

On the nature of the two anterior asetigerous rings in Dorvilleidae and Dinophilidae (Annelida, Polychaeta)

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ABSTRACT

Members of the order Eunicida are apparently characteristic in possessing two more or less clearly separated rings between the prostomium and the first setiger. In the family Eunicidae it has previously been shown that these rings represent a subdivision of the peristomium related to the manner in which the longitudinal muscles are attached to the body wall. Nevertheless, this character may be a synapomorphy for Eunicida, provided that it is homologous among its members. This hypothesis is tested in members of the families Dorvilleidae and Dinophilidae through light microscopic studies of the body area in question. Recent publications have proposed that Dinophilidae is closely related to or actually a subtaxon of Dorvilleidae; this conclusion is not contradicted by the results of this investigation.

RÉSUMÉ

Sur la nature des deux anneaux asétigères antérieurs réunis chez les Dorvilleidae et les Dinophilidae (Annelida Polychaeta)

Les membres de l'ordre Eunicida paraissent caractérisés par la possession de deux anneaux plus ou moins nettement séparés entre le lobe céphalique et le premier sétigère. Pour la famille des Eunicidae on a démontré que ces anneaux représentent des subdivisions du péristomium en relation avec la manière par laquelle les muscles longitudinaux sont attachés aux parois du corps. Néanmoins, ce caractère peut être une synapomorphie pour les Eunicida, à condition qu'il soit homologue parmi ses membres. Cette hypothèse est mise à l'épreuve chez les membres des familles des Dorvilleidae et des Dinophilidae par des études microscopiques de cette région du corps. Dans des publications récentes, on a proposé que les Dinophilidae sont effectivement étroitement alliés à un sous-taxon des Dorvilleidae; cette conclusion n'est pas en contradiction avec les résultats de cette investigation.

INTRODUCTION

In most members of the polychaete family Dorvilleidae the peristomium takes the form of two apodous rings between the prostomium and the first setiger. In most species these rings are subequal, but in many the anterior

one is shorter and indistinctly separated from the prostomium. Only few species show no trace of peristomial subdivision, e.g., four of the five hitherto described species of the genus *Exallopus* Jumars, 1974 (the exception is the type species, *E. cropion* Jumars, 1974). Some confusion has surrounded the nature of these two rings. Thus, while many authors have preferred neutral terms, such as rings, others appear to have regarded them as true segments (e.g., JIRKOV, 1989), where Dorvilleidae is characterized as having "two peristomial segments without parapodia, setae or cirri". The use of the word "segment" may in many instances have been coincidental, but in an evaluation of dorvilleid relationships with other polychaete groups it is important to understand the true nature of these rings. Within the order Eunicida conditions similar to those in Dorvilleidae are found in Eunicidae, Lumbrineridae (sensu ORENSANZ, 1990, including Lysaretidae), Hartmaniellidae, Oeononidae (= Arabellidae), and Iphitimidae (members of the families Histriobdellidae and Ichthyotomidae are too strongly modified to allow an assessment of this character). The major group in which only one peristomial ring is present is the family Onuphidae, which is considered the sister group of Eunicidae (ORENSANZ, 1990; FAUCHALD, 1992). Descriptions of the larval development of onuphids are not clear as to whether a peristomial subdivision is present during earlier stages in ontogeny (e.g., HSIEH & SIMON 1987 on *Kinbergonuphis simoni*). In his discussion of larval development in *Nothria elegans*, BLAKE (1975a) refers to the presence of such a subdivision but this is not confirmed by his illustrations.

The term peristomium, as it is currently used, is not applied to homologous structures in various polychaete families. In embryological terms, the peristomium has its origin in the region between the prototroch and the telotroch of the classical trochophora larva (e.g., GEORGE & HARTMANN-SCHRÖDER, 1985). This appears to be the case in Eunicida (see below). However, the adult peristomium of many polychaete families is a compound structure consisting of the peristomium s. str. as well as a variable number of anterior segments of teloblastic origin which have often lost their setae and parapodia and may possess paired tentacular cirri. Examples of these conditions may be seen in families such as Hesionidae, Syllidae, and Nereidae (GILPIN-BROWN, 1958).

