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Structure of the caecilian *Siphonops annulatus* (Amphibia, Gymnophiona): general aspect of the body, disposition of the organs and structure of the mouth, oesophagus and stomach

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Abstract

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The caecilians (or Gymnophiona) constitute one of the least well known groups of terrestrial vertebrates because most species live underground, in quite unaccessible environments. *Siphonops annulatus* is an exclusively fossorial species and is the most extensively distributed caecilian in South America. This work is the first of a series which intends to study the complete morphology of this species. It describes the general anatomy and the initial portion of the digestive system, from the mouth to the stomach. The general aspect of the body and the elongation of the organs seem to be related to adaptation to the fossorial environment.

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Introduction

Caecilians (Gymnophiona) are amphibians restricted to the tropics that have a serpentiform and annulated body and reduced eyes covered with skin. Extant species are limbless and have a pair of tentacles at the snout, an intromittent copulatory organ (phallodeum) (Wiedersheim 1879) and a unique dual jaw closing mechanism (Bemis *et al.* 1983; Nussbaum 1983). They are primarily adapted to a fossorial life, although a few species are secondarily adapted to the aquatic or semiaquatic environment (Nussbaum and Wilkinson 1989).

Because of their distribution and the type of environment in which they live, the caecilians constitute one of the least well known groups of terrestrial vertebrates. Information about physiology, ecology, natural history and behaviour of these animals is very scarce. Lawson (1963) noticed the low number of references about the anatomy of individual species of caecilians; despite the continuous and comprehensive efforts of such authors as M.H. Wake and colleagues and J.-M. Exbrayat and colleagues, data about the morphology of these amphibians are still few.

Siphonops annulatus is an exclusively fossorial species and is the most widely distributed caecilian in South America. Since it can adapt to different levels of humidity, it is found from quite dry regions (semiarid) to rain forests (Taylor 1968). This species is found in Brazil, mainly on the cacao plantations at the south of Bahia State and in many other countries.

In the last 9 years, our group has maintained an interchange with the Cacao Research Center, in Ilhéus, Bahia State, Brazil. We have made 12 expeditions for observation and collection of specimens of *Siphonops annulatus*. During this time, we have also developed a methodology for maintenance of these animals in captivity. This study primarily aims to describe the structure of *Siphonops annulatus* and intends to use these morphological data for assessing the behaviour of these animals. In this initial paper, we present the general aspect of the body, the anatomy of its viscera and the histological structure of its mouth, oesophagus, and stomach.

Materials and Methods

Ten adult specimens of both sexes of *S. annulatus* Mikan (1820), classified according to Taylor (1968) were captured at the Cacao Research Center (CEPEC CEPLAC) in the region of Itabuna and llhéus in the State of Bahia, Brazil. After capture they were kept in a terrarium and periodically fed with minced meat and newborn mice. We therefore studied well fed animals weighing between 23 and 48 g and measuring from 28 to 43 cm.

Some of the specimens are deposited in the collection of the Zoological Museum of the University of São Paulo under numbers 71277, 71278 and 71279. They were submitted to a temperature of 4 °C for 30 min and injected intraperitoneally with 4% paraformaldehyde dissolved in 0.1 M phosphate buffered saline, dissected and further fixed in the same solution. For light microscopy tissues were embedded in Technovit 7100 resin (Heroeus, Wehrheim, Germany) and sectioned with glass knives at 1 and 2 μm. These sections were stained with toluidin blue and fuchsin and mounted in Micromount (Surgipath Medical Industries, Richmond, IL, USA). Alternatively sections were stained with a variant of Romanowsky stain for haemopoetic tissues described by Rosenfeld (1947).

To study the distribution of glycogen and neutral or acid polysaccharides associated with proteins the periodic acid Schiff (PAS) and the Alcian blue methods were applied according to Bancroft and Stevens (1990). Yellow and green filters were used so as to increase photographic contrast.

Decalcification was performed in 5% EDTA diluted in isotonic saline containing 1% paraformaldehyde. As will be seen thin sections of this material processed in our conditions produced figures with higher resolution when compared to paraffin embedded material. This permitted a better understanding of the function of the cells and tissues studied (Junqueira 1995).

Results

General aspect of the body

Figure 1(A) shows a dorsal view of *Siphonops annulatus*. The body is cylindrical and serpentiform, head and tail presenting a similar diameter. The skin is shiny and bluish-grey. The lighter colour of the annulae makes them evident (Fig. 1A). The head is flattened dorso-ventrally and presents a pair of reduced eyes and a pair of white spots (Fig. 1B) that might correspond to the tentacles described for other caecilians (Billo and Wake 1987; Wake 1992). The mouth has an antero-ventral position. The terminal cloaca is round and pleated and lacks pigmentation (Fig. 1C).

Anatomy of the viscera

The gross distribution of the viscera of *S. annulatus* is presented in Fig. 2.

