

Structure of Head and Stoma
in the Marine Nematode
Genus *Deontostoma*
(Enoplida: Leptosomatidae)

W. DUANE HOPE

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ABSTRACT

W. Duane Hope. Structure of Head and Stoma in the Marine Nematode Genus *Deontostoma* (Enoplida: Leptosomatidae). *Smithsonian Contributions to Zoology*, number 353, 22 pages, 5 figures, 1982.—The cuticle of the head region, the location of the esophageal gland ducts and their external apertures, sensory receptors within the wall of the stoma, labial apodemes, the stoma, microlabia, mandibular ridges, and armature of the cheilostome are described for *Deontostoma californicum* Steiner and Albin, 1933, through the study of wholmount specimens, histological sections, and scanning electron micrographs. The cheilostome armature of *Deontostoma coptochilus* Hope, 1977; *D. timmerchiorum* Hope, 1974; and *D. antarcticum* (Linstow, 1892) Filipjev, 1916, are described and figured with scanning electron micrographs, and the homologous parts are compared among those species and with *D. californicum*. The stomatal armature of other taxa within Enoplida and a theory concerning their homologies and evolutionary relationships are discussed. It is postulated that members of the genus *Deontostoma*, and possibly other leptosomatids, are mucus trap feeders. *Thoracostoma zeeae* Inglis, 1964, is transferred to the genus *Deontostoma*.

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Contents

	<i>Page</i>
Introduction	1
Acknowledgments	1
Methods and Materials	2
Abbreviations	2
Observations	2
Cuticle of the Head	2
Esophageal Glands	3
Sensory Receptors of the Stoma	4
Labial Apodeme	4
Stoma	5
Microlabia and Mandibular Ridges	5
Armature of the Cheilostome	5
Discussion	6
Cuticle of the Head	6
Esophageal Glands	7
Sensory Receptors of the Stoma	10
Labial Apodeme	11
Stoma	12
Microlabia and Mandibular Ridges	12
Armature of the Cheilostome	13
Cheilostome Armature of Other Enoplids; Homologies and Evolutionary Origin	14
Structure of the Stomatal Armature and Niche Partitioning	16
Literature Cited	17
Figures	19

Structure of Head and Stoma in the Marine Nematode Genus *Deontostoma* (Enoplida: Leptosomatidae)

W. Duane Hope

Introduction

The genus *Deontostoma* was proposed by Filipjev in 1916 and it, along with the genera *Thoracostoma*, *Pseudocella*, and *Triceratonema* comprise the subfamily Thoracostomatinae. Four species were originally assigned to *Deontostoma* by Filipjev, with 15 species in the genus at present.

Our knowledge of the head structure among species of *Deontostoma*, as well as other leptosomatids, is derived in part from studies devoted specifically, in part at least, to the head region. Such studies are those of Rauther (1907), Wieser (1953), Inglis (1964), and Platonova (1979). Other substantial contributions concerning the head and stoma of *Deontostoma* and related genera are found in various taxonomic descriptions. This is especially true of the stoma (mouth cavity) and its armature, which are features likely to be used for diagnostic purposes. Such studies, notable for their detailed nature, are those by Jägerskiöld (1901), Türk (1903), Filipjev (1921 and 1927), and de Man (1904), especially in his study of *Deontostoma antarcticum* (von Linstow, 1892) Filipjev, 1916.

During recent studies of species of *Deontostoma* (Hope, 1967, 1974, and 1977), and in the course

of a revisionary study of the genus now underway, it has become apparent that the structure of the head among species of this genus, and among other members of Leptosomatinae, is still not well understood. These same studies have revealed that certain morphological features of the head, and especially of the stoma, may contribute substantially to an understanding of the evolutionary relationships of taxa within the family Leptosomatidae and, possibly, among other members of the order Enoplida. The purpose of this study is to provide a more accurate and complete description of the head based upon histological sections, whole mounts, and scanning electron micrographs; to provide an interpretation concerning the function of several features of the head; and to identify homologous characters of the stomatal armature, especially the odontia. A theory regarding the evolution of the armature of the cheilostome among families of Enoplina is proposed.

For the purposes of this investigation the genus *Deontostoma* is defined as those species of Thoracostomatinae lacking a tropis or keel on the ventral side of the cephalic capsule, but which is present in species of *Thoracostoma*, *Pseudocella*, and *Triceratonema*.

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taking the scanning electron micrographs. Gratitude is also expressed to Mrs. Vernetta Williams for preparing wholemount slides; to Carolyn Gast, illustrator for the Department of Invertebrate Zoology, for preparing the cut-away illustration of *Deontostoma californicum*; to Abbie Yorkoff for editorial assistance; and to Dr. Armand Maggenti, Dr. Meredith Jones, and Dr. Kristian Fauchald for reviewing the manuscript. This work has been supported by a Smithsonian Research Award, No. S3380487, for which the author is most grateful.

Methods and Materials

Wholemounts, histological sections, and SEM preparations have been used during the course of this study.

Specimens to be mounted whole for light microscopy were relaxed in sea water through which CO₂ was bubbled. They were then fixed in 4% formalin in sea water and processed into glycerine by the slow evaporation method as described by Goodey (1957).

Histological sections for light microscopy were prepared by embedding specimens in a 19 to 1 mixture of polyethylene glycol 1540 and 4000, respectively by a method described earlier (Hope, 1969). Sections were cut at 5 μ m on a rotary microtome and stained for 5 minutes in 0.1% aqueous hematoxylin at pH 2.4 using the method of Craig and Wilson (1937).

The scanning electron micrographs are of specimens that were originally permanent mounts in glycerine for light microscopy. They were selected from among other specimens as suitable for SEM because each has its mouth open and does not contain debris. Such specimens were rehydrated by a vapor diffusion method that entailed placing each in a BPI dish containing glycerine, and placing this dish in a covered Petri dish, previously filled with water to a depth of 2 or 3 mm, for approximately 24 hours at room temperature. Distilled water was then added to the hydrated glycerine at the rate of 1 drop every 15 minutes over a period of about 8 hours, during which time

the glycerine was replaced. The specimens were then cleaned by 5 seconds of sonication in a Rapidograph Ultrasonic Cleaner (3069 USCZ) and either freeze dried for 24 hours in a Virtis EF-Freeze-Dry Unit at 5 μ m of Hg at -30 C or critical-point dried in a Denton Vacuum DCP-1 Critical Point Dryer. For the latter technique specimens were processed through a graded series from distilled water to absolute ethanol and then to pure amyl acetate. Liquid carbon dioxide was used as the transitional fluid.

Abbreviations

CC	Cephalic capsule	NE	Nerve in esophagus
CH	Cheilostome	OD	Odontium
EK	Eukampter	OGD	Orifice of gland duct
EN	Endocuticle	ON	Onchium
ES	Esophastome	PK	Pseudokampter
EX	Exocuticle	RC	Radial arm of lumen
GD	Gland duct	RM	Radial muscle of esophagus
H	Hypodermis	SEG	Subventral esophageal gland
LA	Labial apodeme	SR	Sensory receptor
LM	Labial dilator muscle	X	X layer of cephalic cuticle
ME	Mesocuticle	Y	Y layer of cephalic cuticle
MG	Mandibular groove	Z	Z layer of cephalic cuticle
ML	Microlabium		
MLG	Microlabial groove		
MR	Mandibular ridge		

Observations

CUTICLE OF THE HEAD.—The cuticle that covers the head is continuous with that covering the remainder of the body, but the histological organization of the cuticle in these two regions, as observed with the light microscope, is quite different. The cuticle of the body posterior to the cephalic capsule, when observed from histological sections for light microscopy, has three readily observable layers, to which herein will be applied the nomenclature of Maggenti (1979:94). These layers (Figures 1a,b, 4) are the endocuticle (EN), which in *Deontostoma* stains very light blue with hematoxylin and a mottled mixture of medium blue and orange with Mallory's triple stain; the

mesocuticle (ME), which also stains light blue with hematoxylin and dark blue with Mallory's triple; and the exocuticle (EX), which stains dark blue with hematoxylin and medium blue with Mallory's. The epicuticle is not distinctly resolvable with the light microscope.

The most prominent feature of the cuticle of the head region is the cephalic capsule (Figures 1a-d, 2a, 4 (CC)), a distinctly light-refractive layer of the endocuticle that stains orange in Mallory's triple and does not stain in hematoxylin. This specialized layer forms a band around the head that tapers from a relatively thick, rounded, posterior margin to a thin anterior margin (Figures 1a,b, 4). In contrast to the posterior margin, the anterior margin is difficult to resolve in whole-mount specimens because of its thinness. The anterior edge lies a short distance anterior to the cephalic setae, the posterior margin a short distance posterior to the level of the base of the stoma (Figures 1a,b, 4). The posterior portion is divided into six lobes by the posterior margin being looped anteriorly beyond the point where the nerves of the two lateral and two pairs of subdorsal and two pairs of subventral cephalic setae pass through the cuticle. Posteriorly the loop forms a narrow separation, or "incision" (terminology of Wieser, 1953:71), between lobes, but it is dilated anteriorly to accommodate the passage of the nerves.