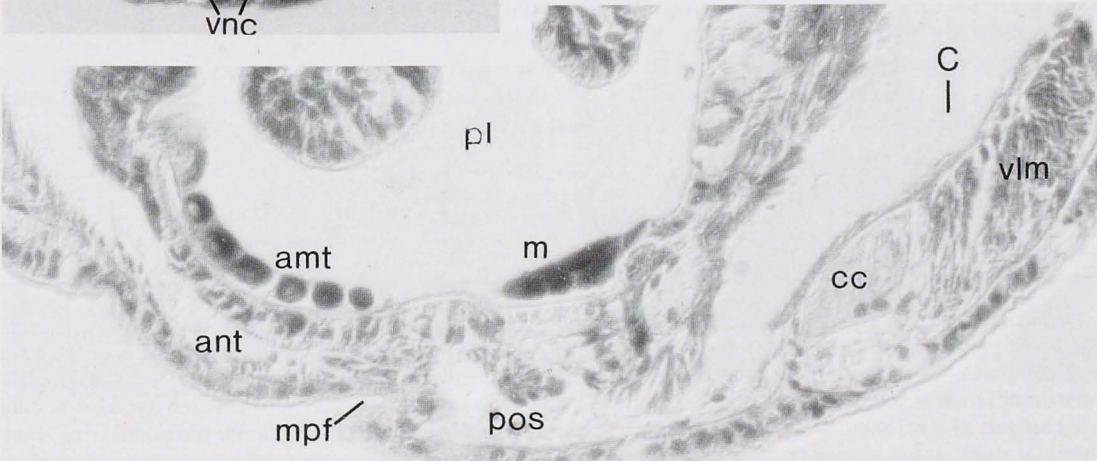
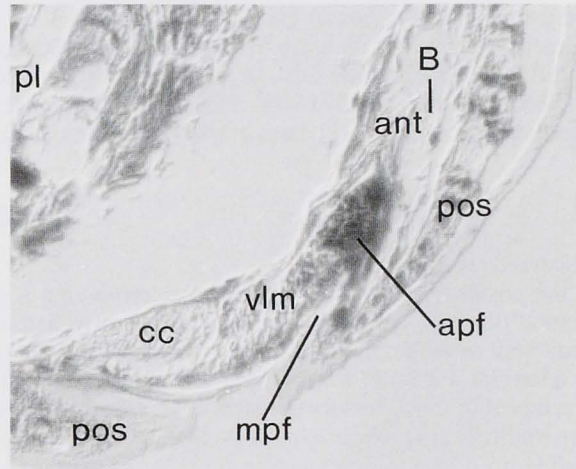
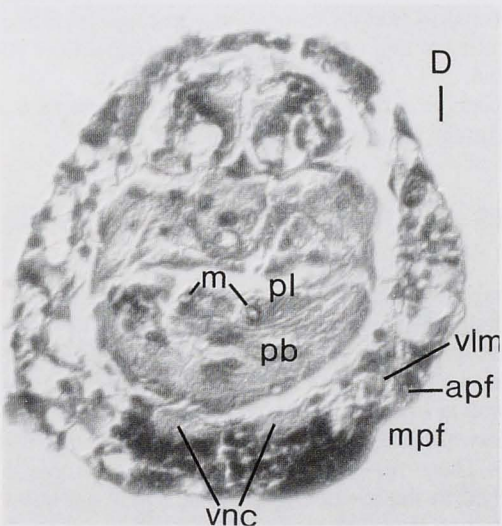
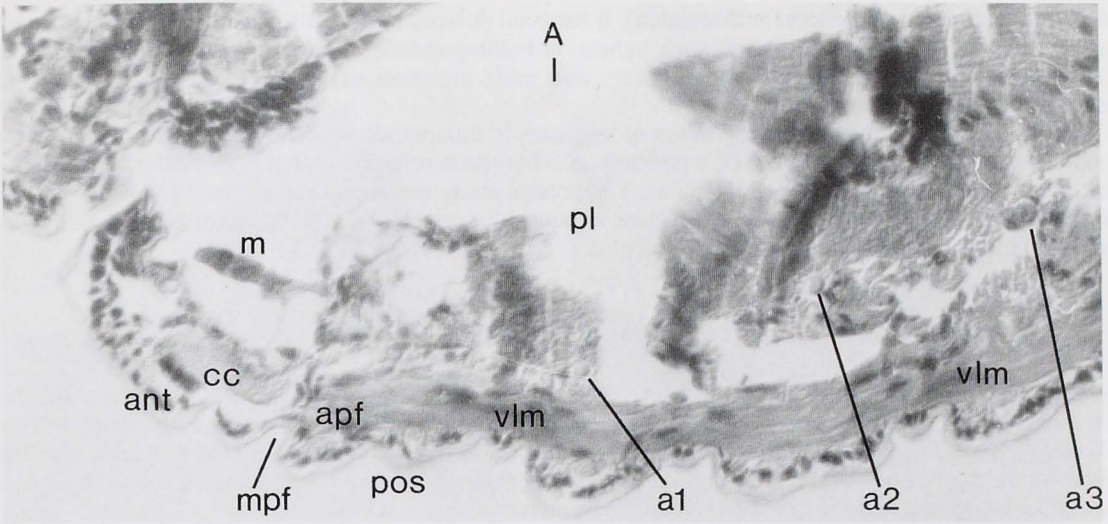
For *Eunice kobiensis* (Eunicidae), ÅKESSON (1967a) gave a very convincing account of the embryological origin of the peristomium. According to his studies, the first setiger of adults corresponds to the first larval segment; the peristomium, including both rings and the peristomial cirri, must be interpreted as presegmental. ÅKESSON also provided an anatomical explanation for the strongly developed peristomial subdivision, which is found in this species. His studies showed that in the posterior region of the peristomium a number of fibres belonging to the ventral longitudinal muscle bands branch off in a lateral direction and attach themselves to the body wall at the level of the subdivision (ÅKESSON, 1967a: Fig. 11). In a similar manner, fibres of the dorsal longitudinal muscles give rise to the dorsal component of the visible, non-segmental furrow.

