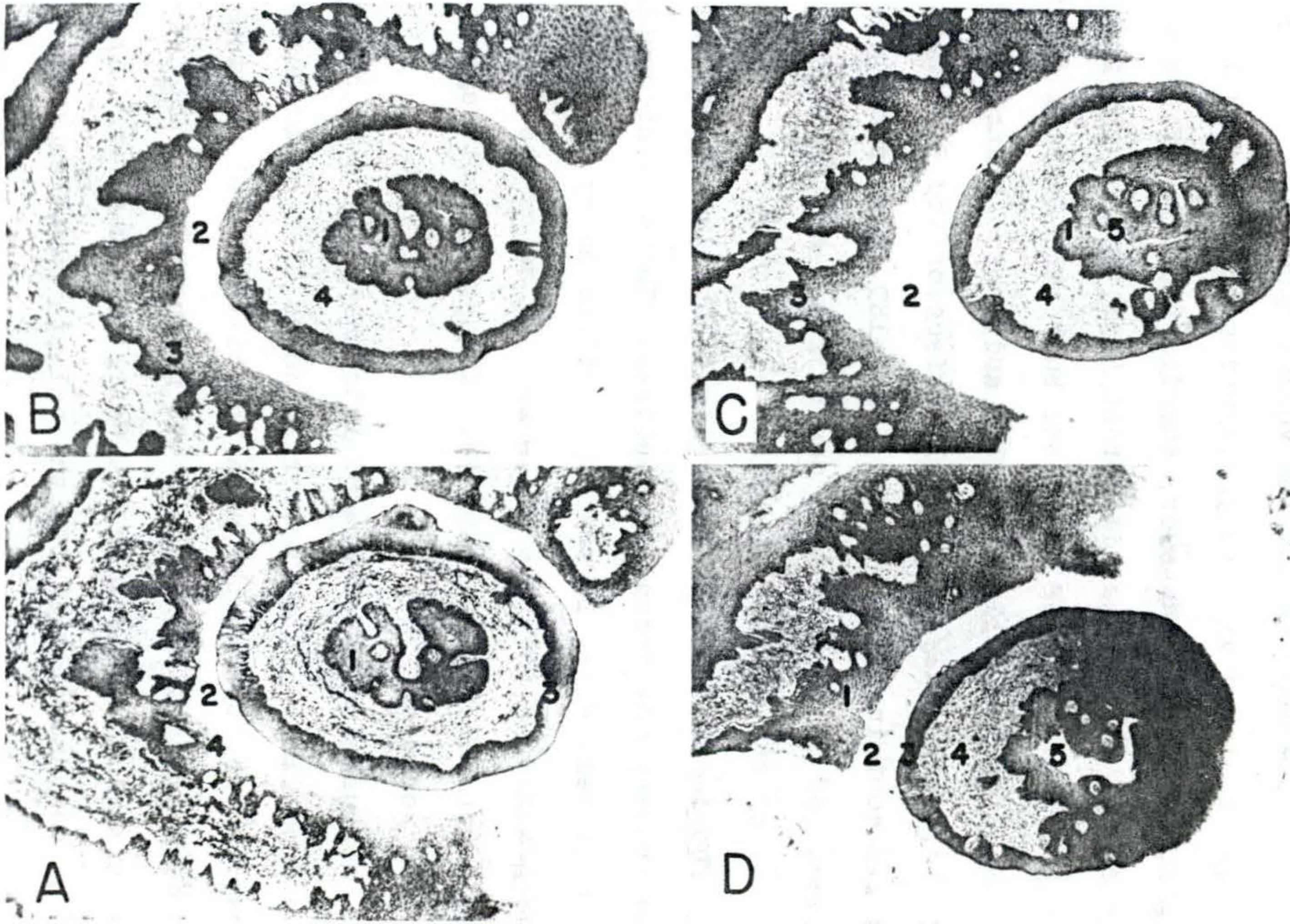
Fig. 17. The dorsal portion of the frontal sections of the vallate papilla

A. 1. Epithelium of the dorsal depression of the vallate papilla
2. Moat or trench. Note that it is open on the right hand side of the picture; this is an indication that the papilla rises above the surrounding mucosa
3. Vallate papilla wall. Note the relative absence of taste buds in this area
4. Wall of the moat or trench

B. 1. Epithelium of dorsal depression of the vallate papilla
2. Moat
3. Trench wall
4. Dermal core of the vallate papilla

C. 1. Epithelium of the wall of the depression on the dorsal portion of the vallate papilla
2. Moat, becoming very wide as the entrance is approached
3. Wall of the trench. Note the dermal core of the ring that surrounds the vallate papilla proper
4. Dermal core of the vallate papilla
5. Crypt within the depression on the dorsal portion of the papilla

D. 1. A portion of the ring of mucosa which surrounds the vallate papilla
2. Moat or trench, mostly absent in this section
3. Wall of papillae proper. Note that there are still some taste buds embedded in this epithelium
4. Remaining dermal core. Note the round shapes in the epithelium lining the crypt, these are taste buds
5. Crypt, just before it opens dorsally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the vallate papilla, serous glands (glands of von Ebner) were identified. The ducts of these glands empty into the bottom of the moat around the vallate papilla.

The isolated vallate papilla resembled a very large fungiform papilla. However, the distribution of the taste buds on the papilla was different from that of the fungiform papilla. Most of the taste buds were located on the side wall of the vallate papilla and on the trench wall, Fig. 16, while only the dorsal surface of the fungiform papilla contained taste buds. Fig. 18D illustrates that at 20 weeks of age, taste buds can be found on the dorsal surface of the vallate papilla.

The dermal core of the vallate papilla may be divided into primary and secondary papillae. The present problem demonstrated, Figs. 16 and 19, that secondary dermal papillae were present on the side walls as well as on the dorsal surface of the vallate papilla. These were not reported by earlier workers.

Serous glands penetrated into the basal part of the dermal papilla. In dogs over 16 weeks of age, mucous glands were demonstrated in the area around the basal portion of the dermal papilla. Large nerve plexuses, Fig. 19, were seen entering and leaving the papilla. There were more taste buds associated with the vallate papillae than with either of the other types of papillae. Therefore, the nerve

Fig. 18. Transverse sections of the vallate papillae of the dog

A. Low power, 57X
   1. Opening of trench or moat
   2. Secondary dermal papilla
   3. Taste buds on side wall of vallate papilla
   4. Primary dermal papilla
   5. Lymphatic nodule

B. Low power, 57X
   1. Opening of crypt on the dorsal surface of the vallate papilla
   2. Dorsal opening of the moat or trench
   3. Ventral portion of the epithelium at the bottom of the depression on the dorsal surface of the papilla
   4. Lateral wall of the vallate papilla
   5. Large nerve plexus entering and leaving the dermal papilla

C. High power, 95X
   1. An epithelial depression or invagination on the dorsal surface of the vallate papilla
   2. Dorsal opening of the moat or trench
   3. Primary dermal papilla

D. High power, 95X
   1. Secondary dermal papilla
   2. Bottom of the crypt in the dorsal surface of the vallate papilla
   3. Taste bud on the lateral papilla wall
   4. Dorsal entrance to moat or trench
   5. The trench wall that surrounds the vallate papilla

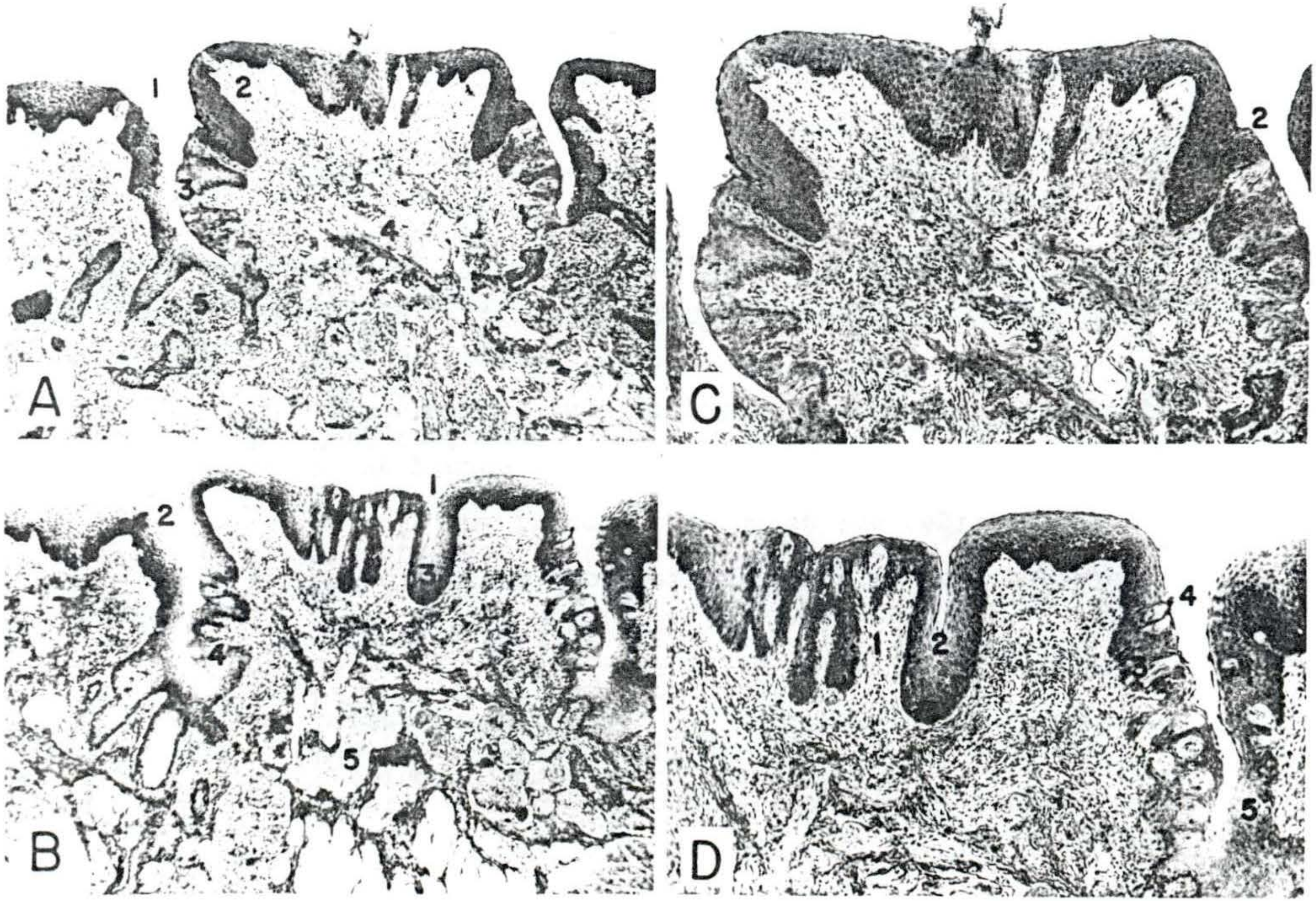
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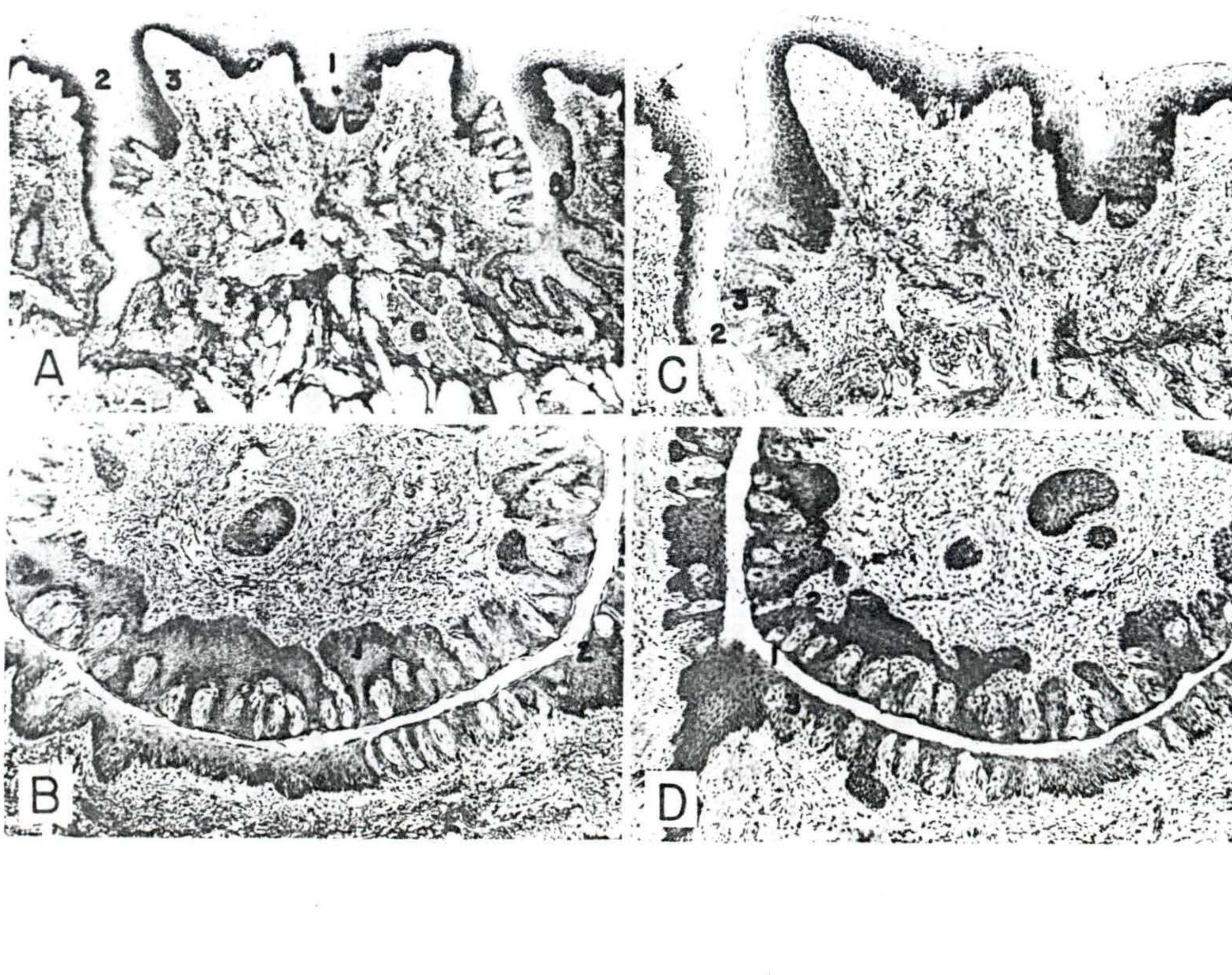
Fig. 19. Transverse and frontal sections of vallate papillae