The cephalic capsule lies within the endocuticle and, from histological sections stained with Mallory's (Figures 1a,c,d, 2a, 4), it appears that a very thin layer of the somatic endocuticle extends anteriorly, passing between the cephalic capsule and hypodermis. This observation has been substantiated by preliminary observations with the transmission electron microscope. At the anterior end of the cephalic capsule, where the cephalic cuticle begins to arch mesad, this thin layer of cuticle appears to become thickened and is anteriorly overlain by a second very lightly stained layer. Both extend medially to the cuticle that lines the lumen of the esophagus (Figures 1a, 4). The anterior layer is herein termed the Y layer

and the posterior layer is termed the Z layer.* It must be stressed, however, that the Z layer, as perceived with the light microscope, appears to include not only endocuticle, but hypodermal tissue and the basement membrane of the esophagus as well. Again, that has been verified by preliminary observations with the transmission electron microscope.

The mesocuticle of the somatic region extends to near the midlength of the cephalic capsule but tapers to an end so that for a short distance the endocuticle and exocuticle are adjacent to one another (Figures 1a, 4). A mesocuticle with the same staining properties as in the somatic cuticle does not occur in the head region. The exocuticle continues anteriorly without any apparent change in structure, arches over the lip region, and turns inward into the stoma where it becomes subjacent to the cuticle lining the esophagus and, in fact, may merge with the latter (Figures 1a,b, 4).

The last layer of cephalic cuticle to be described is the X layer, which extends anteriorly from about the midlevel of the cephalic capsule. Its tapered posterior margin lies between the endocuticle and exocuticle. As it proceeds anteriorly it increases substantially in thickness and arches over the anterior end of the esophagus between the exocuticle and layer Y. It remains contiguous with the exocuticle on its external, anterior, and oral surfaces (Figures 1a, 4). Layer X of the cephalic cuticle stains medium blue with Mallory's and has numerous, irregularly shaped inclusions. In hematoxylin-stained sections of *Deontostoma*, layers X, Y, and Z all stain light blue (Figure 1b). The Y and Z layers are not distinct but the X layer is slightly darker than any of the other layers.

ESOPHAGEAL GLANDS.—The esophagus and esophastome (page 5) of *Deontostoma* species has a cuticularly lined triradial lumen, the rays of

* Formal naming of these layers should wait until the head region has been studied further with transmission electron microscopy and the homologous layers are identified. One or both of these layers may correspond to the endocuticle of Belogurov and Belogurova (1975).

which divide the tissue of the esophagus into a dorsal and two subventral longitudinal sectors (Figures 1*c,d*, 2*a*, 4). (The reader is referred to Wright (1976) for further discussion on the terminology applied to the oral opening of nematodes.) Each sector contains radial muscles whose origin is believed to be on the external basement membrane of the esophagus and whose insertion is on the thickened regions of the cuticle on each side of each ray, a condition designated as "concentrated" by Chitwood and Chitwood (1950:78). One esophageal gland cell extends longitudinally through each of the subventral sectors and three extend through the dorsal sector, one dorsal and two subdorsal. The closed end of each cell lies in the posterior region of the esophagus. Each subventral gland is in the center of its respective sector and lies between the radial muscles. In all species of *Deontostoma*, the dorsal esophageal gland lies in the center of the dorsal sector and opens into the lumen of the esophagus at a level somewhere between the paired eyespots and the posterior margin of the cephalic capsule. This opening is a narrow longitudinal slit in the dorsal wall of the lumen.

Each subdorsal gland lies at the dorsal side of the distal end of its corresponding subdorsal ray. The subdorsal glands can be followed in serial cross sections to the anterior end of the esophagus. But the diameter of each lumen becomes so small, as it enters the cuticle covering the anterior surface of the head, that the locations of the external orifices are uncertain. It may be, however, that each duct converges upon and opens into the base of the dorsal mandibular groove.

The subventral esophageal glands are very evident in wholemount preparations where they can be observed extending into the general region of the stoma. At this level the course of the glands becomes less evident and their openings to the exterior are not apparent. Serial cross sections reveal, however, that near the base of the stoma each gland cell becomes continuous with a cuticularly lined duct (Figures 1*c,d*, 4) that enters the cuticular wall of the esophagome near the level of the onchium. The duct proceeds anteriorly in

the subventral walls of the cheilostome (Figures 2*c,d*, 4) to the base of the groove between the mandibular ridge and the microlabium. It is in the base of this groove, the mandibular groove, that the subventral esophageal gland duct opens to the exterior (Figures 2*d*, 3, 4) as a narrow slit.

SENSORY RECEPTORS OF THE STOMA.—The center of each sector is the passageway not only for an esophageal gland but for nerve cell processes as well. These processes enter the tissue of the esophagus directly from the medial surface of the circumesophageal commissure and proceed in both anterior and posterior directions. Those proceeding anteriorly are at first situated peripheral to the esophageal gland ducts, but then shift medially as the esophagome is approached. The bundle of nerve cell processes in each sector (Figures 1*b,c*, 4) then terminates in a circular depression about 2 μm deep in the cuticular lining of the esophagus at the base of the stoma (Figures 1*a,c*, 4). Each depression is at the point of convergence between adjacent rays, and each of the several nerve endings, where they terminate in the depression, appear to be slightly swollen. In Mallory's triple-stained sections the nerve cell processes are blue, but the enlarged tips are slightly pink. These depressions are interpreted herein to be innervated and to be sensory receptors.

LABIAL APODEME.—The center of each sector at the anterior end of the esophagus is also occupied by a labial dilator muscle (Figure 1*a-d*, 2*a*, 4). Each of these muscles, like the radials, is believed to have its origin on the peripheral basement membrane of the esophagus, from which it extends anteriorly and somewhat mesad toward the anterior end of the esophagus. Through much of its length each muscle is inserted upon a labial apodeme (Figures 1*a,b,d*, 2*a,b*, 4). Each apodeme is branched at its posterior end, presumably to increase the surface area for muscle attachment, but extends anteriorly as a single, rod-like structure through the anterior end of the esophagus and into the cuticle that forms the anterior surface of the head. Here each apodeme is inserted upon the base of the mandibular groove of its

sector (Figures 1*b*, 2*b,c*, 4). The attachment in the case of the apodeme of the dorsal sector is to a rather broad central region of the groove and, in the case of those of the subventral sectors, attachment is on each side of the esophageal gland duct orifices. The apodeme, cuticular though it may be, retains its identity as it passes through the cuticular covering of the head, and it is readily demonstrable in histological sections by its staining properties. In the case of sections stained with Mallory's triple, the apodeme stains orange like the cephalic capsule and medial layer of the cuticle lining the stoma, while, as mentioned above, the cuticle covering the anterior surface of the head is stained different shades of blue. In hematoxylin-stained sections, the apodeme, cephalic capsule, and lining of the stoma do not stain, while, again, the cuticle covering the anterior end of the esophagus and forming the head stains blue.

STOMA.—The stoma, or mouth, is defined herein as that region extending anteriorly from the sensory receptors described above to the external oral opening. The stoma, when viewed in cross section, may have the shape of a relatively large equilateral triangle when fully opened (Figure 5*a,b*), or the shape of a smaller triangle with a narrow extension radiating from each corner when the stoma is closed (Figures 3, 5*d*). The narrow extensions are the corners of the stoma that come together with the relaxation of dilator muscles. The corners of the open triangular stoma are herein termed the eukampters, and the corners of the closed stoma are pseudokampters (Figure 3).

The stoma or mouth is comprised of anterior and posterior parts to which are applied respectively the terms cheilostome and esophastome, adapted from Inglis (1966:57). The esophastome (Figures 1*c,d*, 2*a*, 4) of *Deontostoma* extends anteriorly from the sensory receptors of the stoma to the cephalic cuticle covering the anterior surface of the esophageal tissue. Being a modification of the anterior end of the esophagus, the esophastome is surrounded by esophageal tissue and the lumen, in at least its posterior region, is triradiate

(Figure 1*d*). Although the walls of the lumen of the esophastome have the form and staining properties typical for the adjacent region of the esophagus, they are unique in that the dorsal wall bears a single, large, solid (it is not perforated by a gland duct), immovable tooth or onchium, and each subventral wall accommodates the duct of the corresponding subventral esophageal gland.

The cheilostome lies between the anterior extremity of the lip region and the anterior margin of the esophageal tissue (Figures 2*c,d*, 3, 4). The cheilostome is lined by a thin layer of cuticle continuous with the cuticle lining the lumen of the esophagus, which in turn is surrounded on all sides by the cuticle that covers the head region. The cheilostome, then, is that portion of the stoma that lies within the cuticular covering of the head.

MICROLABIA AND MANDIBULAR RIDGES.—Three narrow lips, termed microlabia (Hope, 1967:324), exist on the anterior surface of the head at the opening of the cheilostome (Figures 3, 4, 5*a-d*). One microlabium extends between each pair of eukampters. The microlabium is set off from the surrounding surfaces of the head by narrow grooves that also extend between pairs of eukampters. These grooves, termed microlabial grooves, are approximately 4 μm deep. Mesad to, and paralleling each of the microlabia, is a narrow ridge termed the mandibular ridge (Hope, 1977:942). The mandibular ridge (Figures 3, 4, 5*a-d*), which usually lies between pairs of pseudokampters and, therefore, is not as long as the microlabium, may be incorporated into other structures (see Armature of the Cheilostome). The mandibular groove, separating the mandibular ridge from the microlabium, is also about 4 μm deep and extends between pairs of pseudokampters (Figures 3, 4, 5*a-d*). Both microlabia and mandibular ridges are manifestations of the exocuticle.