Assuming that the absence of any peristomial subdivision in Onuphidae may be regarded as a secondary phenomenon (possibly related to their being mostly tubicolous), the presence of two rings of true peristomial origin may be regarded as an autapomorphic character of Eunicida. Embryological observations indicate that ÅKESSON's observations on *Eunice* are valid for members of Dorvilleidae (e.g., ÅKESSON, 1967b, 1973a, and b on various species of *Ophryotrocha*; BLAKE, 1975b on *Dorvillea rudolphi*) in the sense that the two asetigerous rings are of peristomial origin. However, it remains to be demonstrated that a true homology exists, i.e., that a homologous pattern of muscle attachment is present.

The primary purpose of this paper is to examine whether anatomical observations on various species of Dorvilleidae can confirm a homology on this point.

The family Dinophilidae was previously placed in Archiannelida, which was usually accorded order or class rank. In recent years, a body of evidence has grown that points to a close relationship between this family and Dorvilleidae (ÅKESSON, 1977; WESTHEIDE, 1985, 1987; ORENSANZ, 1990; EIBYE-JACOBSEN & KRISTENSEN, in press). However, since dinophilids are greatly reduced and highly specialized, much of the evidence is

FIG. 1. — A-C. *Protodorvillea kefersteini*, sagittal section showing ventrolateral longitudinal muscle band and attachment of accessory peristomial fibres to body wall at mid-peristomial furrow (A); cross section showing accessory peristomial fibres (in close proximity to ventrolateral longitudinal muscle band) attached to body wall (B); cross section 15-20 mm further posterior through anterior margin of mandible showing as yet undivided, strongly developed ventrolateral longitudinal muscle band (anterolateral, accessory mandibular teeth visible on left side) (C). D. *Ophryotrocha* cf. *hartmanni*, cross section, on right side corresponding to B (pharynx protruded). All scales = 10 mm. Nomarski differential interference contrast used on all figures. Abbreviations: a1 = aciculum of first setiger; a2 = aciculum of second setiger; a3 = aciculum of third setiger; amt = accessory mandibular teeth; ant = anterior peristomial ring (first post-prostomial ring); apf = accessory peristomial fibres; cc = circumesophageal connective; m = mandible; mpf = mid-peristomial furrow; ol = oesophageal lumen; pb = pharyngeal bulbus; pl = pharyngeal lumen; pos = posterior peristomial ring (second post-prostomial ring); vc = ventral ciliation; vlm = ventrolateral muscle band; vnc = ventral nerve cord.