A.
1. Crypt in dorsal surface of the vallate papilla
2. Opening of the moat or trench
3. Secondary dermal papilla
4. Larger nerve plexus
5. Wall of the trench or moat
6. Serous glands located in the basal portion of the primary dermal papilla

B.
1. Dorsal lateral epithelium of the vallate papilla
2. Trench wall. Note the arrangement of the taste buds on both the trench wall and on the papilla proper

C.
1. Nerve plexus
2. Moat or trench
3. Taste buds on the lateral wall of the papilla proper

D.
1. Moat or trench
2. Secondary dermal papilla
3. Trench wall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plexus must be large enough to supply all of these end organs of taste. In the basal dermal papilla aggregates of lymphatic tissue were identified, Fig. 18. These lymph nodules became more prevalent and more extensive in the dogs over 20 weeks of age.

The stratified squamous epithelium covering the vallate papillae had a very thin (one or two cells thick) layer of keratinized epithelium. The epithelial portion of the vallate papilla was smooth, with no projections, as described in the human vallate papillae, Maximow and Bloom (1953). There was a depression in the center of the dorsal surface of each vallate papilla. Fig. 17 illustrates this depression in the frontal section and Figs. 18 and 19 demonstrate the depression in the transverse section. Taste buds were present in this depression through 28 weeks of age, however there were no taste buds on the dorsal surface of the four-year old vallate papillae. Taste buds were not always located on the apices of the secondary dermal papillae of the vallates. They often penetrated the epithelium directly from the primary dermal core. Fig. 19B shows a high power view of the taste buds on the papilla and on the trench wall. The taste buds on the papilla proper did not all seem to be penetrating the full depth of the epithelium because the section was cut near the top of the papilla at an oblique angle.

d. Foliate. The foliate papillae were best studied from sections cut on the frontal (horizontal) plane. Not all of the papillae were cut at right angles as those papillae located on the posterior and anterior portion of the group were cut obliquely. It will be noted on Fig. 20C, that the papilla is very similar to the transverse section of the vallate papilla. However, the crypts or gustatory furrows were not as deep in the foliate papilla as the moat was on the vallate papilla. The foliate papilla proper, rested on a broad expanse of lamina propria mucosa. The submucosa had an abundance of serous glands. The excretory ducts of these glands emptied into the bottoms of the gustatory furrows. In dogs over ten weeks of age, mucous glands were mixed with these serous glands. The nerve plexus were not as obvious in the submucosa of the foliate papillae.

It was interesting to note, Fig. 20B, that on the ventral portion of the papilla, there was a true crypt where the gustatory furrow became separated from the surface epithelium. These crypts, however, did communicate with the gustatory furrows dorsally.

Fig. 21, A and B, shows a foliate papilla cut transversely. This illustrates the oblique cut on either the posterior or anterior end of the group of foliate papillae. There were secondary dermal papillae located on the primary dermal papilla. Fig. 21C, demonstrates how the excretory ducts of the serous glands empty into the bottom of the gustatory furrow.

Fig. 20. Frontal sections of the foliate papillae of the dog

A. 1. Lateral opening of the gustatory furrow
   2. Secondary dermal papillae with a taste bud on its summit
   3. Bottom of the gustatory furrow
   4. Primary dermal papilla of the foliate papilla

B. 1. Surface epithelium. Note that the crypt below does not communicate with this surface epithelium
   2. Secondary dermal papilla
   3. Crypt at the bottom of the gustatory furrow
   4. Epithelium of the crypt with taste buds embedded within it

C. Low power, 57X of the foliate papilla
   1. Gustatory furrows between foliate papillae
   2. Lateral wall of a foliate papilla
   3. Dorsal epithelium of a foliate papilla
   4. Secondary dermal papilla of a foliate papilla
   5. Broad primary dermal papilla
   6. Serous glands within the primary dermal papilla
   7. Intrinsic, striated lingual muscle

D. Low power, 57X, of the crypts at the bottom of the gustatory furrows
   1. Surface epithelium
   2. Secondary dermal papilla
   3. Crypts at the bottom of the gustatory furrow
   4. Wall of the crypts showing taste buds embedded within the wall
   5. Serous glands located under the crypts

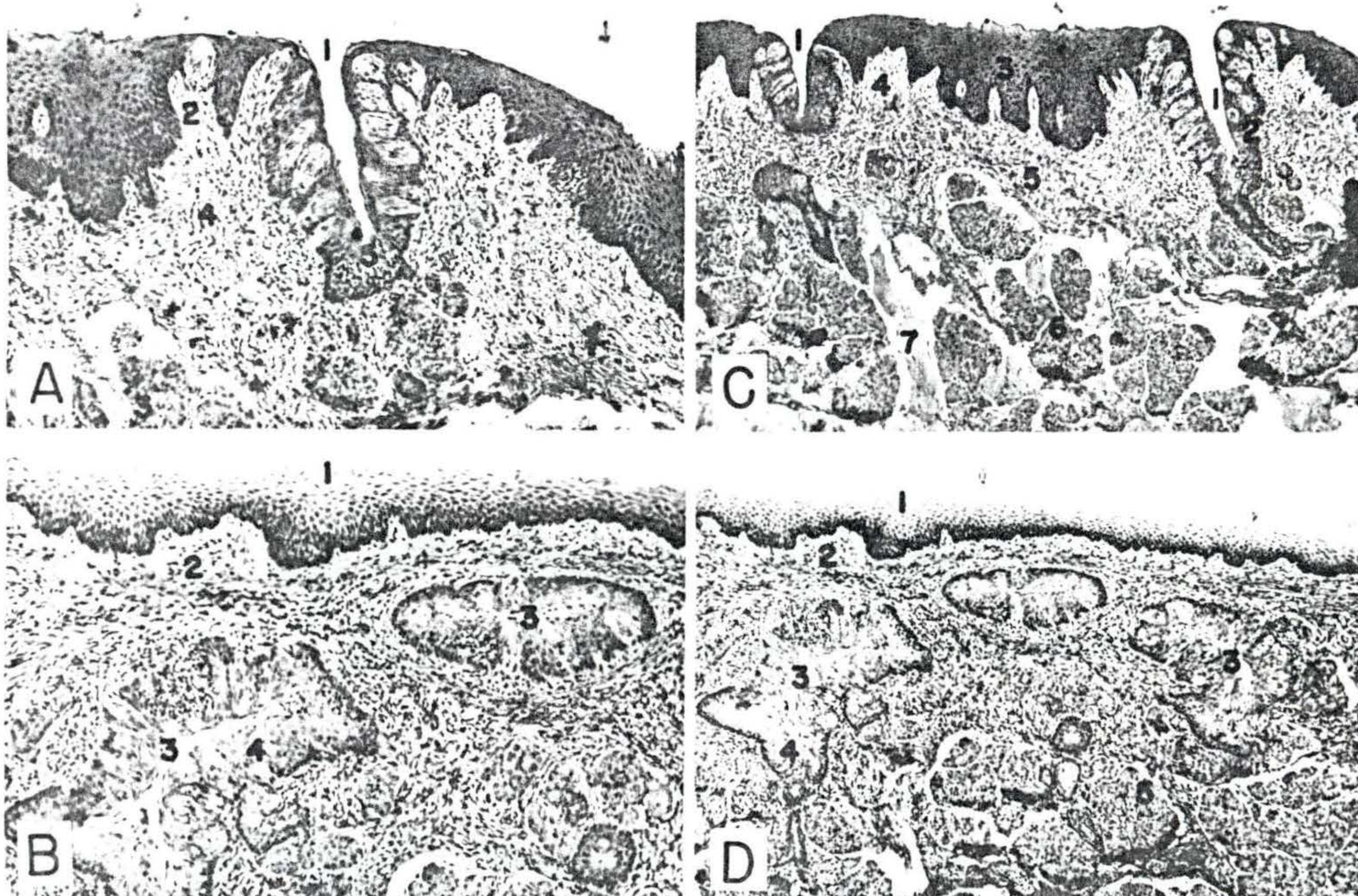
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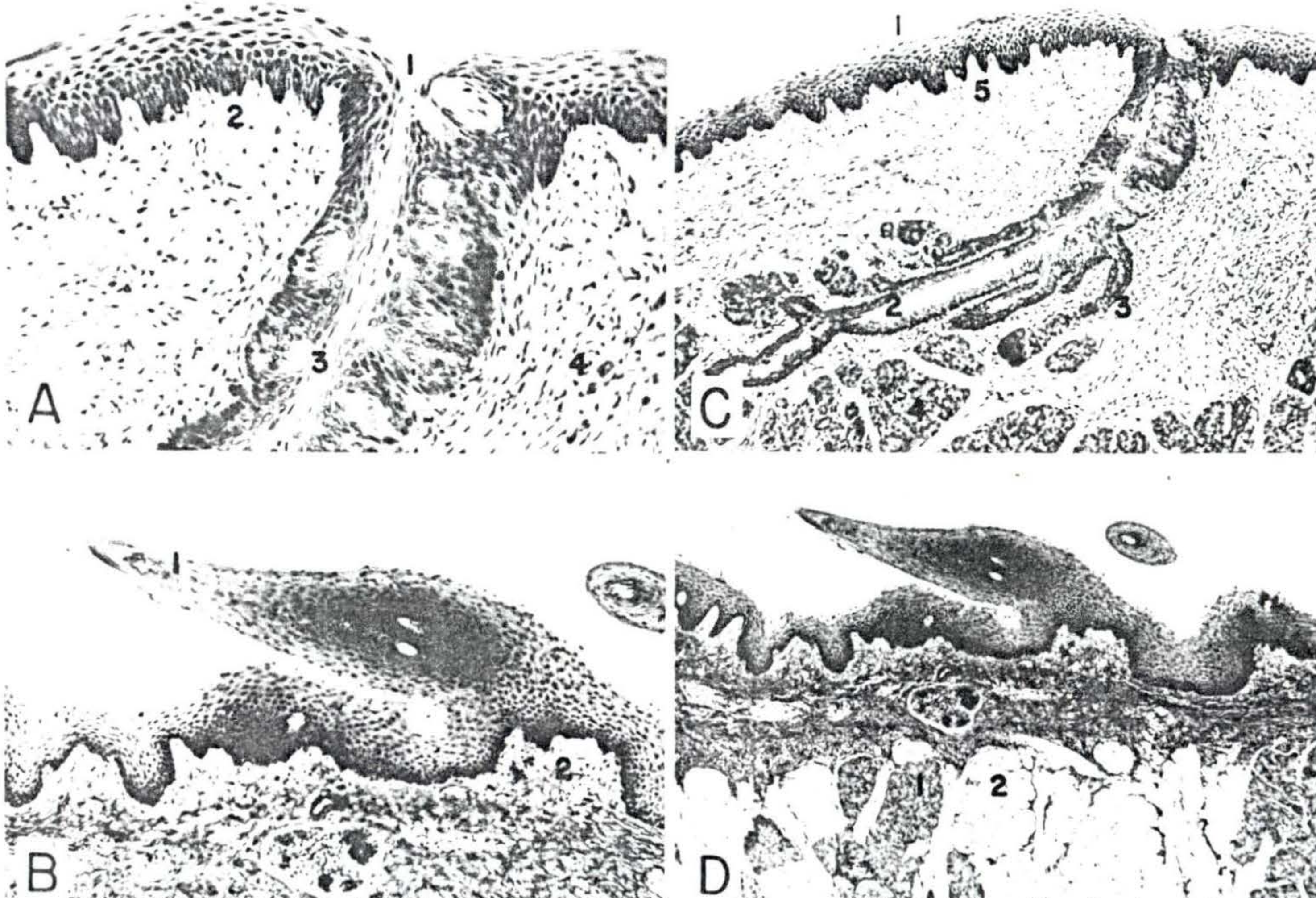
Fig. 21. Transverse sections of foliate papillae and sagittal sections of conical papillae

A. High power, 95X, of a foliate papilla through the gustatory furrow
   1. Lateral opening of the gustatory furrow
   2. Secondary dermal papillae
   3. Gustatory furrow
   4. Primary dermal papilla of a foliate papilla

B. High power, 95X, of a conical papilla
   1. Keratinized tip of a conical papilla
   2. Basal portion of the primary dermal papilla

C. Low power, 57X, of the foliate papilla through the gustatory furrow
   1. Lateral surface of the papilla
   2. Excretory duct of the serous glands opening into the bottom of the gustatory furrow
   3. An excretory duct of a serous gland

D. Low power, 57X, of the conical papillae
   1. Serous glands under the submucosa
   2. Intrinsic, striated lingual muscle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The epithelium covering the foliate papilla was smooth with a very slight amount of keratinization. The taste buds, for the most part, were located on the side walls facing the gustatory furrow. However, Fig. 20A illustrates an exception, with a taste bud opening onto the dorsal surface of the papilla.

e. Conical. The conical papillae, cut transversely, were easily mistaken for fungiform papillae. This was true when the cut passed through the anterior basilar portion of the papilla.