The digestive tube. The mouth presents short conical teeth of various sizes forming a single row in the lower jaw and a double row in the upper jaw (Fig. 3A,B). The tongue is a soft and short structure firmly linked to the lower jaw. The mouth communicates with a long, flattened and thin-walled oesophagus presenting an average diameter of 5 mm. At the height of the heart the oesophagus ends and the stomach begins. This structure has a thicker wall and its diameter gradually increases to an average of 8 mm, ending at the level of the lower portion of the liver. Both oesophagus and stomach are elongated structures. The transition of the stomach to the small intestine is abrupt; the small intestine is much thinner and forms a series of irregular curved loops, constituting the only nonlinear portion of *S. annulatus*'s digestive tract.

An elongated liver of dark colour is situated at the right of the stomach beginning just below the heart and extending as far as the end of the stomach. It is formed by the superposition of $\approx$ 20 leaflets of hepatic tissue linked one to another by a thin structure at their central region. The whole structure has an emarginated aspect. The gall bladder is found behind the lower caudal liver leaflets and communicates with the small intestine by a short and conspicuous bile duct. The spleen and pancreas appear bound to the dorsal region of the first intestinal loop.

The large intestine is a much wider thin-walled structure that ends at the cloaca shortly before the anus. The elongated urinary bladder, inserted at the lower portion of the cloaca, is a very thin walled tube orientated toward the cranial region. From the caudal third of the cloaca a slim structure formed by smooth muscle, the musculus retractor cloacae, emerges. This structure divides itself in the cranial direction assuming the form of an 'Y'; its terminal portions are bound to the lateral muscular wall of the body.

The respiratory system. The trachea, an elongated and thin (1 mm) structure presenting superposed incomplete cartilage rings, begins immediately behind the tongue and ends near the heart, where it bifurcates. The right branch gives rise to a long (2 mm) thin red lung situated between the stomach and liver, which ends as a blind sac at the level of the lower third of the liver. The left branch ends in a reduced lung with a length of $\approx$ 10% of the right lung.

The urinary system. The kidneys assume the form of a red and long ribbon, which is flattened and continuous, covering the dorsal midline of the animals inner surface. This ribbon is constituted in its central part by a large artery and vein bound laterally to the parenchyma of the left and right kidneys. This organ begins just below the heart level and proceeds caudally ending at the cloaca. In the cranial region the ribbon is formed by segments