ARMATURE OF THE CHEILOSTOME.—*Deontostoma californicum* is the only species in which the armature of the cheilostome has been examined in histological sections for this study. In this species the cheilostomatal armature consists of small,

anteriorly directed cones that arise from near the base of the oral surface of each microlabium at each end of the mandibular ridge (Figures 2*c,d*, 3, 4, 5*a-d*). Hence, when the stoma is closed, there is a pair of odontia at each pseudokampter, one contributed by each of the adjacent walls of the cheilostome (Figure 2*d*). Because these projections are a manifestation of the labial region, they are, according to the definition given by Cobb (1919:215), properly termed odontia.

It is evident from histological sections that each odontium has a core of cuticular substance unlike its outer wall, thus giving the impression that the odontia are hollow (Figure 2*c,d*). Sections cut through the base of the cones and stained with Mallory's triple stain reveal that the external wall of each odontium is formed by an outfolding of the orange-stained layer of cuticle that lines the cheilostome. The underlying blue-stained layer of cuticle (exocuticle) projects into the fold and becomes the core of the odontium as it tapers to a point. The same histological sections also reveal that the very base of each odontium has a minor degree of continuity with the adjacent mandibular ridge. Each odontium then extends anteriorly paralleling, but separate from, the end of its adjacent mandibular ridge (Figures 4, 5*a*).

Discussion

The present observations and interpretations concerning the head structures of *Deontostoma*, which are summarized in Figure 4, combine and confirm previous information extant in the literature but largely overlooked. They also provide the bases for new theories concerning the functions and homologies of the structures under consideration.

CUTICLE OF THE HEAD.—The cuticle that covers the anterior end of the esophagus and forms the anterior surface of the head has been known for many years to be thicker than the cuticle posterior from the head. However, the structural basis for the greater thickness has not yet been agreed upon or adequately understood.

Filipjev took the position that the cuticle cov-

ering the anterior end of the head in members of the order Enoplida is doubled (1929:281) or reduplicated (1934:8), the cuticle of the head possibly having been turned back upon itself at the stoma. That interpretation has been followed by Chitwood (1937:77), and Filipjev and Schuurmans Stekhoven (1941:42). The same character was used by Clark (1961:129) and de Coninck (1965:649) to diagnose the superfamily Enoploidea. Inglis (1964:268), on the other hand, was of the opinion that the cuticle of the head is not doubled, but rather there occurs a fluid-filled space anterior to the esophagus that he termed the cephalic ventricle (p. 269). Inglis postulated that the cephalic ventricle evolved because of the fusion of the esophagus with the anterior body wall. With such a fusion he believed that the tissue of the esophagus would have been unable to effect movement beyond the line of attachment so that it "built up at the anterior end of the body to form the cephalic ventricle" (p. 290). Belogurov and Belogurova (1975:30) have described the cephalic cuticle in oncholaims (*Oncholaimina*: Enoplida) as being split into additional layers. They speak of this process as "delamination" or "disintegration" of the cephalic cuticle, although it is unclear as to what is meant by those two terms.

Platonova (1978:502) has observed from studies of wholemount specimens that there are four different combinations of cuticular layering within the head among the genera *Leptosomatum* Bastian, 1865; *Leptosomatides* Filipjev, 1918; *Anivanema* Platonova, 1976; *Pseudocella* Filipjev, 1927; *Anticoma* Bastian, 1865; and *Odontanticoma* Platonova, 1976. She concluded that a particular structural pattern of cuticular layering within the head is consistent only within a genus or group of related genera. Because Platonova did not base her work on histological sections, it is difficult to compare the structure of the cephalic cuticle of the above genera with *Deontostoma californicum*.

The present study provides no evidence to support the concepts that the cuticle anterior to the esophagus is double, reduplicate, or that it contains a fluid-filled cavity. Rather, this study

has shown that the cuticle at about the midlength of the cephalic capsule undergoes a structural change that results in the four layers of cuticle that extend over the anterior end of the esophagus. Because each layer is different in both thickness and staining properties from the other layers of the head, and because the number of layers is not double the number posterior to the head, there is no evidence that the cuticle is doubled upon itself or reduplicated. There does not appear to be any continuity of one layer with another due to it being folded back upon itself.

As for the concept of a fluid-filled cavity, even the lightest staining layer, layer Y, definitely absorbs stain and has texture. It is interpreted herein that no fluid-filled cavities exist in the head of species of *Deontostoma*, nor by extrapolation, in any other members of Leptosomatidae. Rather the increase in thickness of the cuticle covering the anterior end of the esophagus is due to a gradual increase in the thickness of layer X of the head cuticle. Preliminary observations from transmission electron micrographs also clearly show that all layers of the head are structural. None are fluid filled.

The Y and Z layers (more likely the Y) of the cephalic cuticle are readily observable in whole-mount specimens of members of the genus *Deontostoma* due to their light absorptive or refractive properties. These layers have been spoken of as the arch of the internal part of the head capsule (Filipjev, 1916:20–21), the pharyngeal capsule with the stomodaeal ring being its point of attachment to the cephalic capsule (Wieser, 1953:70), and the esophageal capsule (Inglis, 1964:288). Wieser (1953:70) states that the pharyngeal capsule "is a thickening of the outer semicuticular lining of the anterior portion of the pharynx." It appears from this study that layer Z is a combination of the basement membrane of the esophagus, the hypodermal tissue between the anterior end of the esophagus and the cephalic cuticle, and a thin layer of endocuticle. I believe, however, that the pharyngeal capsule (esophageal capsule), as seen in wholemount specimens, is comprised not only of the complex of layers des-

ignated in this study by the letter Z, but also includes the Y layer. This is assumed to be the case because the Z layer by itself is less than 2 μm thick. The two layers combined would have a thickness of about 4 μm , and would be more readily observable in wholemounts.

The stomodaeal ring (Wieser, 1953:70), or cephalic ring (Inglis, 1964:289), is probably the point at which the Z layer (slightly thickened at this point) arches away from the cephalic capsule. It does not physically divide or in any way directly involve the cephalic capsule.

Wieser (1953:69) is of the opinion that the buccal and pharyngeal capsules comprise a morphological unit that he terms the stomodaeal capsule. The observations and conclusions of the present investigation provide no justification for emphasizing that the buccal and pharyngeal capsules are a special morphological unit other than the fact that both are manifestations of the cephalic cuticle. It is suggested that use of this term be discontinued with reference to leptosomatids.

The increased thickness of the cuticle forming the anterior surface of the head may have important implications. With an increase in the thickness of the cephalic cuticle and corresponding increase in the depth of the cheilostome, there must have been a reciprocal loss of efficiency with which the muscles of the esophagus could dilate the stomatal aperture. The successful development of the cheilostome, then, has also been dependent upon the development of the labial apodemes by which specialized muscles of the anterior end of the esophagus dilate the oral aperture and cheilostome. The presence of an apodeme seems to suggest that direct attachment of specialized (longitudinally oriented) muscles of the esophagus to the cephalic cuticle at the anterior end of the esophagus would not be an effective mechanism for dilating a deep cheilostome. Possibly, without the presence of an apodeme extending to the exocuticle, contraction of muscles would result in stretching of the cuticular layers of the head, with negligible dilation of the stomatal aperture.

ESOPHAGEAL GLANDS.—The location of the or-

ifice of the dorsal gland has been documented for various taxa of the Leptosomatidae (Chitwood and Chitwood, 1937:523; Ditlevsen, 1926, pl. 12: fig. 1; Filipjev, 1918:42, 46; Filipjev and Schuurmans Stekhoven, 1941:42; Hope, 1967:313, 315, 318, 321, 324, 327, 331; Inglis, 1964, fig. 172; Platonova, 1979:1120; Rauther, 1907:731; Vitiello, 1975:343, 348, figs. 1A, 3B, 4C,F) which is not surprising since the anterior end of the gland and its duct to the site of the orifice are usually readily visible a short distance behind the head. Among species of *Deontostoma* the location of the orifice of the dorsal gland may vary from just anterior to the eyespots to the posterior margin of the cephalic capsule, but for a given species the location is fairly restricted. The orifice always opens, however, directly into the lumen of the esophagus and, therefore, I assume that the secretion produced by the dorsal gland has a digestive function.

Not only do the orifices of the subdorsal glands remain undetected in this study, as well as in those that preceded it, but the glands themselves have seldom been mentioned. In his description of *Leptosomatum elongatum* (= *L. gracile* Bastian, 1865), de Man (1893:105) identified the presence of three tubes in the dorsal sector of the esophagus, the laterals (subdorsals) of which he believed to open into the stoma at the level of the cephalic suture (posterior margin of the cephalic capsule). While de Man observed three ducts in the dorsal sector, he also states (1893:105) that "il y a donc aussi probablement trois glandes oesophagiennes au côté dorsal au lieu d'une seule, mais c'est douteux."

Chitwood and Chitwood (1937:525) describe the presence of a single dorsal esophageal gland in all members of the Enoplida studied by them except *Phanodermopsis longisetae*. That species is described as having "the glandular tissue of the dorsal sector . . . distinctly subdivided into a dorsal and 2 subdorsal marginal lobes, each of which may represent a separate gland."

Timm (1953, fig. 2C) illustrates the subdorsal esophageal glands of *Leptosomatum acephalatum* Chitwood, 1936 and labels them as such, but makes no mention of them in the text. The pres-

ent study confirms the presence of subdorsal glands in *Deontostoma* but apparently the terminal canal for each of these glands and the orifice are so small that their detection must await studies by transmission electron microscopy.