Fig. 21, B and D, illustrates the sagittaly cut conical papilla. There was only one long pointed papilla similar to the primary filiform, but was much longer and had a broader base.

The dermal papilla went further into the tip of the conical papilla than did the dermal core of the primary filiform. The whole base and papilla proper was directed posteriorly, Fig. 22A. The blood supply was rich in the submucosa of this region, possibly because of the great many serous glands located in this area. The primary dermal core or papilla had only a few secondary dermal papillae.

The epithelium covering the dermal core was stratified squamous and only a thin layer was keratinized, except at the extreme tip of the papilla where it was mostly kera-

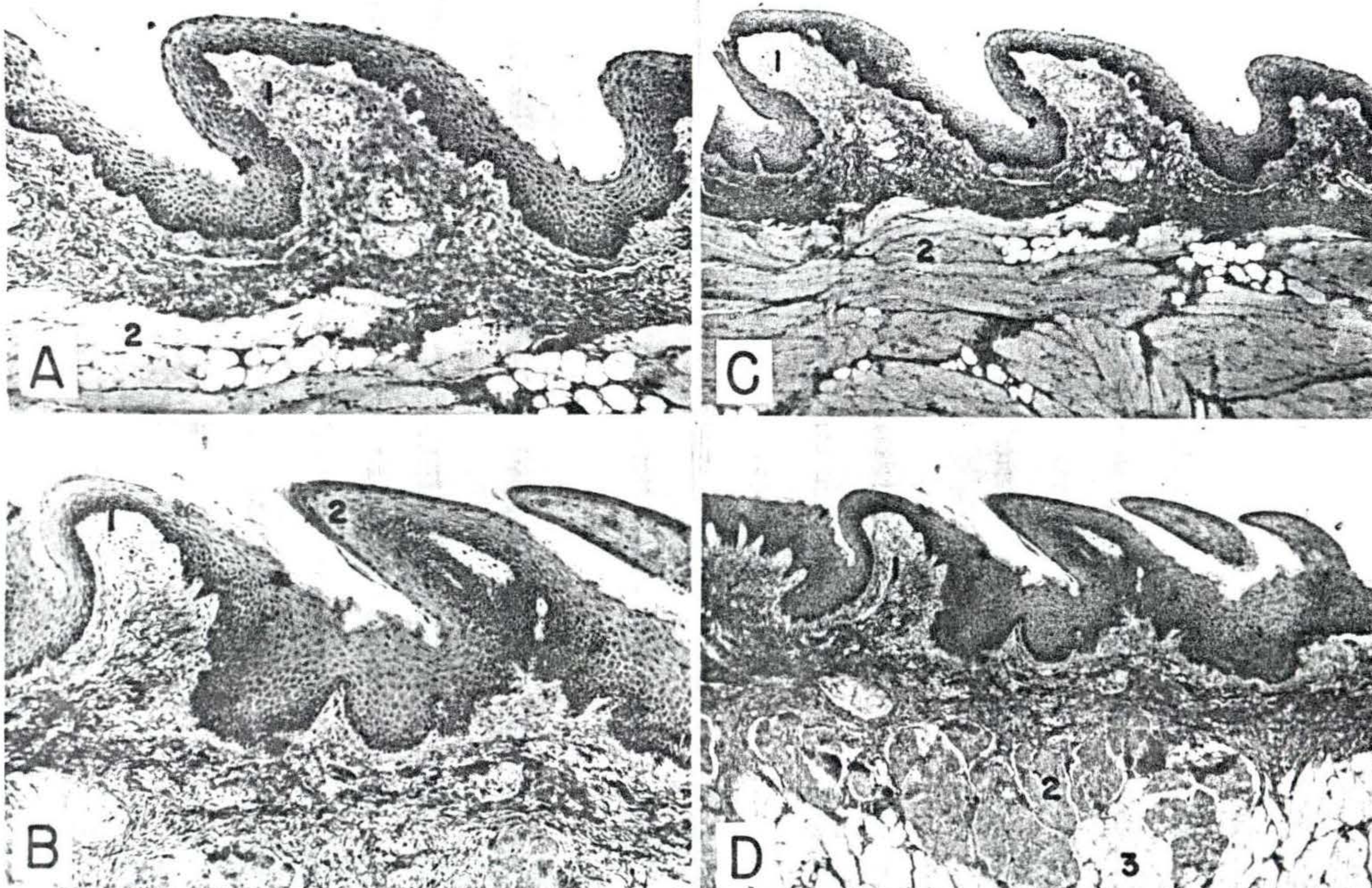
Fig. 22. Sagittal sections of conical papillae located on the posterior third of the dogs tongue

A. High power, 95X
   1. Dermal core of conical papilla. Note the comparative thickness of the epithelium and the thin layer of keratinized epithelium
   2. Intrinsic, striated lingual muscle

B. High power, 95X
   1. Tip of dermal papilla. Note the thin epithelium. If this particular papilla were cut transversely, it could be confused with a fungiform papilla
   2. Tip of epithelial portion of conical papilla. Note the keratinized layer of epithelium covering the very tip of the papilla
   3. Basilar portion of the primary dermal papilla

C. Low power, 57X
   1. Primary dermal core or papilla
   2. Intrinsic, striated lingual muscle

D. Low power, 57X
   1. Primary dermal core or papilla
   2. Serous glands located deep among the lingual muscles
   3. Intrinsic, striated lingual muscle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tinized. The author has never seen taste buds associated with these papillae in the slides studied in this investigation. However, the epithelium was thinner than the filiform epithelium and may in prenatal existence contain taste buds. This study indicates that the character of the epithelial covering determines where taste buds will be found. Thick epithelium with a heavy layer of keratinized epithelium was not associated with the presence of taste buds in the dog.

In addition to an abundance of serous glands, mucous glands were very numerous in the area of the conical papillae (at 20 weeks of age). The lymphatic nodules were also very prominent in this area. They are not true lingual tonsils since there are no crypts opening on the dorsal surfaces.

2. Age changes in the lingual papillae

a. Fungiform and filiform. There were no epithelial papillae on the anterior portion of the tongue at birth. The fungiform papillae were differentiated from the filiform papillae strictly by the differences in their dermal cores. The fungiform papilla had a well developed primary dermal papilla or core, while the filiform papilla had a very small dermal papilla, Fig. 23.

The epithelium was relatively thick over the dermal papilla of the filiform papilla. There was evidence of cell

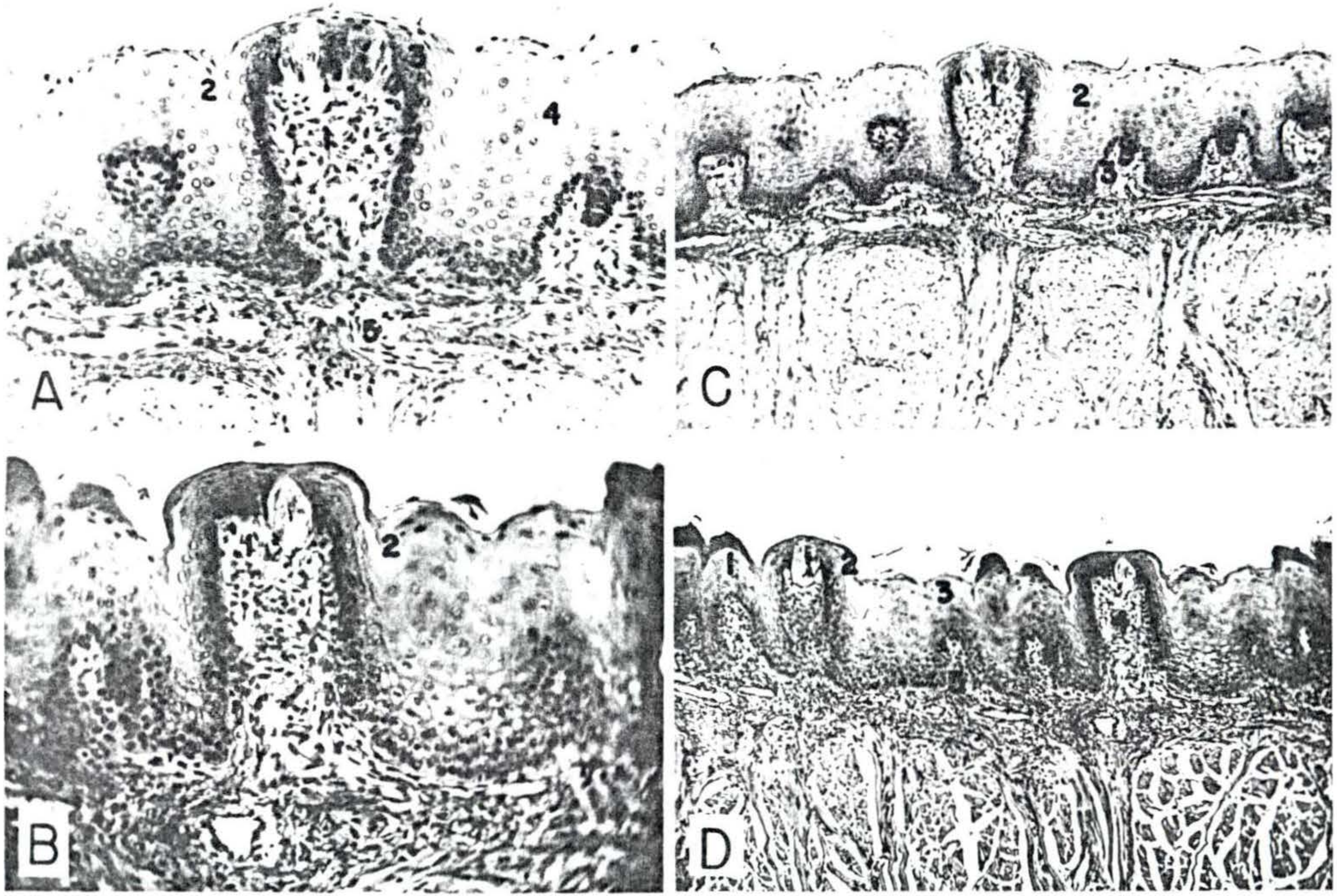
Fig. 23. High power, 190X, and low power, 116X, of the dorsal lingual mucosa at birth. A and C numbered 65TF2, and B and D numbered 65TF4

A. 1. Primary dermal core of the fungiform papilla
   2. Cleavage line between a fungiform and filiform papillae
   3. Epithelium covering fungiform papilla. Note that the taste buds are not situated on the summits of secondary dermal papillae
   4. Epithelium over filiform papilla. Note the large round nuclei and the extreme thickness compared to the fungiform epithelium
   5. Nerve plexus in the submucosa

B. 1. Primary dermal core or papilla of a fungiform papilla. Note the position of the taste bud
   2. Cleavage line between fungiform and filiform papillae. Note that in the fourth block taken from the tongue, the epithelial papillae are beginning to rise above the surface

C. 1. Primary dermal papilla of a fungiform papilla
   2. Epithelium covering a filiform papilla
   3. Dermal core of a filiform papilla

D. 1. Filiform papillae. Note the keratinized layer of epithelium over this papilla
   2. Fungiform papilla
   3. Epithelial covering of filiform papillae
   4. Primary dermal papilla of a fungiform papilla



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division in the stratum germinativum. The nuclei of the stratified squamous epithelium were large and round. The cells were not flattened except in the thin keratinized layer on the surface. A line of cleavage could be seen between the epithelium of the fungiform and the filiform papillae. This cleavage or separation is best illustrated in Fig. 23.