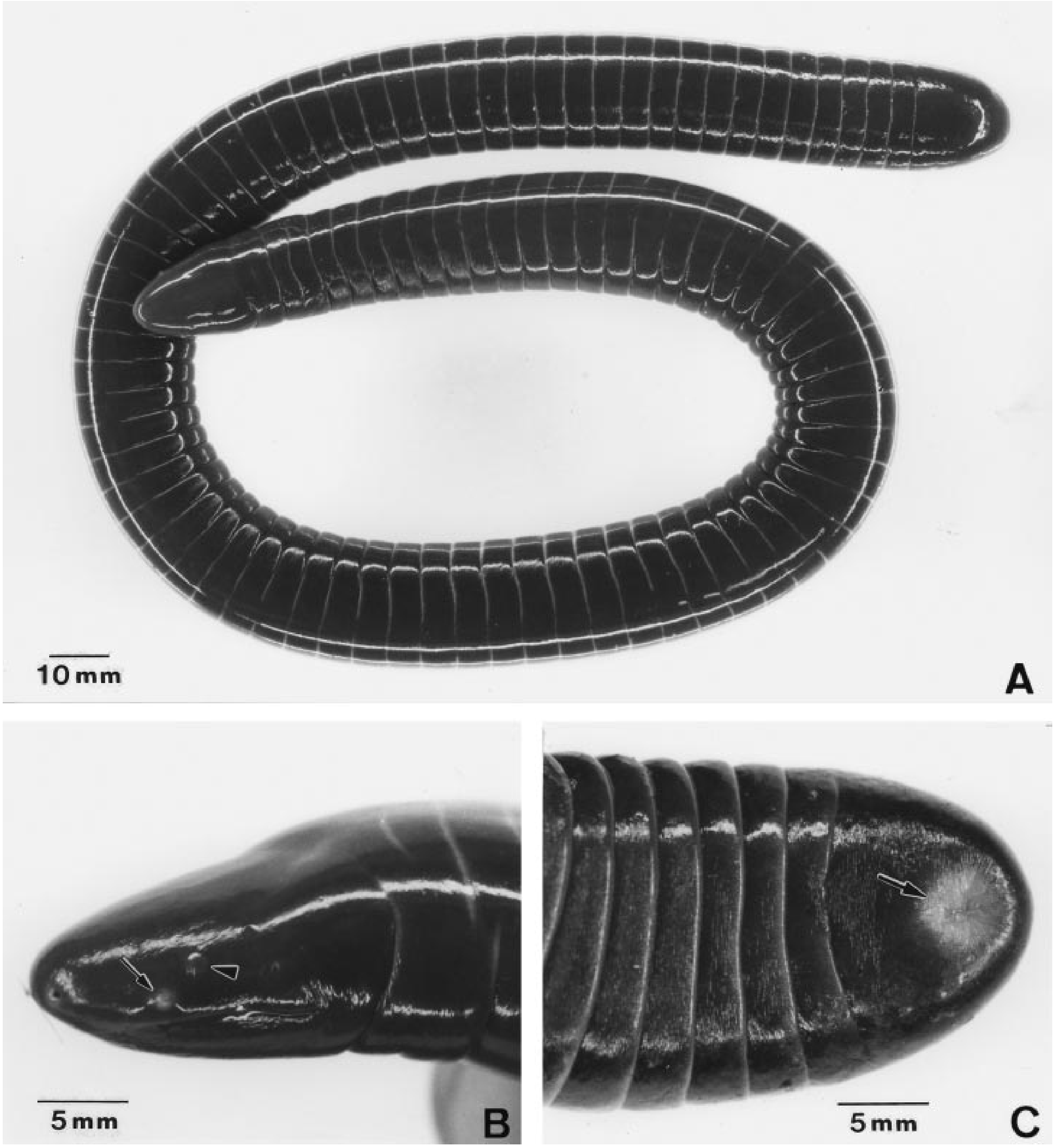


Fig. 1.—*Siphonops annulatus*.—**A,** Entire body. — **B,** Head. From left to right, the nostril is followed by a white spot (arrow) that corresponds to the region of the tentacle of other species and the eye (arrowhead). — **C,** Posterior end with anus (arrow).

separated by constrictions; as it progresses caudally these constrictions disappear.

The reproductive system. The ovaries and testes are paired organs disposed laterally at the height of the small intestine. Each testis presents 3–5 short elongated white lobes. During the periods of sexual inactivity the ovaries usually present small eggs disposed vertically and forming a rosary parallel to the small intestine.

The paired fat bodies are disposed laterally, occupying a region which corresponds to the large intestine and cloaca. They form a sequence of elongated almond-like structures, tied one to another by a thin thread of connective tissue.

Histology of the mouth, oesophagus and stomach

The mouth. The tongue's body is formed mainly by striated muscle. In its anterior region, septa formed by aggregates of muscle fibers are interspersed with venous sinuses

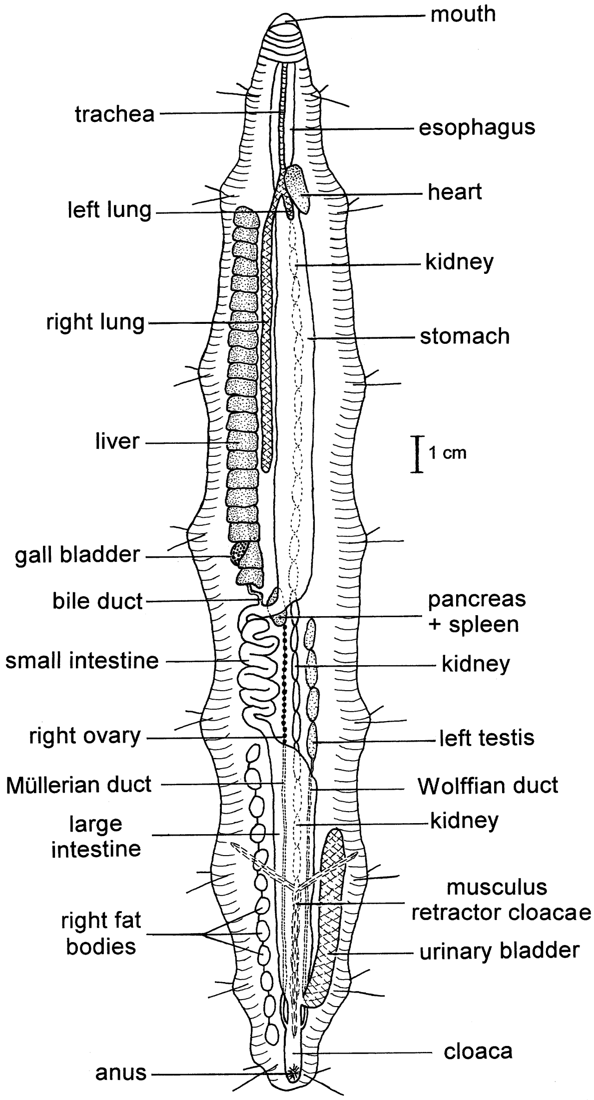


Fig. 2.—Drawing showing the disposition of the visceral organs in *Siphonops annulatus*.

(Fig. 4A,B). The posterior region of the tongue, however, is formed mainly by a solid muscular mass and presents at its posterior end a cartilaginous structure, the ceratohyal bar. This region is covered by prismatic ciliated epithelial cells which are intercalated with mucous goblet cells (Fig. 4D). The anterior portion of the tongue's surface as well as the surface of the mouth's cavity are covered by a stratified squamous nonkeratinized epithelium with occasional mucous goblet cells (Fig. 5B).