While the presence of the subventral glands has been well documented for leptosomatids, including *Deontostoma*, the location of the orifices of these glands is commonly misinterpreted for all subfamilies of Leptosomatidae.

De Man (1893:105), in his description of *Leptosomatum elongatum* (= *L. gracile* Bastian, 1865) stated that the two subventral glands open into the internal tube of the esophagus at the level of the cephalic suture, and Chitwood and Chitwood (1937:523) stated that they open into the lumen near the anterior end of the esophagus. Filipjev (1918:42), in his diagnosis of the genus *Leptosomatum*, stated that "the two subventral esophageal glands open far anteriorly, while the dorsal gland opens more posteriorly." Timm (1953) illustrated the gland ducts in en face view (fig. 1I) of *L. acephalatum* and stated (p. 230) that "three oval sclerotized prominences next to the ridges of the stoma indicate the orifices of the dorsal and subventral esophageal ducts." However, he may have been describing the mandibular ridges instead of the gland orifices because the dorsal gland duct is not present in his cross sections through the stoma (fig. 2A), which demonstrates that the dorsal gland orifice is located posterior to the stoma as it is in *Deontostoma*.

Steiner accurately determined the orifices of the subventral glands in his investigation of *Leptosomatides steineri* Filipjev, 1922 (= *Leptosomatum gracile* sensu Steiner, 1916). Steiner observed (1916:612) that the subventral glands "führt nicht etwa in die Mundhöhle, sondern wendet sich noch vorn, tritt aus dem Gewebe des Ösophagus aus, durchquert die Körperhaut in einem gewundenen Gang und mündet aussen an den Lippen auf die Körperoberfläche."

Uncertainty concerning the location of the orifices of the subventral glands also prevails for the subfamily Thoracostomatinae. De Man (1904:30), in speaking of the subventral glands of *Thoracostoma setosum* states that "ces glandes de-

boucheriant donc dans la cavité buccal à la hauteur des organes latéraux, peut-être même en avant de la dent dorsale,” and he made a similar observation for *Deontostoma antarcticum* (1904:39). Subsequent investigators of members of this subfamily (Hope, 1967:313, 315, 318, 321, 324, 327, 331, figs. 2A, 3A, 4E, 6A, 7B, 8B, 9B; Inglis, 1964, fig. 172; Murphy, 1965, fig. 1E; Siddiqui and Vigliorchio, 1977:79; Timm, 1953:237; Vitiello, 1975:343, 348, figs. 1A, 3B, 4C,F) have also indicated in their descriptions and/or illustrations that the subventral esophageal gland ducts either extend into the region of the stoma or actually open into it.

Likewise, in the case of *Synonchus acuticaudatus* (Jägerskiöld, 1901) Filipjev, 1916, within the subfamily Synonchinae, Jägerskiöld (1901:43) observes, “Ihre Mündungen habe ich an Schnitten nicht mit Sicherheit finden können, ich glaube jedoch, dass sie, wie die Totopräparate zeigen, ein wenig noch hinten von der Linie liegen, welche die beiden Seitenorgane verbindet.” In table 1, fig. 1, however, he labels what is herein interpreted to be the subventral sensory receptors of the esophagus as the subventral gland duct openings. Furthermore, he clearly illustrates in the same figure what I believe to be the subventral gland ducts extending well into the anterior region of the stoma.

Platonova (1979:1120) states that in the genus *Sadkonavis* each subventral gland opens into a special lenslike expansion of the lumen of the esophagus, each of which is situated considerably posterior from the amphids. The dorsal gland, according to her, opens in the region of the stoma. In the case of *Synonchus gorbunovi* Platonova, 1979, Platonova (1979:1121) alleges that the subventral glands open into the oral cavity and the dorsal gland into a lens-shaped expansion of the esophageal lumen. She does not give information regarding the opening of the esophageal glands in other genera of Synonchinae. Since Platonova's observations have been limited to wholmount preparations, it is likely that her interpretations are incorrect and that the subventral ducts course through the walls of the stoma and terminate on the lip region.

In the one remaining subfamily of Leptosomatidae, namely Cycicolaiminae, there has been a misunderstanding concerning the location of the gland openings in question, while there is also evidence that they also open to the exterior on the surface of the head. Jägerskiöld, (1901:6) in his description of *Cycolaimus magnus* (Villot, 1875) de Man, 1889, writes, “Am Boden der Mundhöhle finden wir drei kurze durchbohrte Zähne, die nach innen und vorne gerichtet sind. Der dorsale Zahn liegt ein wenig weiter nach hinten als die zwei subventralen. Die unten besprochenen Oesophagealdrüsen haben ihren Ausgang durch die Kanäle dieser Zähne.” In contrast, text figure one (1901:6) shows the subventral gland ducts of this species within the subventral walls of the stoma, precisely as they are in *Deontostoma* spp., at the level of the cephalic setae and well anterior to the stomatal teeth. The supposition that the subventral glands open onto the lip region of members of this subfamily is also strongly supported by the observations of Rauther (1907:731, 732). In his study of an unknown species of *Cycolaimus* he states:

Die Ausmündungen dieser Drüsen findet Jägerskiöld bei *Cycolaimus* entsprechend der dorsalen auf den zahnartigen Vorsprüngen des Mundhöhlenbodens; bei meinen Formen liegen sie nicht hier; zwar wendet sich an dieser Stelle der Drüsengang etwas einwärts, aber nur, um in jenen oben erwähnten Cuticularkanal der Mundhöhlenwand einzutreten, vermittels dessen er am äussersten Rand der Mundkapsel, unmittelbar hinter der gezähnten Querleiste, zur Ausmündung gelangt.

The transverse ridge of which he speaks is likely the mandibular ridge on each side of the stoma, each ridge bearing several teeth.

From the data provided in this study, the observations of Steiner (1916) and Rauther (1907), and the circumstantial evidence in the literature, it seems quite apparent that the subventral esophageal glands open onto the surface of the head in all species of the family Leptosomatidae, with the possible exception of *Tuerkiana strasseni* (Türk, 1903) Platonova, 1970 where they do appear to open into the lumen of the stoma (Türk, 1903:310, pl. 11: figs. 5–7 (ao), table 11).

The opening of the subventral gland ducts in

the mandibular groove may be an important diagnostic character of the family Leptosomatidae. To what extent this situation exists in other families of the order Enoplida is not known, although personal unpublished observations of serial sections of *Enoplus groenlandicus* Ditlevsen, 1926 reveal that all three esophageal gland ducts open into the stoma, each near the base of its respective mandible, thus confirming the observations of Rauther (1907:723) and Chitwood and Chitwood (1937:522).

The functional implications of the subventral esophageal glands opening onto the lip region are of interest. Generally, these glands are believed to be involved in some aspect of digestion, but it would seem to be disadvantageous to have glands of such a function opening onto the lip region where dilution, if not loss, of the enzymes would occur immediately. The position of the apertures also suggests that the secretions could serve to adhere the anterior end to substrates just as the caudal glands serve to attach the posterior end. There is no evidence, however, that leptosomatids attach themselves to a substrate at their anterior ends under any circumstance. A more likely possibility is that the secretions take the form of mucus threads that entrap small detritus particles, bacteria, and possibly macromolecules that are subsequently browsed. Feeding behavior of this type has been postulated by Riemann and Schrage (1978) for several species of aquatic nematodes representing different taxonomic orders. Their observations (p. 82) have shown that aquatic nematodes can "release large amounts of mucus from their mouths" that are believed to at least contribute to the mucus trap. It seems very likely that since the subventral and, probably, the subdorsal esophageal glands actually open to the exterior lip region in members of *Deontostoma* species, and other leptosomatids as well, they most likely do secrete mucus. Thus members of these taxa are very likely to be mucus trap feeders. The dorsal gland, which opens into the lumen of the esophagus between the level of the eyespots and the posterior margin of the cephalic capsule, may

produce digestive enzymes swallowed with ingested food.

The phylogenetic significance of the position of the subventral esophageal gland duct openings in Leptosomatidae is difficult to assess without more knowledge of the openings in other taxa. On the other hand representatives of the order Enoplida, which are regarded by some as being closer to the ancestral form of nematodes (Filipjev, 1934:11; Maggenti, 1963:276), typically have subventral esophageal glands opening rather far anteriorly, either into the lumen of the esophagus or the stoma. Whether the presence of the orifices in the lip region is the most primitive expression of that condition or a derived state is not known.

SENSORY RECEPTORS OF THE STOMA.—What have been described in this study as sensory receptors have been almost entirely overlooked, with exceptions possibly being apparent in the illustrations of *Leptosomatum gracile* Bastian, 1865 by de Man (1893, pl. 6: fig. 9b; = *L. elongatum*) and of *Synonchus acuticaudatus* by Jägerskiöld (1901, table 1, fig. 1), the latter being misidentified as the apertures of the dorsal and subventral esophageal glands. Filipjev (1918:51) noted in his diagnosis of the genus *Leptosomatides* that there are enlargements on the internal ventral angles of the esophagus, making small chambers, but the apertures of the esophageal glands are apparently disposed otherwise. These small chambers may be what have been identified in this study as sensory receptors.

Sensory receptors in the esophagus have been studied by way of electron microscopy for the soil nematode *Caenorhabditis elegans* (Maupas, 1900) Dougherty, 1953 by Albertson and Thomson (1976), the animal parasitic nematode *Nippostrongylus brasiliensis* (Travassos, 1914) Travassos and Darriba, 1929 by Wright (1976), and the plant parasitic nematodes *Xiphinema diversicaudatum* (Micoletzky, 1927) Thorne, 1939, and *Longidorus leptocephalus* Hooper, 1961 by Robertson (1975 and 1979).