The dermal cores of the filiform papillae were only a third of the height of the dermal cores of the fungiform papillae at birth. There were secondary dermal papillae on the primary filiform dermal papillae, but none were observed on the dermal core of the fungiform papillae. The taste buds were resting directly on the primary dermal core or papilla of the fungiform papilla. There were no primary, secondary or tertiary filiforms observed on the filiform papillae at birth. The mucosa was smooth at birth.

When the dog was only 12 hours old, striking changes in the lingual mucosa were noted. The papillae were beginning to differentiate grossly as well as microscopically. The relative thickness of the epithelium was less than at birth, probably because the papillae were pushing toward the surface at a much faster rate. The fungiform papillae were beginning to form secondary dermal papillae. However, fungiform papillae possessing taste buds did not have any secondary dermal papillae.

On the posterior half of the tongue (12 hour old dog), the filiforms were beginning to form, Fig. 24A. On the anterior portion, the filiform papillae were not observed to have filiforms.

Development became slower at one week, Fig. 24B. The filiform papillae were much slower in differentiating than were the fungiform papillae. The filiforms were found on the posterior portion of the tongue, but were still absent on the filiform papillae of the anterior half of the tongue.

At three weeks of age, the fungiform papillae were almost completely separated from the adjoining filiform papillae. The epithelium was composed of flattened cells. The keratinized layer was thicker than before. The fungiform papillae were almost mature in structure. The filiform papillae had primary filiforms that protruded above the basal portion of the parent papillae, Fig. 24C.

At six weeks of age, the fungiform papillae resembled those of the mature animal. The secondary dermal papillae were completely developed on the fungiform papillae of all areas of the tongue. A comparison of the fungiform papilla in Fig. 24D with the fungiform papillae in Figs. 25, A, B, C and D, will serve to show that the fungiform papillae had reached structural maturity.

The filiform papillae, at six weeks of age, were forming ear-like projections on their dorsolateral borders. These

Fig. 24. Representative samples of fungiform and filiform papillae of various ages

A. A section taken from block 34TF3, 12 hours of age, approximately 60X
   1. Fungiform papillae
   2. Filiform papillae
   3. Intrinsic, striated lingual muscle

B. A section taken from block 66TF1, one week, approximately 60X
   1. Fungiform papillae
   2. Filiform papillae. Note that the filiforms are beginning to be seen on the lateral edges of the filiform papillae
   3. Intrinsic, striated lingual muscle

C. A section taken from block 68TF1, three weeks, approximately 60X
   1. Fungiform papilla. Note the primordia of the secondary dermal papilla
   2. Filiform papilla. Note the circles of tissue on either side of number 2, these are the caudal projections of the primary filiforms

D. A section taken from block 42TF1, six weeks, 60X
   1. Fungiform papilla. Note that the taste buds are now resting on secondary dermal papillae
   2. Filiform papilla. Note the thick keratinized layer on its dorsal surface

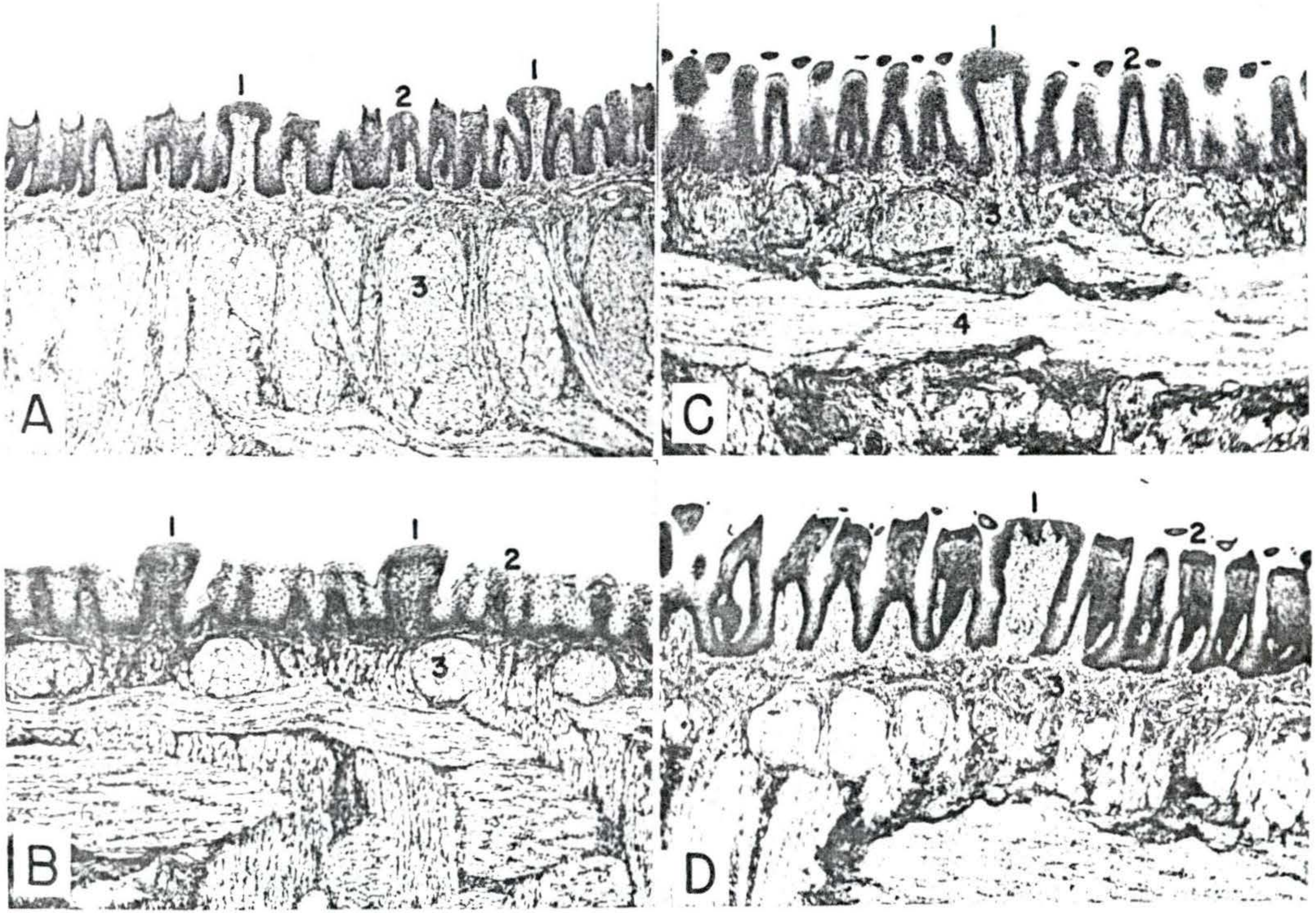
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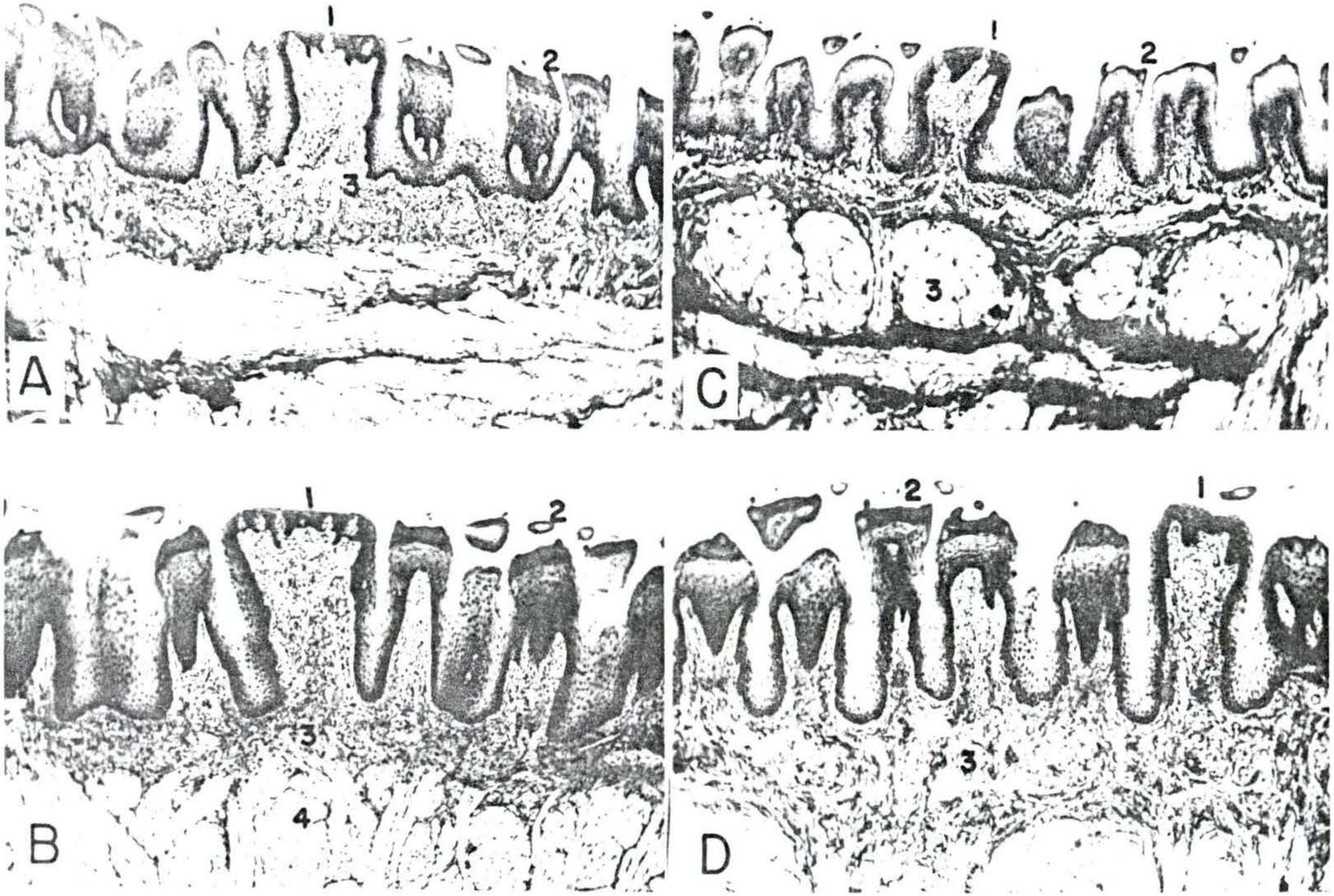
Fig. 25. Representative samples of fungiform and filiform papillae after structural maturity

A. A section taken from block 46TF1, eight weeks, 60X
   1. Fungiform papilla. Note secondary dermal papillae
   2. Filiform papillae. Note the secondary filiforms (ear-like projections)
   3. Submucosa beneath primary dermal papilla of fungiform papilla

B. A section taken from block 6TF4, ten weeks, 60X
   1. Fungiform papilla. Note the number of taste buds in its dorsal epithelium
   2. Filiform papillae and some primary filiforms
   3. Submucosa beneath fungiform papilla
   4. Intrinsic, striated lingual muscle

C. A section taken from block 19TA1, 16 weeks, 60X
   1. Fungiform papilla
   2. Filiform papilla
   3. Intrinsic, striated lingual muscle

D. A section taken from block 55TF2, four years, 60X
   1. Fungiform papilla
   2. Filiform papilla. Note the thickness of the keratinized layer of epithelium on the dorsum of the papillae
   3. Submucosa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projections were the beginnings of the secondary filiforms. The keratinized layer was much thicker at six weeks than at three weeks of age.

The filiform papillae continued to change up through 16 weeks of age. The secondary filiforms increased in size through eight and ten weeks. At 16 weeks of age, the filiform papillae were structurally mature. The primary, secondary and tertiary filiforms did not change appreciably after this age.

Fig. 26, A, B and C, illustrates the age changes that occurred in the modified filiform papillae on the anterior lateral portion of the tongue. At birth, the fringe of epithelial and dermal papillae was very extensive. Fig. 26B illustrates the dorsal concavity of the dog's tongue at birth, with the extensive, modified filiform papillae on its dorsal lateral border. The fringe was rarely seen to extend much behind section TF3 (see Fig. 1).