The lamina propria of these regions presents a third layer of abundant simple tubular mucous glands. These glands present two regions with two distinct mucus-producing cells. The upper region, which constitutes the greater part of the glands, is formed by large cells with large secretory granules that stain irregularly with the PAS method. In the basal portion of these glands flattened cells appear, containing small granules strongly stained by PAS (Fig. 4C). The mouth's palatal region also presents a conspicuous and continuous layer of tubular mucous glands and, as in the tongue, is also covered by a stratified squamous nonkeratinized epithelium with goblet cells. Based on the distinct distribution, morphology and histochemical reactions presented by the mouth's mucous cells, we verify that the mouth in *S. annulatus* not only presents a very high content of mucus secreting structures but also seems to secrete three different types of mucus.

The study of the tongue revealed the presence of an unique disposition in which striated muscle fibers are directed from the muscular layer to the organ's surface. These fibers run in parallel forming periodically disposed septa of striated muscle. These septa are separated in their initial portions by the venous sinuses and in their terminal portions by the tubular mucous glands (Fig. 4A,E). These muscle fibers, as they approach the subepithelial connective tissue, become thinner and end in the aponeurosis linguae, a specialized region of the lamina propria which is known to be a site of muscle insertion in the mammalian tongue (Krstic 1984) (Fig. 4F). In these regions one can observe the insertion of the muscle fibers in fibroblasts disposed in parallel (Fig. 5A). In several sections of mouths of adult specimens all stages of odontogenesis were found to occur simultaneously. Aspects of this process are illustrated in Fig. 5C,D,E.

Although no serial sections were performed, taste buds (Fig. 5B) were observed only on the tongues of three specimens, suggesting that these structures are not abundant; an extralingual distribution was not observed.

The oesophagus. This organ is covered internally by a stratified prismatic ciliated epithelium interspersed with mucous goblet cells that stain strongly with PAS and weakly with Alcian blue (Fig. 5F,G). At the basal region of this epithelium small round cells are visible, which are probably the stem cells responsible for the epithelial continuous renewal. A basement membrane separates the epithelium from the lamina propria. This layer presents an abundant capillary vascularization (Fig. 5F,G) but no muscularis mucosae was observed.

The oesophagus presents two exceptionally thin layers of smooth muscle.

The stomach. The inner surface of this organ is formed by a layer of prismatic mucous cells that covers another layer formed by gastric glands. These glands vary in number, appearing as isolated structures at the transition oesophagus/stomach, increasing in number in the stomach mid-region and finally decreasing in quantity at the caudal portion of this organ. A thin muscularis mucosae separates the tunica propria from the submucosa. The stomach