circumstantial (larval resemblances, connections through theoretical morphological reduction series, parasite relationships; see above references for discussion). It has been difficult to find positive apomorphic characters that support a relationship. To date, the best such indication is the presence of an unpaired, pygidial stylus with a specific musculature in certain dorvilleid genera and most members of the dinophilid genus *Dinophilus* (WESTHEIDE, 1985).

There are difficulties in the homologisation of segments in dinophilids with those of other polychaetes, since parapodia and setae are absent. However, a peristomial subdivision resembling that in Dorvilleidae appears to be present, most clearly in the genus *Trilobodrilus*. The present study was in part undertaken to isolate yet another possible character to strengthen the view of a close relationship between these families (or at least, in the present context, the membership of Dinophilidae in Eunicida).

MATERIALS AND METHODS

Several specimens of each of the following species were examined: *Protodorvillea kefersteini* (McIntosh, 1869); *Parougia eliasoni* (Oug, 1978); *Ophryotrocha* cf. *hartmanni* Huth, 1933; *O. puerilis siberti* (McIntosh, 1885); and *Trilobodrilus* cf. *nipponicus* Uchida & Okuda, 1943. The dorvilleid species were taken at various localities along the north coast of Brittany, France. The specimens of *Trilobodrilus* were found in samples of coarse sand and gravel taken off Ellekilde Hage in the southern Kattegat, Denmark.

The specimens were embedded in paraplast using standard techniques, sectioned to a thickness of 4 µm, and stained using a modification of Masson's trichrome method (Weigert's iron haematoxylin, Ponceau's xylydine, and Fast Green). This renders muscle tissue bright red, whereas collagen and other connective structures are stained green. After dehydration, the sections were embedded in Entellan.

The sections were studied with a Leitz Ortholux microscope, whereas photographs were taken on a Zeiss Axiophot microscope, in most cases employing Nomarski differential interference contrast.

RESULTS

Protodorvillea kefersteini

In the posterior part of the second aseptigerous ring a group of muscle fibres (henceforth termed accessory peristomial fibres) leave the lateral part of each ventrolateral longitudinal muscle trunk (Fig. 1C). They attach to the body wall ventrolaterally on either side, midway along the length of the peristomium (Fig. 1B). Figure 1A shows a sagittal section in which a ventrolateral longitudinal muscle band is seen in the anterior setigers as well as the attachment of the accessory peristomial fibres to the body wall at the mid-peristomial furrow.