Fig. 26C illustrates the same area on the tongue of an eight week old dog. In this illustration, the fringe of modified filiform papillae has just about disappeared. The fringe disappeared frequently at six weeks of age.

b. Vallate and conical. At birth, the vallate papillae were not much larger than mature fungiform papillae. The moat around the papilla proper was not always patent at

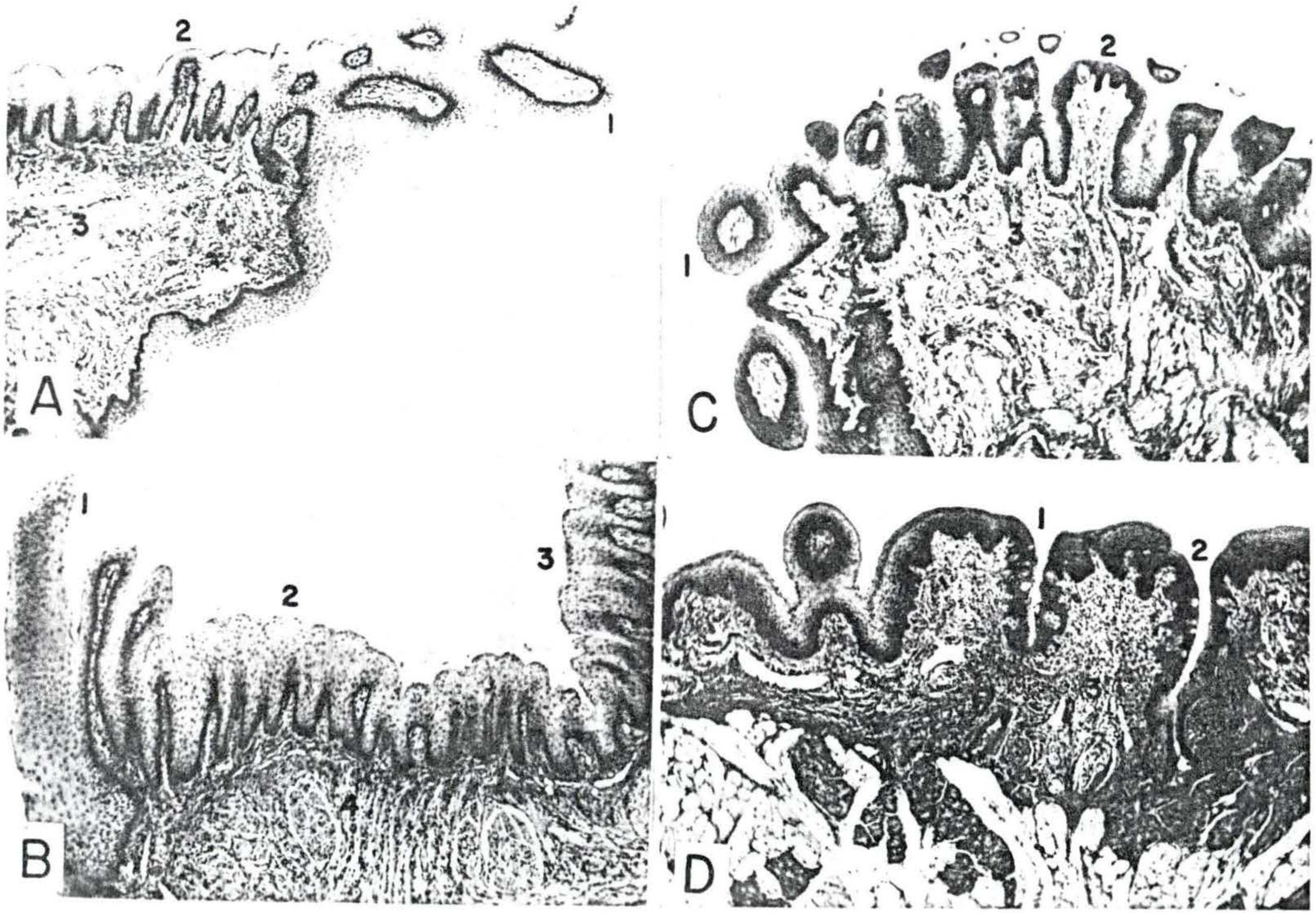
Fig. 26. Some photomicrographs of the modified filiform papillae on the dorsal lateral border of the tongue

A. A section taken from block 65TF1, birth, 60X
   1. Fringe of papillae on the dorsal lateral border of the tongue. Note that in this area, TF1, the tongue does not have a dorsal convexity
   2. Fungiform papilla
   3. Intrinsic, striated lingual muscle

B. A section taken from block 65TF2, birth, 60X
   1. Modified filiform papillae, Note the extreme dorsal curvature
   2. The lateral border of the dorsal convexity
   3. The dorsal portion of the tongue proper. This dorsal convexity, coupled with the long fringe of papillae almost forms a complete tube during the act of nursing
   4. Intrinsic, striated lingual muscle

C. A section taken from block 46TF2, eight weeks, 60X
   1. Note the relative absence of modified fringe papillae at eight weeks of age
   2. Fungiform papilla
   3. Submucosa

D. A section taken from block 19TA5, 16 weeks, 60X
   1. A dorsal crypt in the center of a vallate papilla. This vallate papilla resembles two adjacent fungiform papillae
   2. Gustatory moat or trench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birth. Arey (1954) stated that during the fourth fetal month in man, the epithelial collar around the vallate papilla split and formed the moat or trench. The splitting of the epithelial collar around the vallate papilla of the dog was observed in some cases after birth.

The various vallate papillae on the tongue differentiated at different times. It was found that the posterior medial pair of vallate papillae of the dog matured earliest.

At birth, the taste buds were located exclusively on the dorsal surface of the papillae. However, one animal (12 hours old) displayed taste buds on the lateral wall, facing the moat. There were relatively few taste buds present on the vallate papillae of the youngest animals.

The most obvious age change was the increase in size of the papillae. Figs. 27 and 28 are the same magnification, emphasizing the progressive increase in size from birth to 12 weeks of age; from 12 weeks through four years the size of the vallate papillae is relatively constant.

The serous glands of von Ebner, located in the submucosa and between the striated muscles of the tongue, also changed with age. At birth they were practically absent, Fig. 27A, however, they became maximally developed between ten and 12 weeks of age. Figs. 27 and 28 illustrate the progressive increase in the amount of serous glands and ducts around the base of the vallate papillae.

Fig. 27. Representative samples of vallate papillae from birth to three weeks

A. A section taken from block 65TF6, birth, 60X
   1. Vallate papilla
   2. Primary dermal papilla. Note the absence of serous glands in this photomicrograph
   3. A small group of serous excretory ducts

B. A section taken from block 34TF6, 12 hours, 60X
   1. Vallate papilla
   2. Primary dermal papilla
   3. Serous glands among the striated lingual muscles

C. A section taken from block 66TF5, one week, 60X
   1. Vallate papilla
   2. Primary dermal papilla
   3. Note the relative absence of serous glands in this section

D. A section taken from block 68TF7, three weeks, 60X
   1. Vallate papilla
   2. Primary dermal papilla
   3. Note the scarcity of serous glands even at three weeks of age

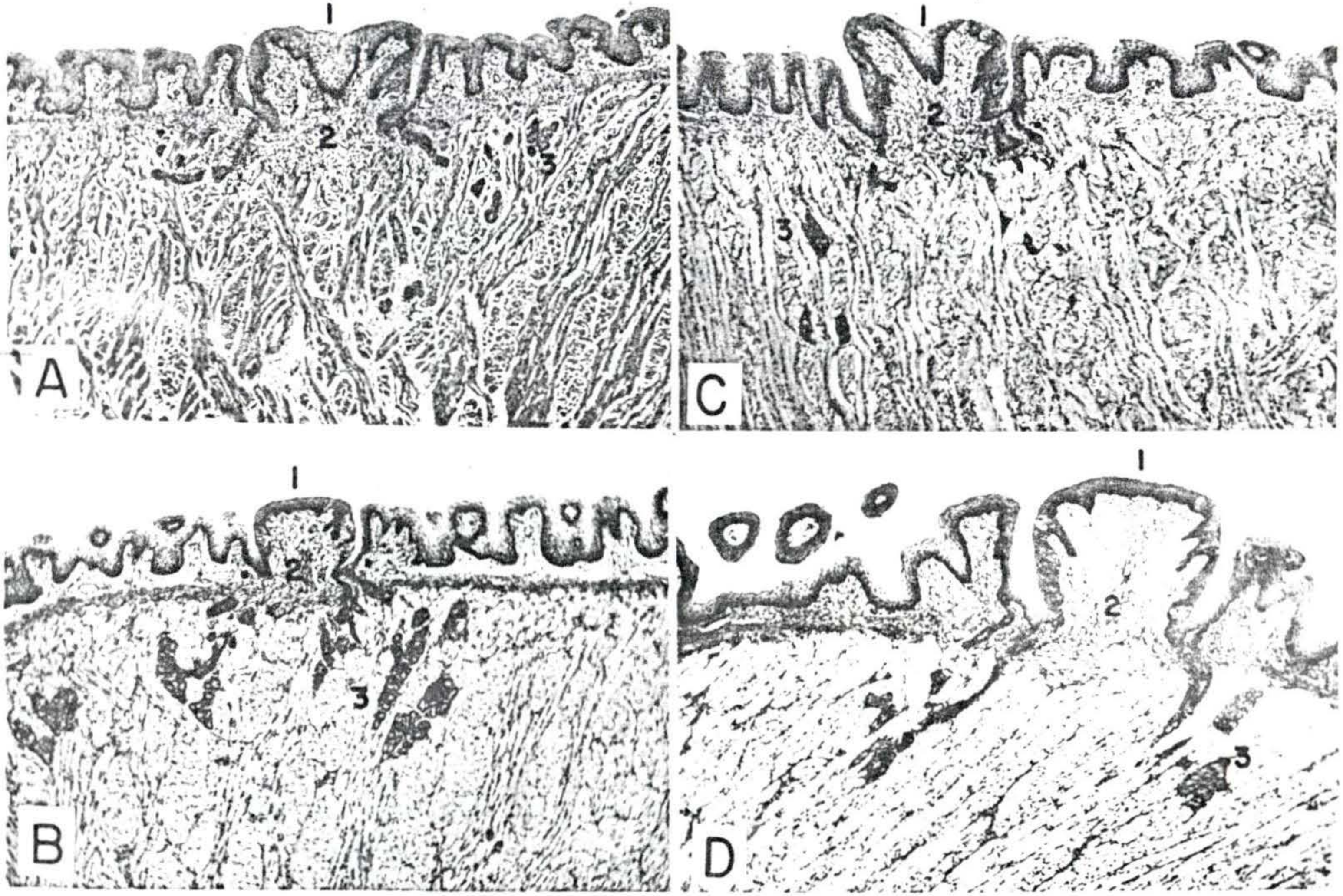
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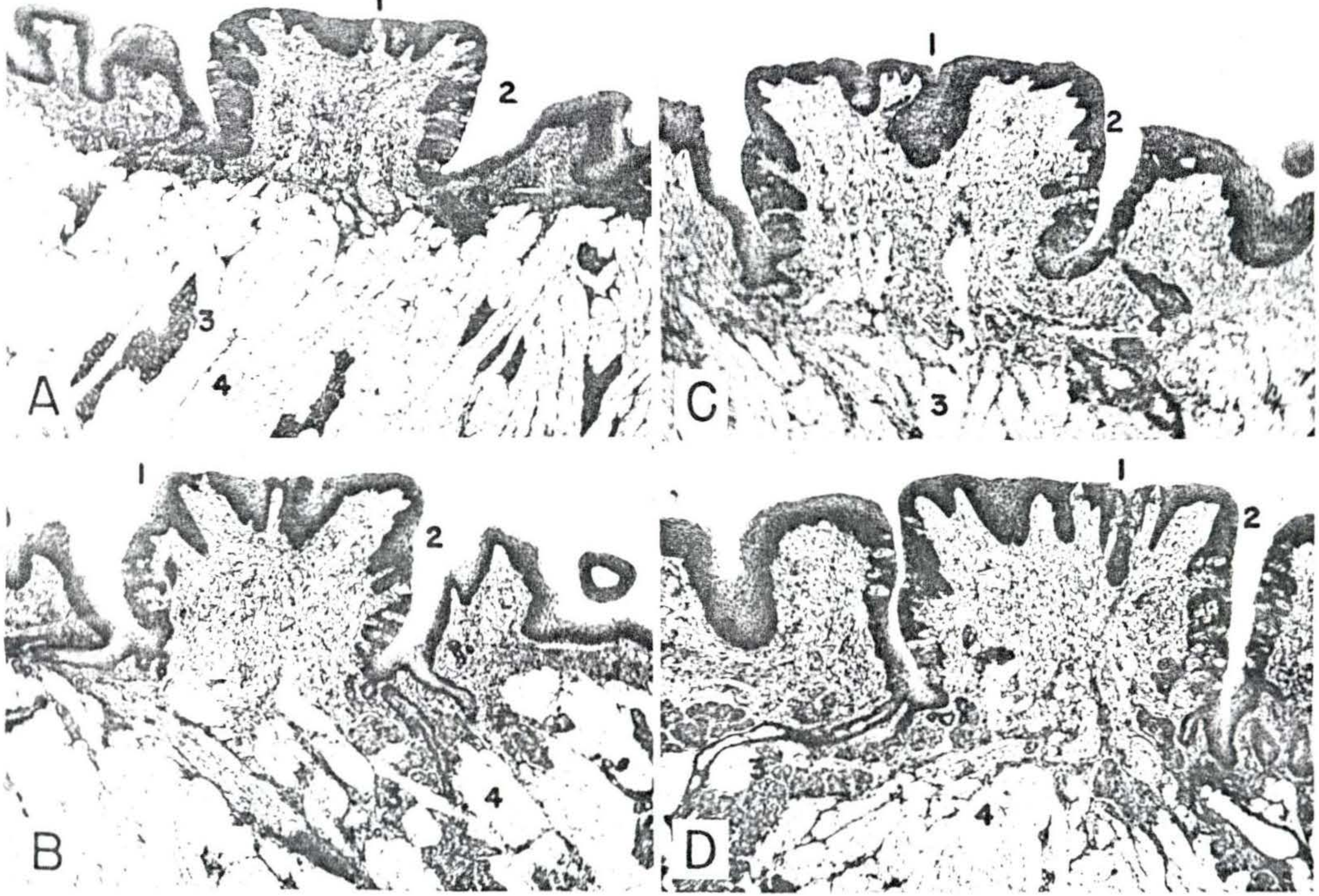
Fig. 28. Representative samples of vallate papillae from four weeks to 12 weeks of age