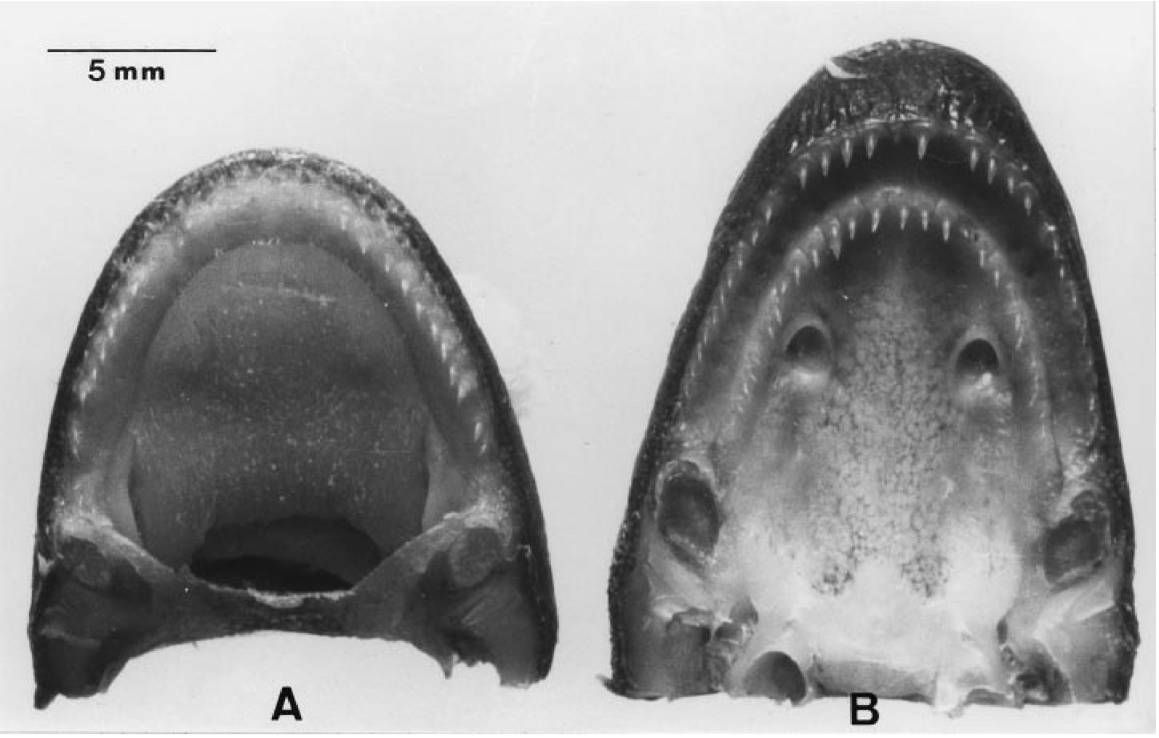


Fig. 3.—Internal views of the mouth of *Siphonops annulatus*. The lower jaw (A) bears the short and flat tongue and has only one row of teeth. The upper jaw (B) has two rows of teeth. Observe the irregular size and distribution of the teeth.

presents circular as well as longitudinal external smooth muscle layers (Fig. 6A).

In the lamina propria gastric simple tubular glands are found containing two different types of cells. The upper parts of these glands contains mucous cells. These cells, as those of the mucous surface epithelium, react strongly with the PAS method and stain weakly with Alcian blue (Fig. 6B). The lower parts of the gastric glands contains cells characterized by a basophilic basal region and an apical region with conspicuous secretory granules, which are not closely aggregated, thus presenting a space between them (Fig. 6C). These cells of the lower portion of the gastric glands do not react to the PAS method or stain with Alcian blue and present the structural characteristics of cells that secrete both pepsin and hydrochloric acid (chloridropeptic cells).

Discussion

The general aspect of the body of *Siphonops annulatus* seems to be related to its adaptation to the fossorial environment. The smooth skin, the tubular body and the antero-ventral position of the mouth facilitate the beginning of excavation and locomotion inside tunnels. The position of the mouth may also protect the animal as it moves inside the earth. It is possible that the bluish grey colour of the skin is a mechanism of protection, which serves as mimicry or advertising colour. Its skin secretion can, in some people, cause irritation in the eyes and in the respiratory system (Sawaya 1940).

Our observations in *Siphonops annulatus* agree with those of Duellman and Trueb (1986), that 'the organs of caecilians are elongated'. With exception for the small intestine that forms loops all other segments of the digestive, urinary and respiratory systems are exceedingly elongated. Its liver results from the superposition of ≈ 20 leaflets of this tissue. The presence of an atrophic left lung agrees with the observation of Baer (1937), Marcus (1937) and Carrier and Wake (1995). Despite this disposition being frequently found in Gymnophiona, the lung anatomy is highly variable in these animals (Goniakowska-Witalínska 1995). The kidneys are the organs that present an unparalleled elongation when compared to all other vertebrates.

S. annulatus's tongue is not protrusible; it is so firmly linked to the mouth's floor that is practically immobile. It therefore does not participate in the capture of food as is common among many other amphibians (Bemis *et al.* 1983). However, the observation of structures similar to taste buds in the tongue suggests a sensory function in this organ. The low number found of these structures contrasts with the situation known to occur in Anura. In *S. annulatus* also, taste