Of the above, the receptors of *Longidorus* and *Xiphinema* seem to be most similar to *Deontostoma*. In the case of *Xiphinema* there are diagonal rows

of indentations in the stylet extension (odontophore) that allow nerve tissue to nearly reach the lumen of the food canal. In *Longidorus*, small, cone-shaped, electron-dense modifications of the odontophore wall merge to form lamellae. These specializations are assumed to be areas of chemoreception since rigidity of the odontophore seems to preclude the possibility of pressure reception.

While a gustatory function cannot be ruled out, it seems quite possible that the stomatal sensory receptors of *Deontostoma* could be stimulated by mechanical stress. Mechanical stimulation might occur when contraction of the labial dilator muscles cause the stoma to open. Conceivably, dilation of the stoma may cause the thin layer of the cuticle between the nerve endings and the lumen of the stoma to bend, thus generating the sensory impulse.

It is postulated herein that the occurrence of sensory receptors in leptosomatids in the stoma is common, but they have either largely been overlooked or observed in wholemounds as a thin spot or depression of unknown function in the wall of the stoma.

LABIAL APODEME.—The labial apodeme of leptosomatids was previously mentioned by de Man (1893:104), Hope (1967:311, 315, 318, 321, 324, 327, and 331) and possibly Filipjev (1918:49). Inglis (1964:288) stated that for *Thoracostoma* and leptosomatids in general (p. 287) the musculature in each sector at the anterior end of the esophagus extends anteriorly as a narrow strip through the "cephalic ventricle" to become inserted upon the wall of the cheilostome. He further contends "that the buccal cavity appeared by a migration outwards of the tissue lining the inner surface of the buccal cavity" (p. 290). This, according to Inglis, is the most marked difference between Leptosomatidae and other families (p. 287).

While Inglis was aware of the fundamentally different manner in which muscles of the esophagus act upon the cheilostome of leptosomatids, he was incorrect in his belief that the esophageal muscles attach directly to the cheilostome. Sections of *Deontostoma* reveal that, not only is there

an apodeme passing posteriorly from the base of the mandibular groove through the cephalic cuticle into the anterior end of the esophagus, but that there is no musculature extending beyond the limits of the esophagus.

Since the labial apodeme, cephalic capsule, and lining of the stoma stain orange in Mallory's triple-stained sections and do not stain in hematoxylin, they are chemically different from the blue-staining cuticle that covers the external body surface. It is also likely that the apodeme, cephalic capsule, and lining of the stoma have unique physical properties such as being more rigid and stress resistant. Hence the stress generated by the contracting labial dilator muscles is transmitted through the apodeme to the base of the mandibular ridge, and not by way of the layers of cephalic cuticle. It is not known whether or not the labial apodeme is structurally separated from the head cuticle and, therefore, freely slides through it.

The function of the labial apodeme is possibly dual. First, it probably permits the labial dilator muscles to draw the labial region posteriorly and laterally so as to dilate the labial region and cheilostome. In addition, however, contraction of the labial dilator muscles may open the subventral and subdorsal esophageal gland duct orifices in preparation for subsequent extrusion of gland contents. However, it admittedly does not make sense that extrusion of the subventral gland contents should necessarily be coincidental with ingestion.

The presence of an apodeme may be tentatively assessed from wholemound specimens by observing whether the muscles in the anterior end of the esophagus are obliquely arranged and extend towards the anterior end. Using this technique, indications of an apodeme were noted in the course of this study for species of *Leptosomatium*, *Platycoma*, *Platycomopsis*, *Syringonomus*, *Thoracostoma*, *Pseudocella*, *Triceratonema*, *Corythostoma*, and *Synonchus*. While its presence in members of the Cylicolaiminae could not be ascertained from wholemounds, face views did seem to demonstrate evidence of its presence. If it does exist in Cylicolaim-

inae, it may be a vestige, because the stoma in members of that subfamily are relatively fixed in an open state. Otherwise the apodeme may serve only to dilate subventral gland orifices.

STOMA.—It is important to emphasize that the cheilostome and esophastome in *Deontostoma* are manifestations of very different structural components of the head. The esophastome is a specialized region of the anterior end of the esophagus. The cuticle lining the lumen of the esophastome is structurally similar to that of the esophagus, and, as in the case of the esophagus, dilation of the lumen of the esophastome is effected by direct action of the radial muscles of the esophagus. The esophastome differs from the esophagus, however, in that the dorsal wall bears the dorsal onchium and the subventral walls accommodate the esophageal gland ducts.

The cheilostome is that region where the stomatal opening is surrounded by the cuticle covering the head, but is also lined by an anteriorly tapering extension of the cuticle that lines the esophastome. In most species of nematodes, the layer of cuticle covering the head is so thin that a cheilostome is too shallow for structural elaboration, especially of the armature. As already stated, the greater depth of the cheilostome in Leptosomatidae is attributable to the fact that the somatic cuticle, which is quite thick to begin with, is almost twice as thick where it covers the anterior surface of the head. The cheilostome is not dilated by radial muscles, but by way of apodemes and anteromedially directed labial dilator muscles.

The cheilostome, however, remains relatively open even when the dilator muscles of the stoma are relaxed and the eukampters are closed, so that the pseudokampters form the corners of the cheilostome. Thus, unlike desmoscolecids and monhysterids, where the lips form a barrier between the digestive system and the external environment, at least the cheilostome in members of *Deontostoma* is open at all times to the external environment. It is herein postulated that the dorsal onchium serves as a wedge-shaped barrier between the cheilostome (external environment)

and the remainder of the digestive system, and that it is not necessarily involved at all in piercing the external surface of prey organisms. Hence it may serve the same purpose, in part at least, as the lips of other nematodes.

MICROLABIA AND MANDIBULAR RIDGES.—There are few references in the literature prior to those of Hope (1967, 1974, and 1977) in which structures were described that may indeed be either microlabia or mandibular ridges. De Man (1893:104), in his description of *Leptosomatium gracile* Bastian, 1865, states: "Si l'on étudie la tête en avant (fig. 9c), on observe trois petites plaques chitineuses de forme ovale: une dorsale, les deux autres subventrales. Elles sont situées contre le milieu des bords chitineux de l'orifice buccal. Je présume que ces plaques chitineuses sont les lèvres." The structures described by de Man as lips are most likely what I have designated as mandibular ridges, since both are immediately adjacent to the lumen of the stoma. The microlabia are also much more difficult to resolve in face-view preparations. In other cases (Kreis, 1928:140; Jägerskiöld, 1901:6) reference to a lip probably refers to the general anterior surface of the head. This is especially apparent in Jägerskiöld's description of *Cylicolaimus magnus*, because he states (p. 6) that the lips "tragen je zwei diminutive Papillen." The papillae are always posteriorly located from the microlabia. Of course, the "fein gezahnte Leiste" in Jägerskiöld's (1901:6) description of *Cylicolaimus magnus*, in Rauther's (1907:732) description of a *Cylicolaimus* species, and in similar references to a toothed ridge or comb in taxonomic descriptions of species of this genus, the authors are referring to what is herein regarded as the odontia-mandibular ridge complex (see "Armature of the Cheilostome"). The microlabia probably do not function to close off the oral cavity from the external environment in *Deontostoma*, because in that genus, as noted above, the cheilostome seems to remain open when the eukampters are closed. The microlabial grooves, which set off the microlabia from the remainder of the head, may add flexibility to the anterior surface of the head, thereby facilitating

dilation of the stoma. Thus it may be that the microlabial groove is more of a functional entity than the microlabia themselves.

Likewise, it may be that the mandibular ridge was not a functional entity in the initial stages of its evolutionary development. Initially it may have been separated from the remainder of the head region with the formation of the mandibular groove, the latter having greater functional importance as the depression through which the esophageal glands opened to the exterior. Even now the mandibular ridge, by itself, seems to bear little more significance than being the anterior-most rim of the cheilostome. It assumes an entirely different functional significance, however, when integrated with the odontia (see "Armature of the Cheilostome").

ARMATURE OF THE CHEILOSTOME.—The number, position, and form of odontia in *D. californicum* (Figures 2*d*, 4, 5*a*) are the same in *D. karachiense* (Timm, 1959) Hope, 1967; *D. magnificum* (Timm, 1951) Platonova, 1962; and *D. washingtonense* (Murphy, 1965) Hope, 1967. This conclusion is based upon examination of the type-specimens of each of these species.

Deontostoma coptochilus Hope, 1977 also has six odontia, each located near its respective pseudokampter (Figure 5*b*). Each odontium is situated on the anterior margin of the mandibular ridge, however, rather than each odontium being attached at its base to the wall of both the microlabium and, to a lesser extent, the mandibular ridge, as is the case in *D. californicum*. The base of each odontium is incorporated into the crest of the mandibular ridge and, of course, in this situation the odontia extend well beyond the crest of the mandibular ridges.