A. A section from block 28TF5, four weeks, 60X
   1. Vallate papilla
   2. Moat
   3. Serous glands
   4. Intrinsic, striated muscle

B. A section from block 42TF5, six weeks, 60X
   1. Vallate papilla
   2. Moat or trench
   3. Serous glands. Note the increase in amount at six weeks of age
   4. Striated lingual muscle

C. A section from block 46TF6, eight weeks, 60X
   1. Vallate papilla
   2. Moat
   3. Striated lingual muscle. The glands were much deeper in between the bundles of lingual muscles in this section

D. A section from block 11TF5, 12 weeks, 60X
   1. Vallate papilla. Note the taste buds on the dorsal surface of this papilla
   2. Moat or trench. Note the depth and inclination of the walls
   3. Serous glands and a large secretory duct
   4. Striated lingual muscle bundles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The moat became deeper and the trench wall more vertical as the age advanced. Fig. 28D illustrates a typical vallate papilla on the tongue of a 12 week old dog. This was the typical papillae found up to four years of age. Fig. 26D illustrates one of the variations found at 16 weeks of age. This papilla resembles two fungiform papillae.

The conical papillae underwent similar age changes. Fig. 29 illustrates typical transverse sections through conical papillae. At birth, the papillae were small, but, relatively speaking, the most mature structurally. The caudally curved projections of the conical papillae were present at birth. After six weeks, the conical papillae changed only slightly in size and structure.

At birth, serous glands were sparse in the TF7 (See Fig. 2) sections of the tongue, Fig. 29A. The serous glands increased in number with age. It may be significant that mucous glands made their appearance in the submucosa of sections TF5, TF6 and TF7 (See Fig. 2) at six to ten weeks of age. Fig. 29C illustrates mucous glands in the submucosa of section TF7. The trichromic stain used on these sections readily differentiated between serous and mucous glands. Fig. 29B illustrates the serous glands mixed with the mucous glands.

c. Foliate. The depth of the gustatory furrow at

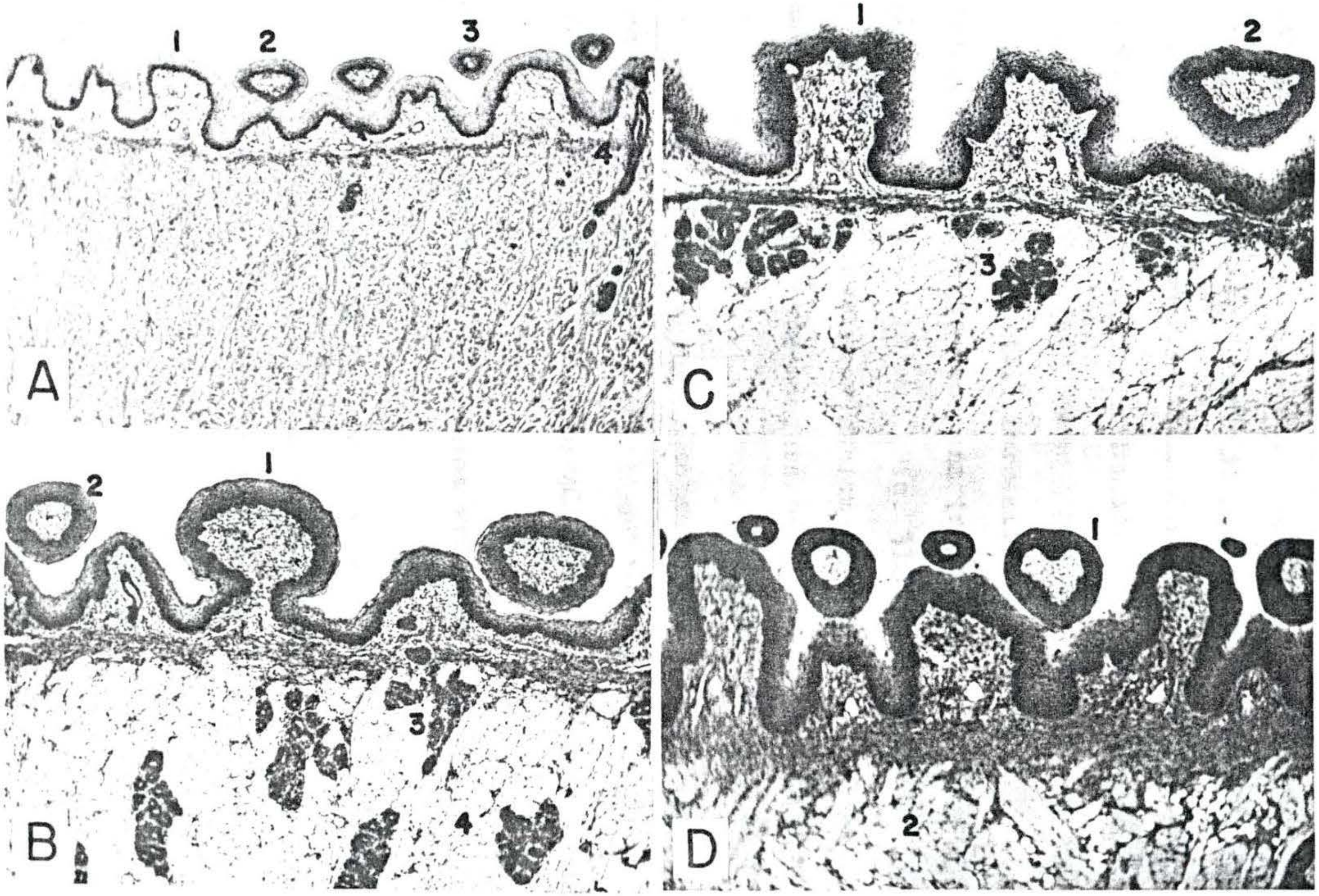
Fig. 29. A representative sample of transverse sections of conical papillae

A. A section taken from block 65TF7, birth, 60X
   1. Basal portion of a conical papilla
   2. Recurved cone shaped papilla showing the separation of the secondary dermal papilla from the basilar portion of the papilla
   3. The caudal end of the cone shaped papilla
   4. Secretory duct of a serous gland

B. A section taken from block 28TF7, four weeks, 60X
   1. Cone shaped papilla still connected by its dermal core to the basal portion of the papilla
   2. Recurved portion of the conical papilla
   3. Serous glands

C. A section taken from block 42TF7, six weeks, 60X
   1. Conical papilla
   2. Recurved portion of a conical papilla
   3. Mixed serous and mucous glands in among the lingual muscles

D. A section taken from block 6TF6, ten weeks, 60X
   1. A recurved portion of a conical papilla
   2. Striated lingual muscle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birth was relatively shallow. It increased in depth and became relatively fixed at six weeks of age. The serous glands are mostly absent at birth, Fig. 30. The secretory ducts were forming at the bottom of the gustatory furrow. The glands increased in size and number and became maximally developed at six to eight weeks of age, Figs. 30 and 31.

The foliate papillae were cut transversely, so only the anterior or posterior sections (obliquely cut) were adequate for study of the papillae. Fig. 31D illustrates a foliate papilla (cut transversely) through one of its furrow walls. Many of the taste buds on this section were cross sections instead of longitudinal sections as normally seen.

It was impossible to make an accurate study of the transversely cut foliate papillae, because the gustatory furrows could not be fully examined, Figs. 30 and 31.

C. Operative Procedures and Associated Anatomy

The operations were performed to facilitate the resection of the chorda tympani, glossopharyngeal, and vagus nerves. The chorda tympani nerve was cut inside the middle ear, which necessitated the removal of the osseous and tympanic bullas. The glossopharyngeal and vagus nerves emerged from the petro-basilar fissure in the dog, Fig. 32. It was located dorsomedial and posterior to the osseous bulla.

Fig. 30. Representative foliate papillae from dogs ranging in age from birth to three weeks of age

A. A section taken from block 65TF6, birth, 60X
   1. Lateral surface of the tongue
   2. Secretory ducts of the serous glands

B. A section taken from block 34TF6, 12 hours, 60X
   1. Lateral surface of a foliate papilla
   2. Secretory ducts
   3. Serous glands
   4. Striated lingual muscles

C. A section taken from block 66TF5, one week, 60X
   1. Foliate papilla with a gustatory furrow
   2. Serous glands
   3. Striated lingual muscles

D. A section taken from block 68TF6, three weeks, 60X
   1. Foliate papilla
   2. Serous glands

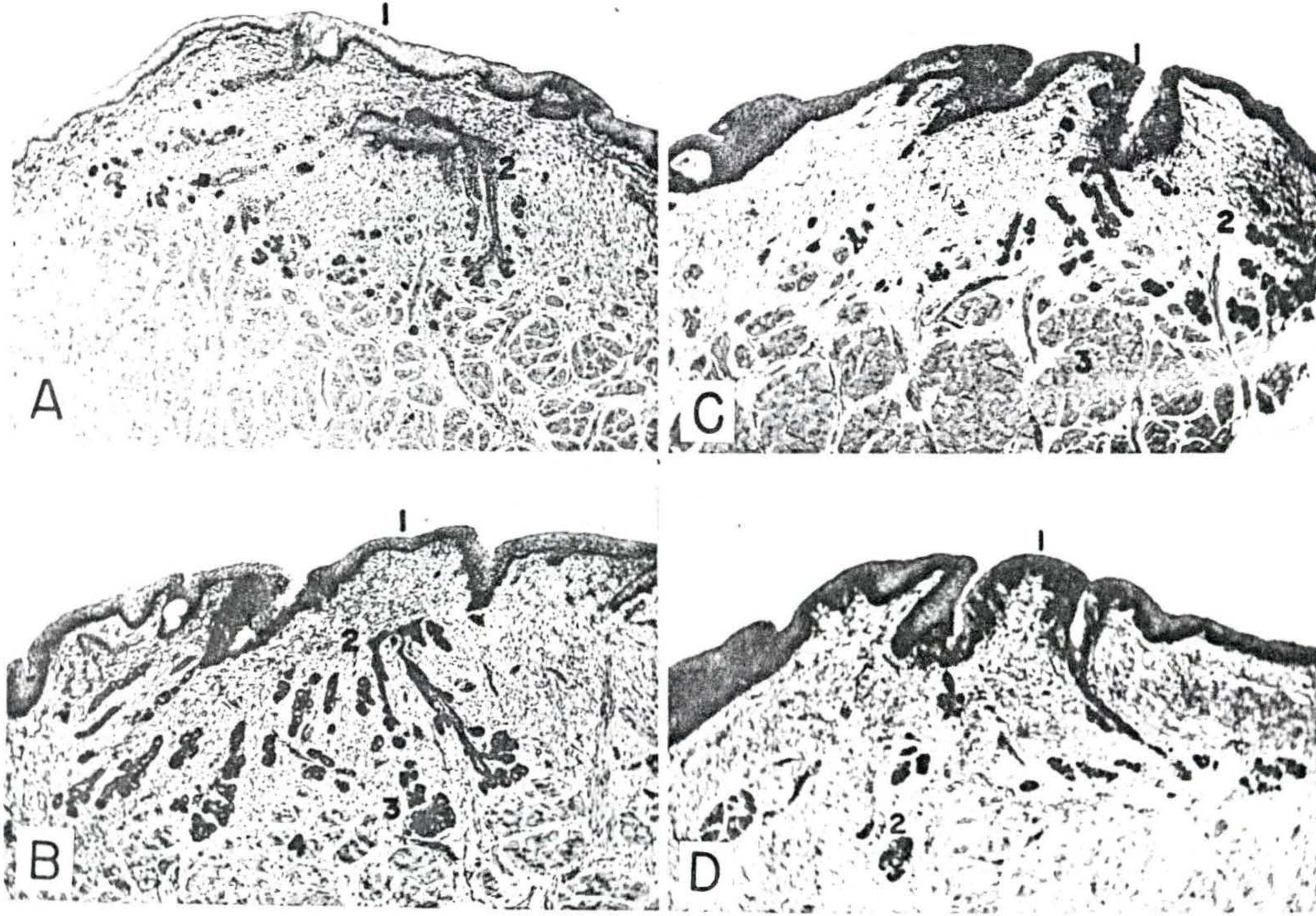
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Fig. 31. Representative foliate papilla from dogs ranging from four weeks to ten weeks in age