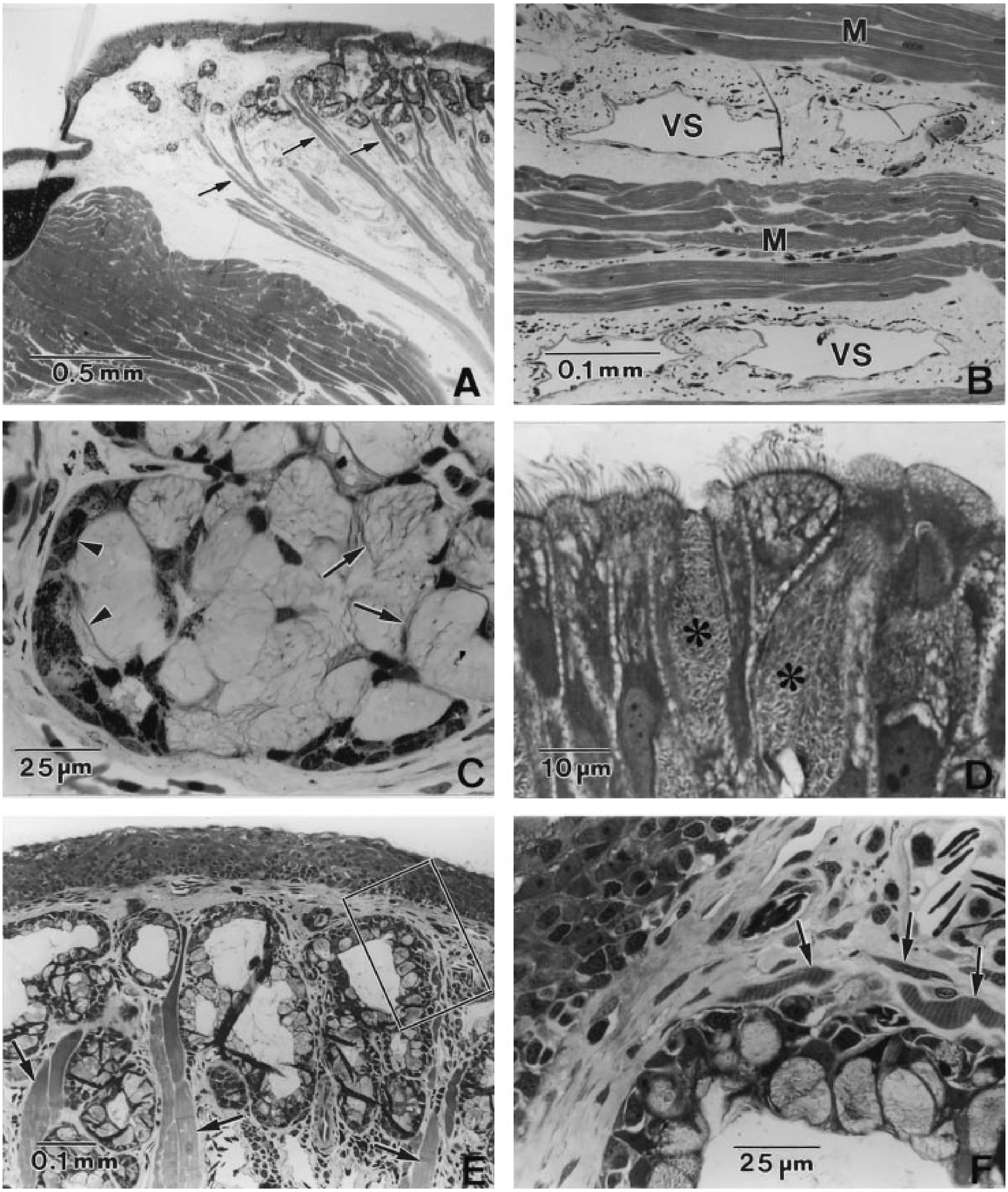
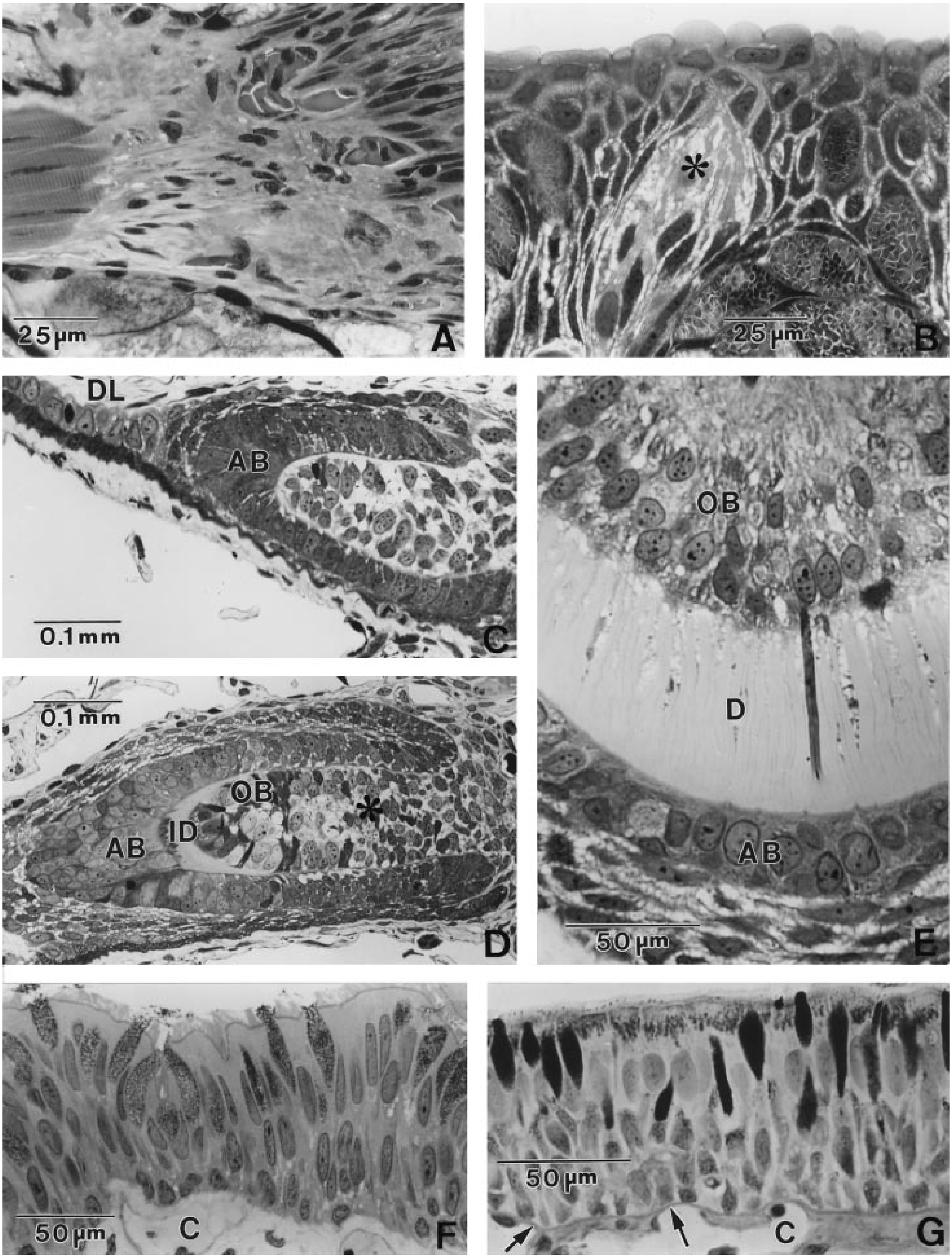