The odontia and mandibular ridges on the subventral buccal walls of *D. timmerchiorum* Hope, 1974 are very similar to those of *D. californicum* with regard to location and point of attachment (Figure 5*c*). The only notable difference is that the odontia are slightly larger and the mandibular ridges relatively smaller than in *D. californicum*. On the dorsal microlabium, however, there appears a structure that resembles a "bifid tooth"

with anteriorly directed cusps, but is, in fact, an odontia-mandibular ridge complex in which the much enlarged odontia are situated on the crest of the mandibular ridge, and the mandibular ridge has become incorporated into a common base for the odontia. A fundamentally similar kind of cheilostome armature may exist on the dorsal microlabium of *D. bruuni* (Wieser, 1956) Hope, 1974. Specimens of this species were not examined during the course of this study, but from the literature it appears that *D. bruuni* differs in that the enlarged odontia have their tips directed laterally, and their bases, which, if connected by way of the mandibular ridge, may be anteriorly obscured by overlap of the microlabium. *Deontostoma zae* (Inglis, 1964), new combination, also appears to have an odontia-mandibular ridge complex on the dorsal lip region, at least that is so if Inglis' figure 172 is correct. However, such a structure is not described in the text.

With the above understanding of how the odontia and mandibular ridge become incorporated to form a "bifid tooth," it becomes equally possible to understand that the "pièce chitineuse cordiforme" described by de Man (1904:37) for *D. antarcticum* (von Linstow, 1892) Filipjev, 1926 is also an odontia-mandibular ridge complex. In the case of *D. antarcticum* (Figure 5*d*), each subventral mandibular ridge has at its dorsal margin an odontium whose shape and position, relative to the mandibular ridge, is very similar to the case in *D. californicum*, differing only in that its size is slightly larger. The odontia at the ventral margin of the subventral mandibular ridges are also similar to the odontia of *D. californicum* with regard to their position and points of attachment, but they are rounded, lobe-like, and much larger (Figure 5*d*). It is easy to understand, then, how the cordiform piece may be comprised of the two large, lobe-like odontia of the dorsal buccal wall, whose bases have become incorporated with the mandibular ridge. A notable difference between the bifid tooth of *D. timmerchiorum* and the cordiform piece of *D. antarcticum* is that the latter

structure is optically more dense and seems to have an almost crystalline structure in some cases.

A cordiform piece may exist in *D. jae* (Inglis, 1964) Hope, 1974 where the incorporated odontia, although large, have retained more of their conical shape. The interpretation that the cordiform piece is an odontia-mandibular ridge complex is contrary to the opinion of Inglis, who interprets the structure in question as being a "large bifurcate dorsal onchium" (1964:288), and it does not support his contention that the onchia in Leptosomatidae tend to be carried much more anteriorly relative to the mouth opening (p. 289).

It may be argued that the cordiform piece of *D. antarcticum*, which also occurs on the dorsal buccal walls of *D. angustifissulatum* (Mawson, 1956) Hope, 1974, and *D. parantarcticum* Vitiello, 1975, is derived from some structure or structures other than the odontia and mandibular ridge. Yet, if this were the case, one would expect to find among the species with a bifid tooth or cordiform piece, one or more species in which the bifid tooth or cordiform piece was present in addition to the mandibular ridge and/or odontia. In all known species, however, the dorsal wall of the cheilostome does not possess a mandibular ridge and/or odontia resembling those in *D. californicum* when a bifid tooth or cordiform piece is present, and vice versa. The two occurrences are mutually exclusive. This observation supports the hypothesis that the mandibular ridge-odontia complex, bifid tooth, and cordiform piece are all homologous structures.

A similar concept of homology was developed by Wieser (1956:246, 248, 249) in his comparisons of the buccal armature of *D. bruuni* (Wieser, 1956) Hope, 1974, *Corythostoma kreisi* (Wieser, 1953) Wieser, 1956, and *Synonchoides galathea* Wieser, 1956. He noted (p. 248) that the cusps on the concave cuticular thickenings of each subventral wall are homologous with the tips of the two triangular plates on the dorsal wall, and those in turn homologous with "the 'pièce cordiforme' in *Thoracostoma* s. str."

CHEILOSTOME ARMATURE OF OTHER ENOPLIDS; HOMOLOGIES AND EVOLUTIONARY ORIGIN.—The

structure of the head in other genera of the suborder Enoplina has not been studied in the same detail as in the case of *Deontostoma*. But enough information has been accumulated to have at least a general impression of the structure of the buccal armature in other taxa and to postulate on homologies of cheilostome armature and on the evolutionary origin of enoplid jaws.

Within the subfamily Thoracostomatinae, microlabia, if not a mandibular ridge, are present in representatives of *Thoracostoma*, *Pseudocella*, and *Triceratonema*. Odontia, however, were not observed in species of *Pseudocella* or *Triceratonema*, but they do occur in at least *Thoracostoma setosum*, *T. parasetosum*, and an undescribed species in the USNM collections (former United States National Museum, collections now in the National Museum of Natural History, Smithsonian Institution).

In considering the cheilostome of other subfamilies of Leptosomatidae, it should be noted that representatives of Cylicolaiminae have well-developed microlabia, mandibular ridges, and odontia. All genera of this subfamily are rather poorly known except *Cylicolaimus*, where the mandibular ridges are provided with odontia in a comb-like or pectinate fashion. In Synonchinae the prominent armature of the lip region in *Fiacra longisetosus* (Southern, 1914) Filipjev, 1927, and *Synonchus fasciculatus* Cobb, 1894, are most likely odontia. Furthermore paired protuberances on each subventral wall in species of *Corythostoma*, *Eusynonchus*, *Fiacra*, *Jaegerskioeldia*, *Sadkonavis* (on one subventral side only), *Synonchus*, *Synonchoides*, *Tuerkiana*, and possibly *Paratuerkiana*, are at least provisionally interpreted to be odontia (phylogenetically derived in the lip region) that are located farther posterior than in *Deontostoma*. Platonova (1979) refers to these paired protuberances as jaws or forklets, while not discussing their homologies. Preliminary observations indicate that microlabia and mandibular ridges are present, but that the latter are not fused with odontia to produce the complex found in *Deontostoma*.

In the case of Leptosomatinae, several whole-mount specimens and face-view preparations of

Leptosomatum were examined with a light microscope and, while they appear to have microlabia and possibly a mandibular ridge, no odontia or onchia were evident.

In most families of the suborder Enoplina, namely Thoracostomopsidae, Anoplostomatidae, Oxystominidae, Ironidae, Anticomidae, and Phanodermatidae, there are no obvious evidences of odontia, microlabia, or mandibular ridges. Furthermore, there is no evidence of an apodeme in these taxa, a structure that seems to be highly correlated with the presence of a mandibular ridge and microlabium. There are teeth on the medial surface of the lips in members of the Ironidae, but they are formed in the tissue of the esophagus. From there they migrate anteriorly to take their place on the lips. Therefore, they are not homologous with the odontia of Leptosomatidae.

In the family Enoplidae, each wall of the stoma may or may not bear an onchium, and typically each wall bears a jaw with a pair of teeth at the anterior end. According to Inglis (1964:290) the jaws of Enoplidae have evolved as follows: "The development of a cephalic ventricle necessitates the development of some kind of supporting structure, particularly for the inner circle of sense organs, and this is represented by the buccal rods of *Dayellus* and *Phanoderma*." Inglis (1964:272) also postulates that the buccal rods were initially a V-shaped cuticular structure in the cephalic ventricle, each of the six V's embracing one of the nerves that innervates a labial papilla. The arm of the V on one side of the nerve was phylogenetically derived from one of three anteriorly projecting lobes of the esophagus, and the other side of the V corresponds to one side of the radial lumen of the buccal cavity. Inglis (1964:290) further argues that something comparable to the early evolutionary development of buccal rods in the Enoplidae can be found today in the head of *Crenopharynx* (Phanodermatidae), and that buccal rods, similar to those that must have existed in Enoplidae, now exist in *Dayellus* and *Phanoderma*. In the meantime, as the depth of the buccal cavity increased, there was an increasing need for

mechanical support of the cuticle surrounding the buccal cavity (1964:291). This led to the formation of a cuticularized mandibular plate in each wall, and, with an increase in the thickness of the specialization of the wall of the buccal cavity, the importance of the buccal/mandibular rods must have been reduced because their functions were progressively taken over by the mandibular plate. Eventually the buccal rods fused with the mandibular plate to become what are now recognized as mandibular rods, as in the case of *Enoplolaimus*, and eventually absorbed into the mandibular plate, as in *Mesacanthion* and *Africanthion*. What was originally a skeletal system has become jaws or gripping organs (Inglis, 1964:291).

The foregoing theories of Inglis are based upon a premise that the region between the anterior end of the esophagus and the cuticle covering the head is a fluid-filled space in need of mechanical support. If the structure of the head cuticle of Enoplidae may be inferred from the present investigation, however, then there is no fluid-filled cavity in the head region. Because the entire structure anterior to the esophagus is most likely cuticular, there seems to be little need for support, especially around the nerves of the labial papillae.

As an alternative to Inglis' theory regarding the development of the enoplid jaws, it is herein suggested that the ancestor of the Enoplidae possessed a microlabium, mandibular ridge, and a pair of odontia on each of the three sides of the oral aperture. With subsequent evolutionary development, the odontia may have fused with the mandibular ridge, perhaps resulting in a structure not unlike that presently extant in leptosomatids. It is further proposed that the mandibular ridge-odontia complex then shifted posteriorly into the stoma to eventually become the jaws of present-day enoplids. A similar shift appears to have taken place in the ancestral line of the Synonchinae. Thus the teeth of the jaws in the Enoplidae may have been derived from odontia, the longitudinal rods derived from longitudinal extensions of the odontia, and the transverse bar representing the mandibular ridge component of

the jaw. Further amalgamation of these components conceivably has resulted in the mandibular plate of such species as those of the genus *Enoplus*.