A. A section taken from block 28TF5, four weeks, 60X
   1. Foliate papilla
   2. Primary dermal papilla
   3. Serous glands. Note their increase over three weeks
   4. Striated lingual muscles

B. A section taken from block 42TF5, six weeks, 60X
   1. Foliate papilla
   2. Primary dermal papilla
   3. Secretory ducts from bottom of gustatory furrow
   4. Serous glands
   5. Striated lingual muscles

C. A section taken from block 44TF6, eight weeks, 60X
   1. Foliate papilla, lateral border
   2. Primary dermal papilla
   3. Serous glands

D. A section taken from block 6TF5, ten weeks, 60X
   1. Gustatory furrow, cut transversely
   2. Primary dermal papilla
   3. Secretory ducts emptying into the gustatory furrow
   4. Serous glands
   5. Striated lingual muscles

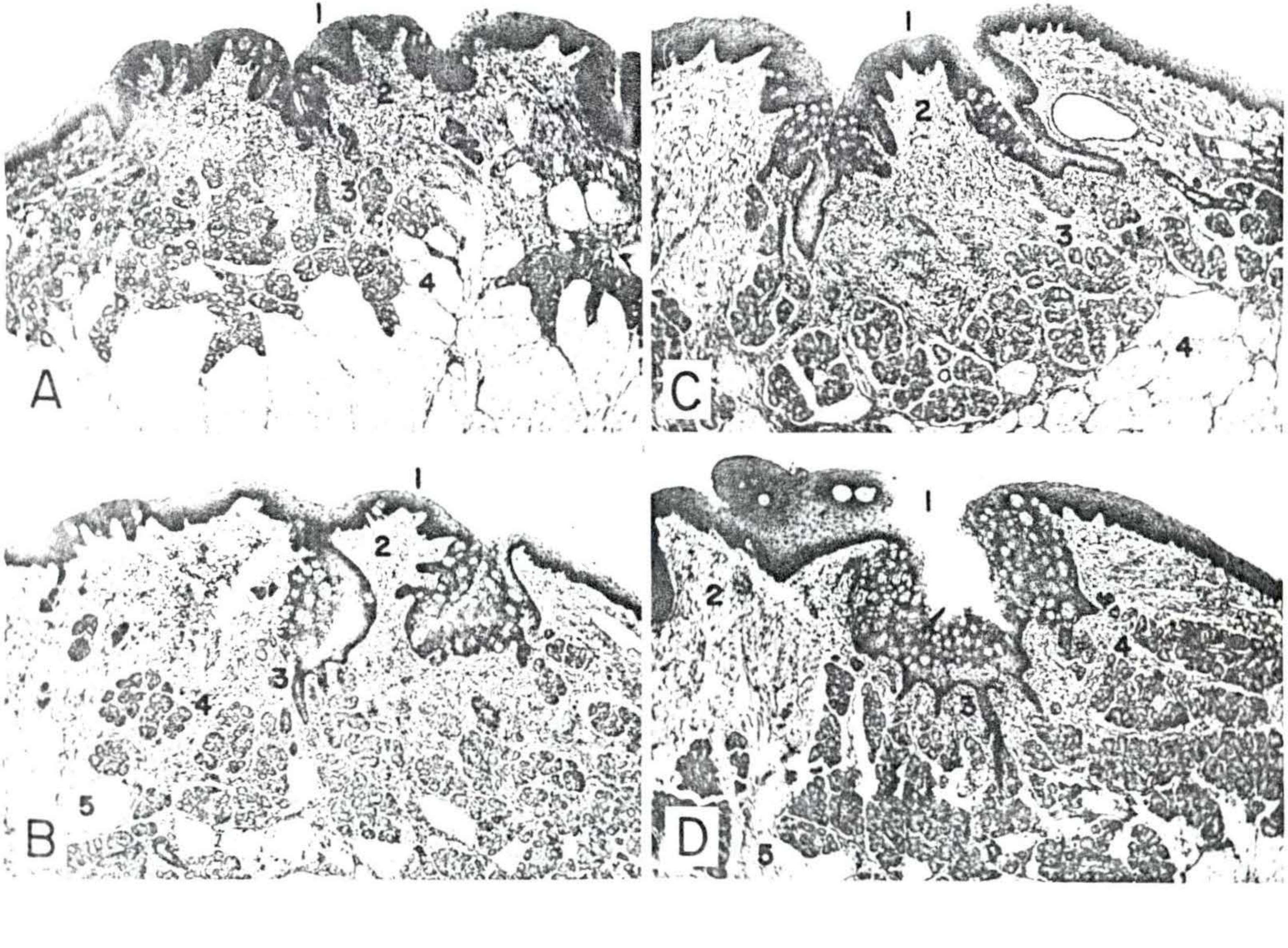
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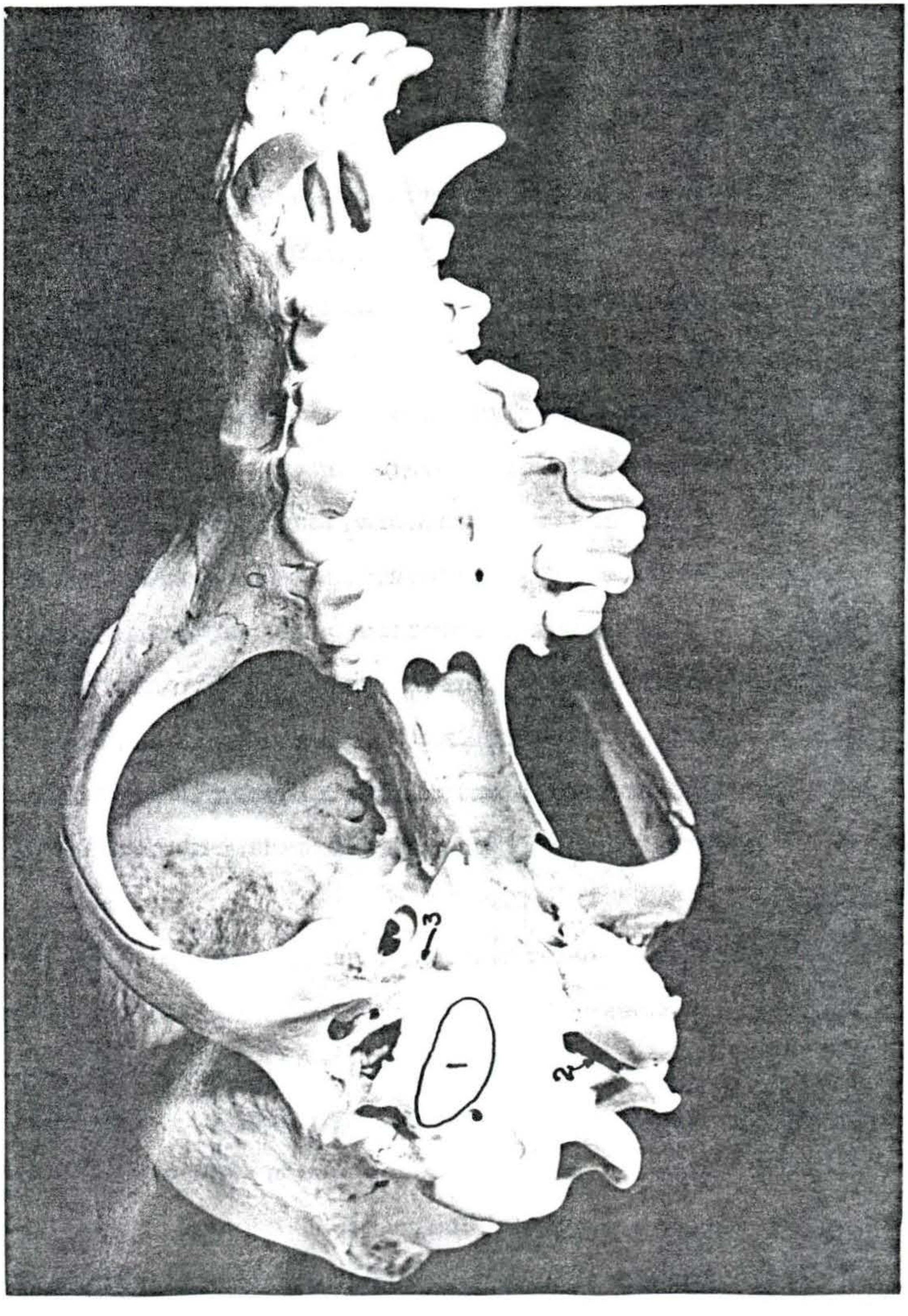
Fig. 32. A three-quarter view of the dog skull, showing the areas involved in the neurectomy experiments

1. Osseous bulla; the encircled area indicates the portion removed to gain access to the cavity of the middle ear
2. Petrobasilar fissure; the foramen by which the vagus, glossopharyngeal and spinal accessory nerves gain an exit from the calvarium
3. Petrotympanic fissure; the foramen by which the chorda tympani branch of the facial nerve leaves the cavity of the middle ear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Since the areas involved in the resection of the three nerves were so closely associated with each other, the operative procedures necessary for each resection were modified only slightly.

The first approach to the middle ear was from the lateral side, just under the external acoustic meatus. The chorda tympani nerve was not visible after the bulla ossea, Fig. 32, was removed from this lateral approach. The site of the operation was progressively moved medially until the most advantageous site for exposing the chorda tympani nerve was found to be on the midline over the larynx.

The area from the symphysis of the mandible to the middle of the neck was clipped, shaved, defatted with ether, and disinfected with 70 percent ethyl alcohol. The dog was intubated, using latex tubing. The surgical site was then shrouded with sterile towels and covered with a large sterile plastic shroud, through which the operation was performed.

An incision was made from a point midway between the symphysis and the caudal angle of the mandible to a point one to one and one-half inches caudal to the cricoid cartilage of the larynx. This large, initial incision was necessary to provide an adequate exposure of the osseous bulla, Fig. 32. The superficial fascia was dissected away from the underlying muscle tissue. The sphincter colli primitivus, profundus and the platysma muscles were laid back with the fascia. The mylohyoideus, stylohyoideus, and parotidoauricularis muscles were transected in this operation, as well as the superficial muscles mentioned above. Natural cleavage lines were used in separating the remaining muscles in the operative field. The stylohyoideus muscle was a small, ribbon-like muscle that took its origin from the stylohyoid bone and swung vertically between the lateral side of the digastricus muscle and the mandibular salivary gland. It inserted on the basihyoid bone. The mylohyoideus muscles originated along the medial aspect of the mandibles as far dorsally as the alveolar line. They came together medially and inserted on the basihyoid bone posteriorly. The parotidoauricularis or depressor suriculae muscle arose from the deep fascia in the area of the larynx and passed anterodorsally across the external maxillary vein and the middle of the parotid salivary gland. It inserted on the antitragus of the auricular cartilage. It was about one centimeter wide.

A large vein was situated ventral to the basihyoid bone. This vein joined the two lingual veins before they drained into the external maxillary veins. A small vein was found on the midline, between the mandibular rami, at the junction of the two mylohyoideus muscles. It drained into the middle of the transverse vein. These veins could have been avoided, but it was best to doubly ligate the transverse veins and cut between the ligatures. Occasionally, they were inadvertently damaged because of their variable position.

After the mylohyoideus, stylohyoideus and depressor auriculae (parotidoauricularis) muscles were cut, the bulla tympanica was reached by blunt dissection. The larynx was pulled to one side. This manipulation required the trachea to be intubated to prevent collapse and suffocation. The carotid artery was pushed laterally as far as the stylohyoid and digrastricus muscles. The lingual artery crossed the field of the operation in most cases. The stylopharyngeus muscle ran from the dorso-medial portion of the stylohyoid bone and inserted on the pharyngeal wall just under the dorsal extent of the hyopharyngeus muscle. The stylopharyngeus muscle had to be severed in most cases. The digastricus and styloglossus muscles were pulled laterally. A retractor was then inserted under the stylohyoid bone and the hyopharyngeus, styloglossus and digastricus muscles were pulled laterally. The longus capitus muscle inserted on the basal portion of the occipital bone at its junction with the basal portion of the sphenoid bone. The ventral straight muscle of the head inserted just posterior to the longus capitus muscle. These two muscles were moved as far medially as possible.

The nerve plexuses that overlaid the osseous bulla were carefully dissected away from the bulla and a bone chisel was used to remove the floor of the osseous bulla, Fig. 32. Hemorrhage was negligible if the operation was properly done. Control of hemorrhage was very important before the osseous and tympanic bullas were removed to prevent blood from entering the cavity of the middle ear and obscuring the field. A head lamp was used to illuminate the narrow, deeply situated cavity of the middle ear. The chorda tympani nerve could easily be seen as a white streak crossing over the anterior process of the malleus. With fine forceps it was easily picked up and the free portion pulled away from the portions still in the bony canals.