Fig. 4.—Light microscopical sections of *Siphonops annulatus* — **A,** Tongue, longitudinal section. At right the anterior portion with the muscular septa. At left, the posterior region with a solid mass of striated muscle and cartilage. Arrows indicate the muscular septa. — **B,** Detail of the muscular septa (M) and thin-walled venous sinuses. (VS). Loose connective tissue between the muscle and sinus. — **C,** Lingual tubular mucous glands showing two types of mucus secreting cells (arrow and arrowheads). — **D,** Prismatic ciliated epithelium of the tongues posterior region. Asterisks in the mucous cells. — **E,** Tongue, showing the muscular septa (arrows) separating the tubular mucous glands. These septa become thinner and end in the subepithelial connective tissue. — **F,** Enlargement of the area limited in the preceding figure. Thin muscle fibers (arrows) ending in the connective tissue and separating mucous glands. At left the epithelium.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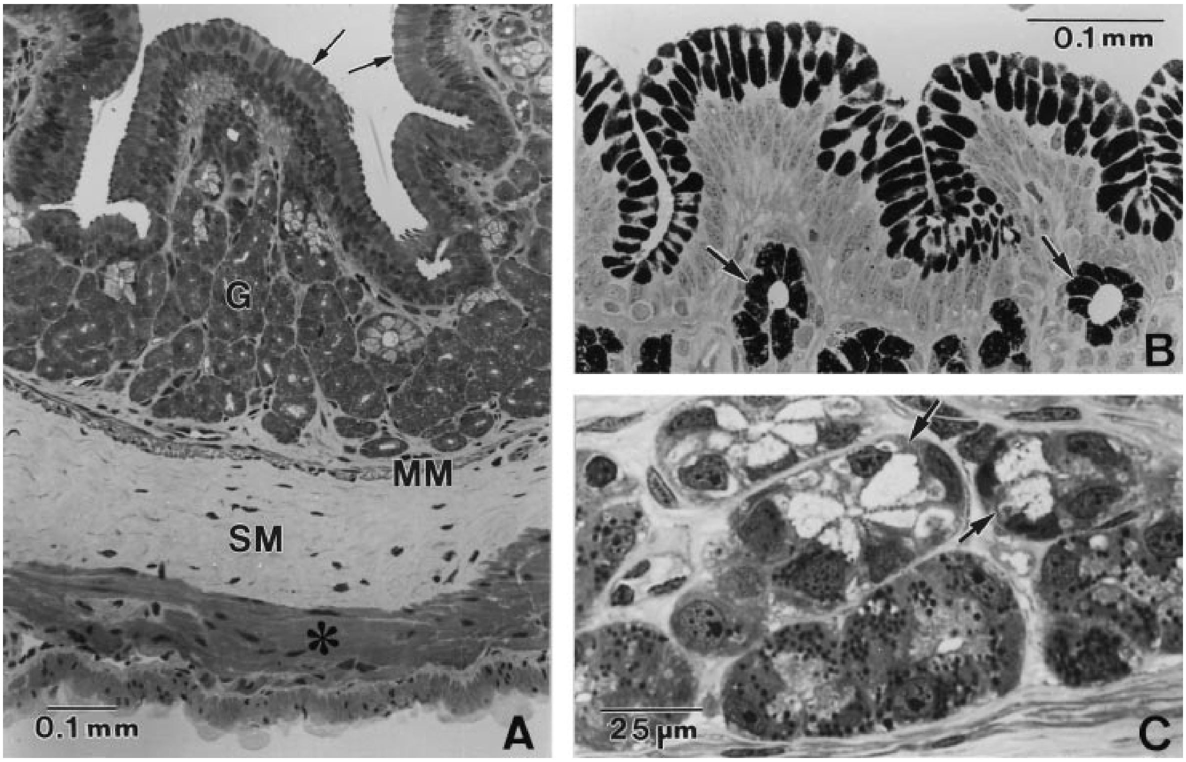

Fig. 6.—Light microscopical sections of *Siphonops annulatus.* — **A,** Stomach with its superficial mucous cell layer (arrows), thick gastric gland layer (G) muscularis mucosa (MM), submucosa (SM) and two smooth muscle cell layers (asterisk). — **B,** Stomach PAS stain. Superficial mucous cells and glandular mucous cells (arrows) strongly stained. — **C,** Peptic gland showing its upper mucous cells (arrows) and lower chloridropeptic cells with secretory granules.

buds were observed only in the tongue and did not present the extralingual distribution described by Wake and Schwenk (1986) in larval *Ichthyophis* and adult *Typhlonectes compressicaudus*. The histological characteristics observed, however, were the same as those described by these authors.