It was noted above that there seems to be a fairly high correlation between the presence of the microlabium and mandibular ridge, if not the odontia as well. Where one exists, all commonly seem to exist (as in Leptosomatidae), and where one is absent, all appear to be absent (as in Thoracostomopsidae, Anoplostomatidae, Oxystominidae, Ironidae, Anticomidae, Phanodermatidae). If the ancestral line of the Enoplidae possessed this suite of traits, then it would be expected that representatives of that family would have microlabia because the mandibular ridge and odontia appear to be present as components of the jaws. Evidence in support of the existence of microlabia seems to exist in low magnification scanning electron micrographs of *Enoplus* species now in my possession.

If it is subsequently demonstrated that representatives of Leptosomatidae and Enoplidae have microlabia, mandibular ridges, and odontia in common, then it may follow that these two families also share a common ancestor not shared by other families presently assigned to the suborder Enoplina. While the information compiled in the course of this investigation has been used to justify the above theories, the data is admittedly limited and further confirmation must await more detailed studies of all the taxa concerned.

STRUCTURE OF THE STOMATAL ARMATURE AND NICHE PARTITIONING.—Virtually nothing is

known about the food or feeding habits of species of *Deontostoma*. Members of this genus are commonly in sediment associated with sessile or semi-sessile marine macro-organisms, but the association appears to be facultative (Hope, 1977:957). Most likely they feed upon micro-organisms, either selectively or nonselectively. Wieser (1953) has assigned genera of marine nematodes to one of four feeding types based entirely upon the structure of the stoma. He assigned both *Deontostoma* and *Thoracostoma*, the latter genus having contained at that time many of the species now assigned to *Deontostoma*, to feeding group 2-A. This group is comprised of species whose stoma is small- to medium-sized and allegedly equipped to scrape or grasp food from an epistrate, such as sand particles. Indeed, it may be that species of *Deontostoma* feed, at least in part, in the manner described by Wieser. Although the location of the orifices of the subventral esophageal glands on the lip region strongly suggests, as described above, that members of the genus *Deontostoma*, and perhaps all leptosomatids, are mucus-trap feeders. Whether they are epistrate feeders or mucus-trap feeders, however, the different forms of buccal armature further suggests that what is ingested, and how it is sorted out and removed from the nematodes environment, differs for each type of buccal armature. Hence differences in buccal armature among species of *Deontostoma* suggest that more than one ecological niche is occupied by members of this genus.

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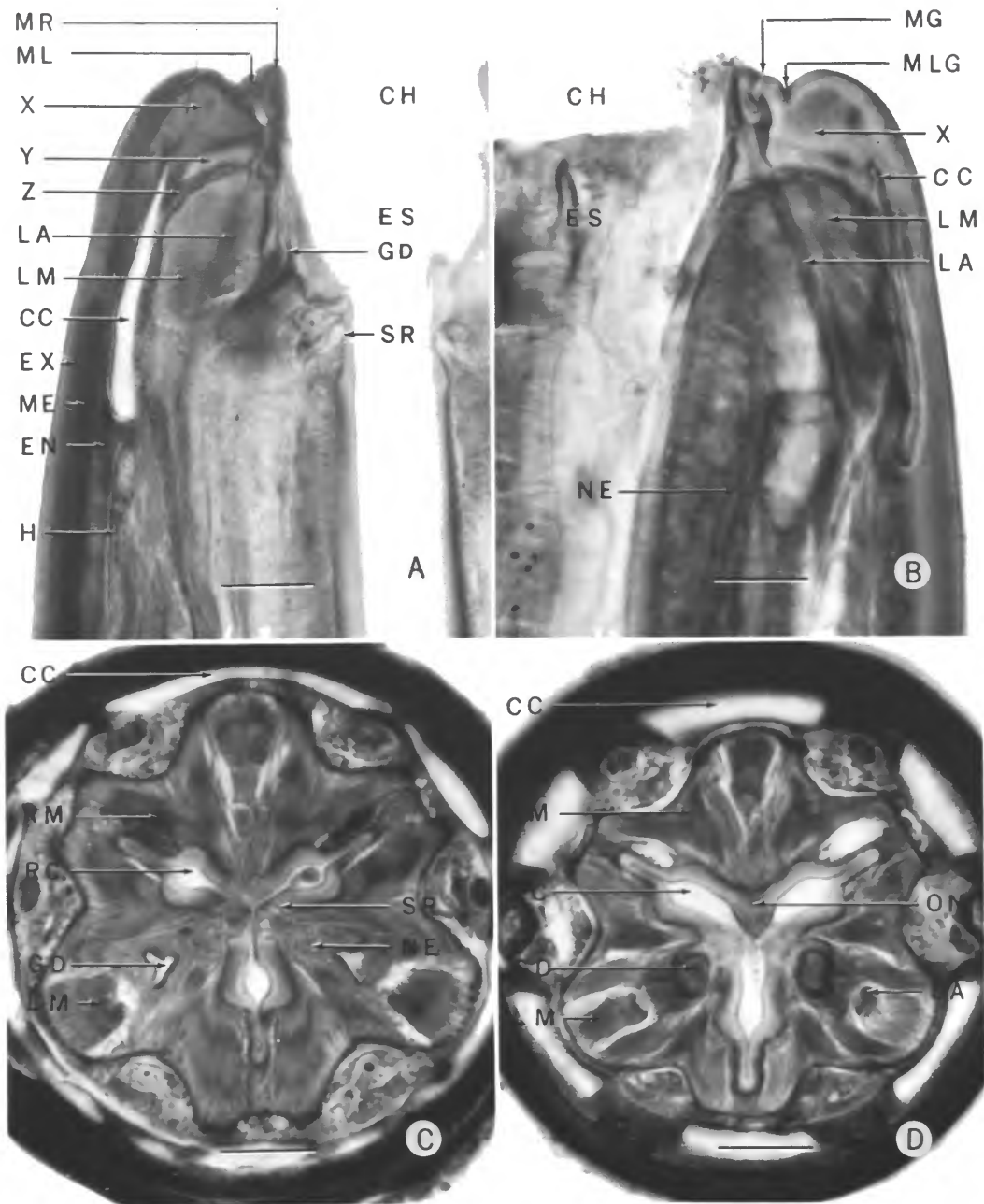


FIGURE 1.—*Deontostoma californicum*: A, Frontal section of head; B, saggital section through dorsal lip region; C, transverse section at level of sensory receptors at base of stoma; D, transverse section at level of onchium (sections A, C, and D stained with Mallory's triple stain; B stained with hematoxylin; scales = 10 μ m).