The cap of the bulla ossea, Fig. 32, was not replaced. The fascia between the muscles was sutured to eliminate pockets. The mylohyoid muscles were placed in apposition and their fascial sheaths sutured with 000 plain catgut. The subcutaneous fascia was sutured with 00 chormic catgut. The skin was closed with interrupted sutures of 00 chromic catgut. The incision was sealed with gauze and Flex-O-Seal (a commercial flexible skin covering). All of the incisions healed by first intention. Two dogs had slight hemorrhage from the nostrils, indicating escape of blood through the eustachian tube.

Neurectomy of the glossopharyngeal and vagus nerves followed essentially the same pattern as that of the chorda tympani neurectomy. The anterior point of the skin incision was on the midline about an inch anterior to the caudal angle of the mandible. The posterior point was three inches behind the larynx. The mylohyoid muscle was not cut, but the stylohyoid and depressor auriculae (parotidoauricularis) were severed. The insertion of the cleidomastoid portion of the brachiocephalicus muscle and the sternocephalicus muscle were also pulled laterally. The longus capitis muscle and trachea were pulled as far medially as possible. The carotid artery was separated from the vagosympathetic nerve trunk. The vagus, glossopharyngeal and spinal accessory nerves emerged from the skull via the petrobasilar fissure. The glossopharyngeal nerve was anterior to the hypoglossal nerve for a short distance.

The glossopharyngeal nerve was severed as close to the petrobasilar fissure as possible. This was very difficult to accomplish successfully since the nerve exited in an acute dorsal angle from the skull. The vagus nerve was severed between the jugular and nodose ganglion. Persistent vomition was the sequel to cutting of the vagus. Difficulty in swallowing was also noticed to a minor extent.

The wounds were sutured in a manner similar to that used in the chorda tympani neurectomies. There was no infection or drainage of the wounds. First intention healing was established in all cases.

Microscopic studies are to be made at a later date on the tissue sections obtained from the neurectomy experiments.

V. DISCUSSION

Arey (1954) stated that in human fetuses of nine to 11 weeks the fungiform papillae could be distinguished grossly as elevations in the mucosa. In the dog, the fungiform papillae cannot be distinguished grossly until the third or fourth postnatal week. According to Arey (1954), the epithelial ring around the vallate papilla splits, by the fourth month of fetal life, forming the moat. In the dog the moat was not formed in some instances until after birth. Arey (1954) also stated that human taste buds disappeared from the dorsal aspect of the vallate papillae before birth. Taste buds were found on the dorsal aspect of the vallate papillae through 28 weeks of age in the dog.

The tongue of the human fetus (nine to 11 weeks) is comparable with the tongue of the dog at birth.

The terminology used in the literature to describe the lingual papillae of the dog is confusing. A distinction is made in this work between the filiform papillae and the conical papillae of the dog. The human has no lingual papillae behind the rows of vallate papillae as does the dog. There is a great deal of morphological difference between the conical and filiform papillae of the dog. The author wishes to suggest that the term "conical", as used by

Sisson and Grossman (1953) and Bradley (1948), be applied to those lingual papillae located caudal to the "V" shaped rows of vallate papillae. The term "filiform papillae" should be restricted to the papillae bearing thread-like projections on the portion of the tongue anterior to the "V" shaped rows of vallate papillae. The largest, most caudal projection is the primary filiform. The next two papillae in size, located just anterior-lateral to the primary filiform, are the secondary filiforms. The five to six lesser projections from the anterior edge of the basal papilla are called tertiary filiforms, Fig. 2.

The gross and microscopic structure of the leaves of the so-called foliate papilla were found to be similar to the vallate and fungiform papilla. The individual leaf of the foliate papilla (currently used term) is a separate entity, and satisfies all the structural requirements of a lingual papilla. It is, therefore, suggested that each individual leaf be termed a foliate papilla.

The distribution of the fungiform papillae were found to conform for the most part with the descriptions in the literature. Bradley (1948) and Sisson and Grossman (1953) stated that fungiform papillae were not found behind the "V" shaped rows of vallate papillae. In this investigation, fungiform papillae were found posterior to the rows of vallate papillae.

Trautmann and Fiebiger (1952) stated that in carnivores the gustatory field on the vallate papilla was restricted to the bottom of the moat and was therefore very small. They further stated that taste buds were usually absent in the surface epithelium of each papilla as well as in the pe-ipheral wall of the moat. These statements are true for the dog, only from birth to six weeks of age. At birth taste buds are found on the dorsal surfaces of the vallate papillae. This work has shown that the gustatory area is extensive in dogs 12 weeks to four years of age. At 20 weeks, taste buds were found on the dorsal epithelium and walls of the vallate papilla as well as in the peripheral wall of the moat.

A description of the fringe of modified filiform papillae on the anterior-lateral border of the tongue was not found in the literature. The shape of the tongue at birth is concave. This concavity, along with the fringe of modified filiform papillae, forms a tube around the nipple of the bitch during the act of nursing. The dorsal concavity changes to a dorsal convexity between six and eight weeks of age. The fringe papillae also disappear at this age. Most puppies are weaned at six to eight weeks of age and the method of prehension must necessarily change from sucking to lapping. This change is gradual and the fringe papillae slowly disappear.

Another change that took place at the sixth to eighth postnatal week was the tremendous increase in the number of submucosal serous glands under the vallate and foliate papillae. These glands may aid in the dissolution of the solid food particles that find their way into the moats or gustatory furrows.

The keratinization increased in thickness between six and eight weeks of age. This may be due to the change in the method of procurement of food by the weanling pup. The fungiform papillae are structurally mature at six weeks of age and the vallate papillae at 12 weeks of age. The tongue and it's membranous covering undergoes an important adjustment at the time of weaning.

Another phase of the experiment was the resection of the various nerves to the taste buds. Olmstead (1922) resectioned the chorda tympani nerve between its emergence from the petrotympanic fissure and its junction with the lingual nerve. Miller (1952) stated that this portion of the chorda tympani nerve is very short and may be impossible to locate in some dogs.

Olmstead's technique (1922) for resection of the chorda tympani nerve was difficult to perform. His procedure resulted in a high degree of trauma and a low survival rate. The technique developed in this investigation was relatively simple and there were no fatalities. The dogs displayed no symptoms other than a slight amount of difficulty in swallowing. Resection of the entire chorda tympani was complete in all cases. It could not be confused with any other nerve because of its isolated location. The chorda tympani nerve was resectioned on five dogs with excellent results, using this new technique.

Olmstead (1922), using one dog, cut the mandibular nerve just cranial to the junction of the chorda tympani with the lingual nerve. The left side of the tongue was paralyzed and it had difficulty in drinking. Miller (1953) stated that the hypoglossal nerve is motor to the entire tongue. The lingual nerve is assumed by Miller (1953) to be sensory to the anterior two-thirds of the tongue. The hypoglossal nerve inadvertently was cut in this investigation, and the dog showed very little changes in its ability to lap water, thus the motor innervation of the tongue of the dog should be investigated further.

Olmstead and Pinger (1936) severed the lingual nerve with its chorda tympani nerve component and anastomosed the distal end of the lingual nerve with the proximal end of the cut hypoglossal nerve. They stated that the hypoglossal nerve can initiate regeneration of the taste buds which had disappeared from the fungiform papillae on the operated side. This is contrary to the commonly accepted findings regarding regeneration of sensory nerve endings.

VI. SUMMARY AND CONCLUSIONS

The tongues of 31 dogs were studied in order to determine age changes of the lingual papillae. A pattern was established for the structure and distribution of the lingual papillae of the dog. Suggested changes in nomenclature are as follows:

1. The cone-shaped lingual papillae behind the "V" shaped rows of vallates should be termed "conical papillae".

2. The lingual papillae (with thread-like projections) which are located anterior to the "V" shaped rows of vallate papillae should be termed "filiform papillae".

3. The thread-like projections on the filiform papillae should be designated as primary, secondary and tertiary filiforms.

4. The term "foliate papilla" should be reserved for each individual leaf of the papilla termed "foliate papilla" by previous workers. This suggested change is consistent with the naming of lingual papillae according to their morphological shape.

The period between six and eight weeks of age (weaning time), was the critical morphological phase of the tongue and its coverings. The shape of the tongue at birth was concave, conforming with its sucking function. At six weeks of age, the tongue changed its concave shape to a dorsal convexity. The change accompanies its new function of prehension of solid food, and lappingfluids. Modified filiform papillae on the anterior-lateral border of the tongue formed a fringed border. This border, which disappeared by the time of weaning, seemed to facilitate the nursing action of the tongue of the pup.

Serous glands, located in the submucosa under the vallate and foliate papillae, developed rapidly at weaning time (six to eight weeks) and were maximally developed at 12 to 20 weeks of age. These serous glands undoubtedly aid in the dissolution of food in preparation for eliciting taste sensations in the taste buds.

Mucous glands began making their appearance along with the serous glands after 12 to 16 weeks of age.

A new technique was devised for the accurate resection of the chorda tympani branch of the facial nerve. This technique was developed to facilitate further study of the innervation to the taste buds on the anterior two-thirds of the dogs tongue.

Sixteen dogs were used in the neurectomy experiments: five dogs were used for the chorda tympani neurectomy; five each for the glossopharyngeal and vagus nerve resections; and one control. The tissues will be studied at a later date.

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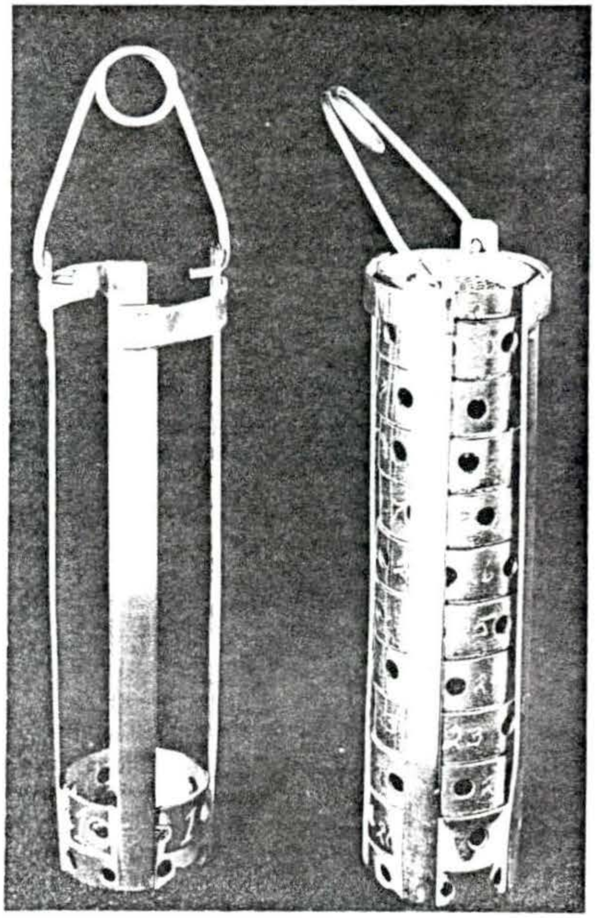
IX. APPENDIX

Fig. 33. Top picture, series of tissue baskets and holding rack

Bottom picture, the embedding tray and movable brass block



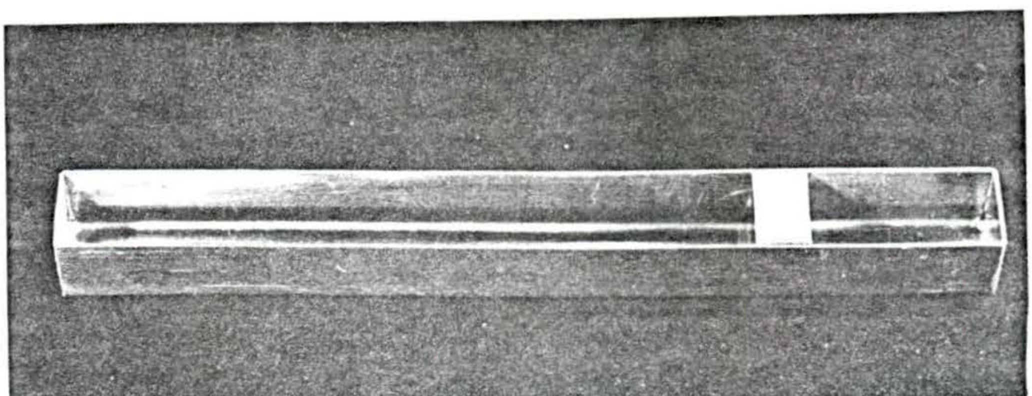


Fig. 34. The data sheet used to keep accurate account of all the varied treatments and times given the tissues while they are in the series of tissue baskets

Specimen No.______ Fixative Used:________________ Date:__________

Breed:______________________ Sex:__________ Notes:______________

Dog No.	Tissue	Block No.	Age	Date Autopsied	Pieces	Capsule

Date	Time	Hours	Reagents