The presence of a single line of teeth in the lower jaw and a double one in the upper jaw, also described in other species, is probably related to the feeding habit. The irregular disposition and size of the teeth and our histological observations regarding the occurrence of teeth in different stages of development in adult animals suggest a continuous process of tooth replacement, as observed in other species of Gymnophiona by other authors (Lawson 1965; Wake 1976, 1980).

The histology of the initial part of the digestive tract of *S. annulatus* presents a series of structures and characteristics such as: (1) presence in the mouth of a stratified squamous epithelium associated with goblet mucous cells; (2) presence of a prismatic ciliated epithelium associated with mucous goblet cells in the tongue (also found in some other amphibians, but unusual in other groups of vertebrates); (3) a great amount of tubular mucous glands in the tongue and palatal region; (4) production of different types of mucous substances in the mouth; (5) presence of venous sinuses in the tongue [also described in the terrestrial caecilian *Dermophis mexicanus* by Bemis *et al.* (1983)]; (6) presence of muscular septa disposed perpendicular to the tongue's surface whose muscle fibers insert in its subepithelial connective tissue; (7) extremely thin layers of smooth muscle in the oesophagus.

Fig. 5.—Light microscopical sections of *Siphonops annulatus.* — **A,** Muscle fibre ending at a group of vertically orientated subepithelial connective tissue cells suggesting local muscle insertion. — **B,** Group of elongated cells with characteristics of taste bud (asterisk) present in the tongues stratified epithelial layer. At lower right mucous gland cells. — **C, D and E,** Different progressive stages of odontogenesis present in adult animals. AB ameloblast; asterisk pulp; DL dental lamina; ID initial dentin; D dentin; OB odontoblasts. — **F,** Oesophagus with prismatic ciliated epithelium showing abundant mucous cells. C indicates blood capillaries. — **G,** Oesophagus PAS stained. Mucous cells strongly stained. The dark granular region below the ciliary layer is due to the local presence of glycogen, probably an energy depot for ciliary activity. Observe the distinct basal membrane (arrows) closely associated with two blood capilaries (C).

These characteristics all might be related with the process of swallowing and food transport to the stomach. They suggest the presence of a synchronized process by which the anterior portion of the mouth would be pressed by the engorgement of the venous sinuses with simultaneous muscular contraction reinforced by ciliary activity. These phenomena may create forces that would press into the oesophagus the food mixed with and covered by mucous secretion. The role of the venous sinuses and muscular sheets in this process might be important to prevent reflux of food and to press the tubular mucous glands. Bemis *et al.* (1983) also suggested the same function for the venous sinuses in *Dermophis mexicanus*. The ciliated lingual epithelium and the different types of mucous substances probably facilitate the swallowing of food.

Very few nerve plexuses were observed in the initial part of the digestive tract when compared to the small intestine and cloaca. This might be related to the relatively reduced motor activity of these regions as compared to the rest of the digestive tract; this supposition is reinforced by the thinner muscular layers observed in these regions.

The exceptional amount of neutral PAS positive mucus secreting glands in the mouth, oesophagus and stomach of *S. annulatus* is possibly related to the facilitation of food transit in the digestive tract. The very weak reaction with Alcian blue suggesting the absence or small quantities of acid mucus attracted our attention, because in mammals neutral and acid types of mucus frequently coexist in the digestive tract.

The presence of chloridropeptic cells in the stomach of *S. annulatus* is in accord with the described presence of these cells in amphibians and reptiles (Welsch and Storch 1973; Junqueira and Salles 1975).

The developed capillary network observed in the oesophagus reinforces the suggestion made by Mendes (1945) that this organ might participate in the respiration of *S. annulatus*.

In all parts of the digestive system presented here the very low number of mitotic epithelial cells suggest a slow rate of epithelial renewal.

In conclusion, the histology of the initial part of the digestive tract of *S. annulatus* regarding the structure of the tongue, distribution of taste buds and mouth mucous cells presents characteristics which might be related to feeding habits and a peculiar process of food swallowing and food transport towards the stomach.

Due largely to the fact of caecilians being rather unaccessible animals and having a limited geographical distribution, many aspects of their biology remain poorly known. In this way any study about caecilians is valuable. The data presented here together with future information about other systems and organs of *S. annulatus* may contribute to a better knowledge of these animals.

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