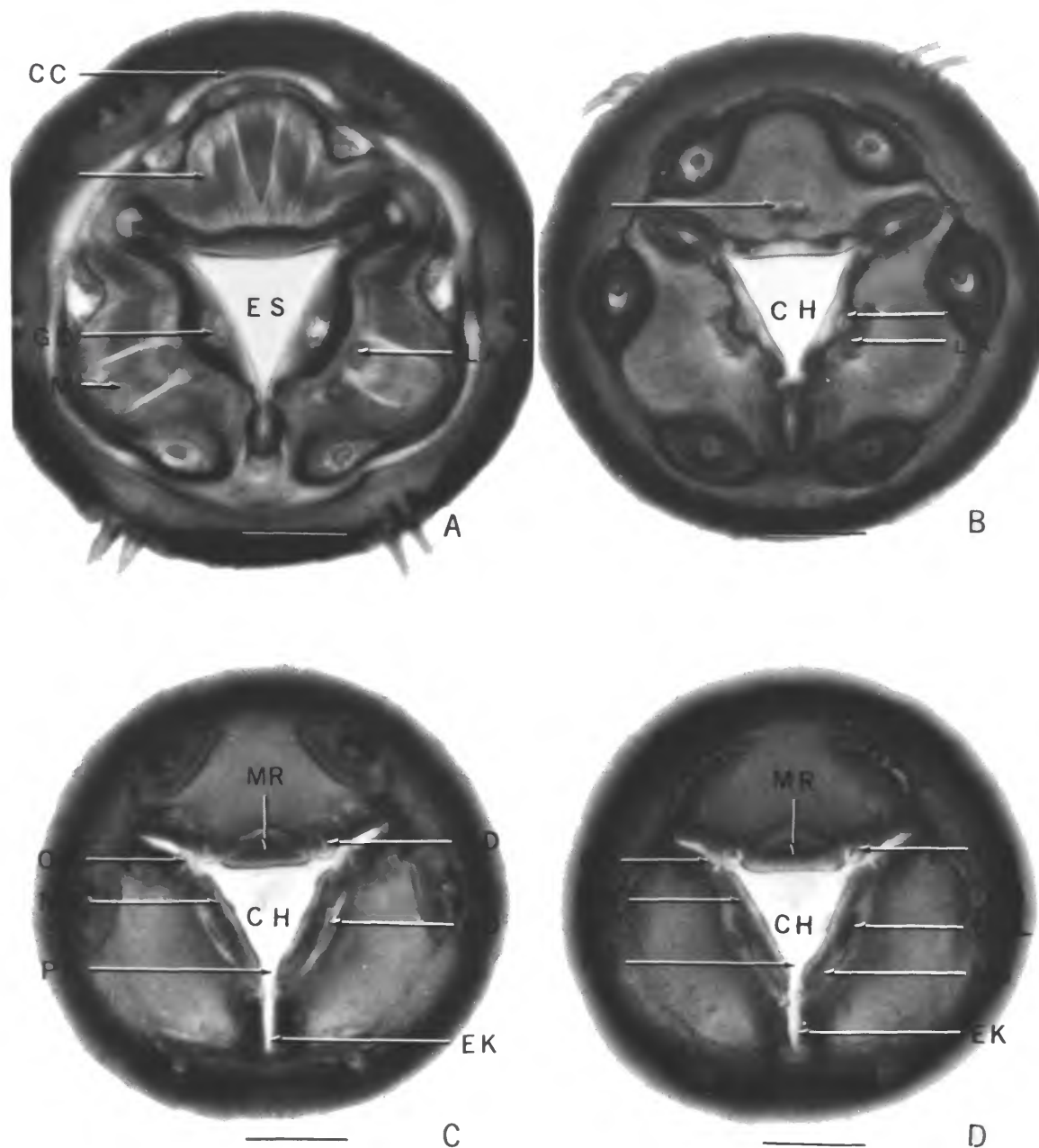


FIGURE 2.—*Deontostoma californicum*: A, Transverse section through anterior region of esophagome; B, transverse section through posterior level of cheilostome; C, transverse section through cheilostome at level where odontia emerge from the cheilorhabdion; D, transverse section of cheilostome at level of odontia (all sections stained with Mallory's triple stain; scales = 10 μm).

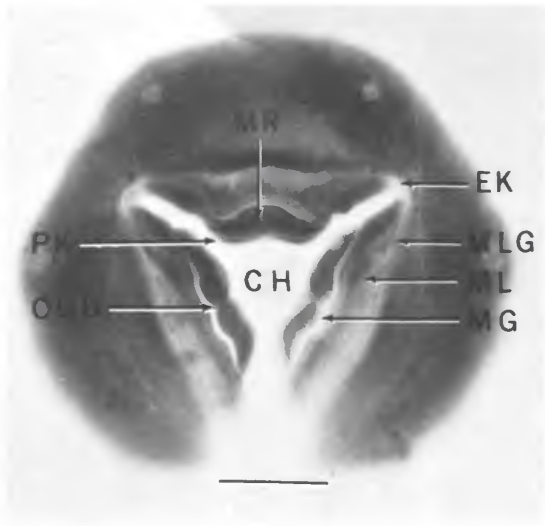


FIGURE 3.—*Deontostoma californicum*: Transverse section at level of mandibular ridges (section stained with Mallory's triple stain; scale = 10 μ m).

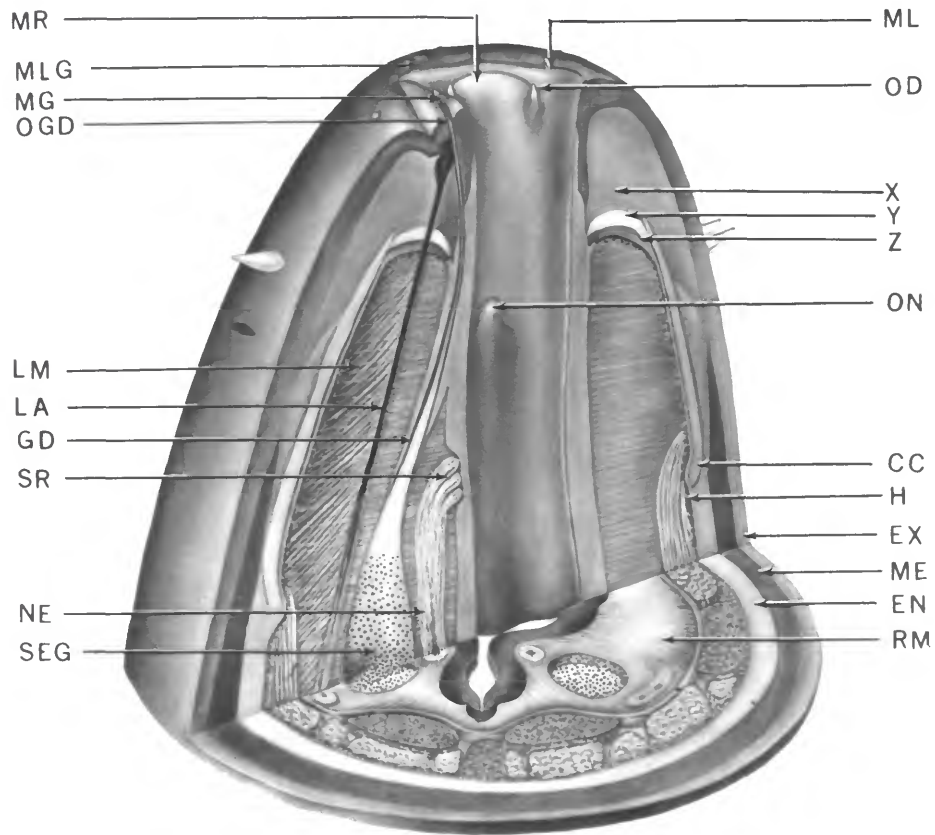


FIGURE 4.—*Deontostoma californicum*: Cut-away illustration showing details of internal head structure; longitudinally sectioned labial apodeme, esophageal gland and duct, and sensory receptor in right subventral sector of esophagus (scale = 20 μ m).

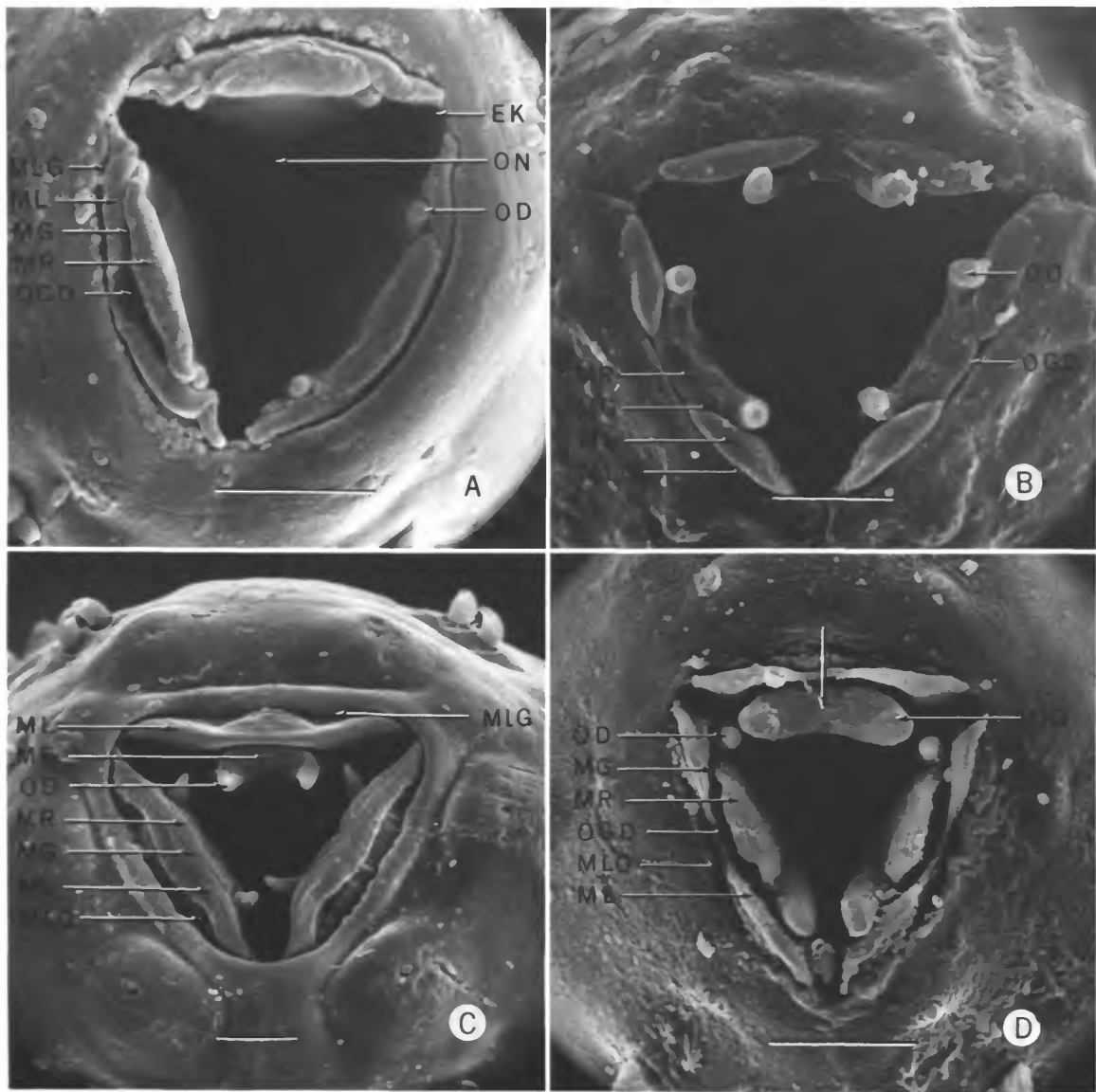


FIGURE 5.—Scanning electron micrographs of oral aperture of: A, *Deontostoma californicum* (scale = 10 μm); B, *D. coptochilus* (scale = 5 μm); C, *D. timmerchiorum* (scale = 10 μm), and D, *D. antarcticum* (scale = 10 μm).

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