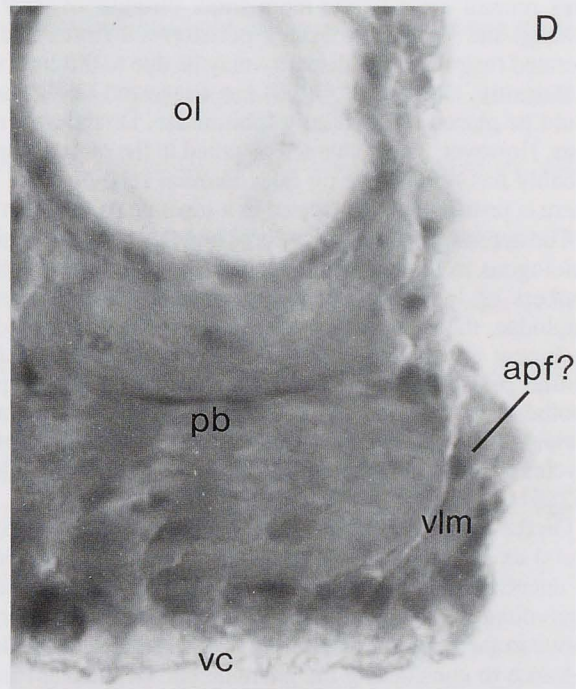
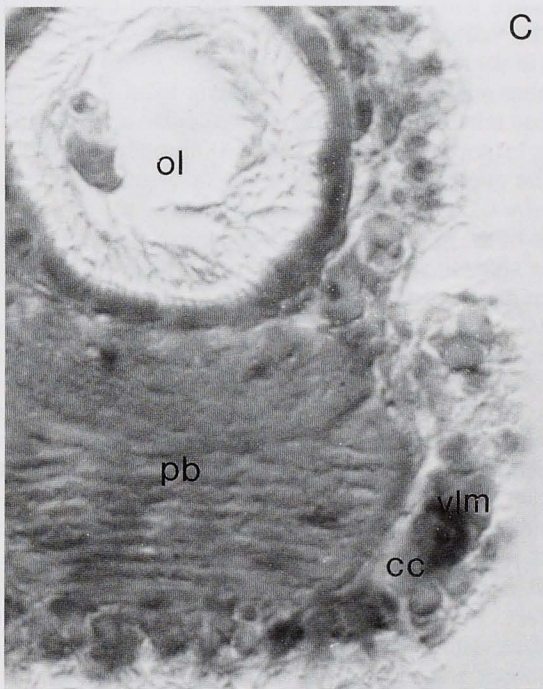
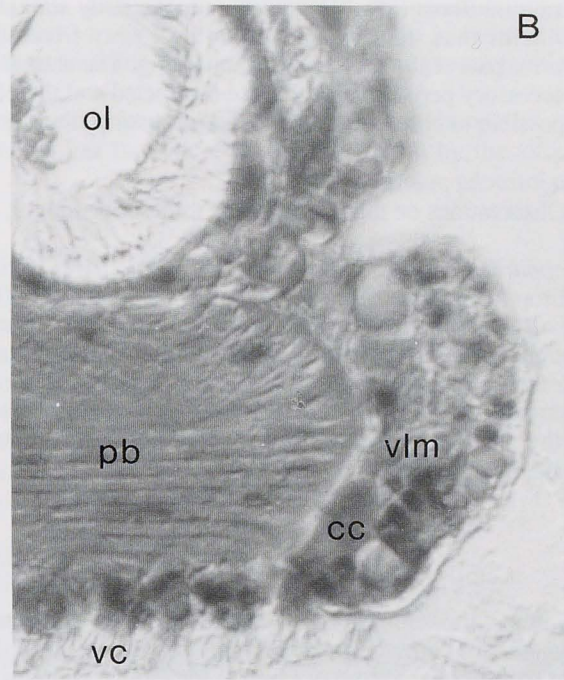
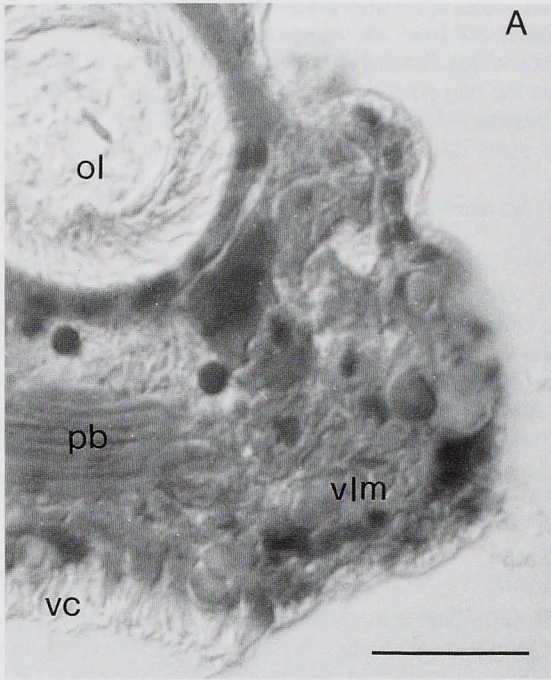
The ventrolateral longitudinal muscle trunks continue forward and insert on the body wall at the lower (posterior) lip of the mouth opening (not visible on Fig. 1A). These fibres may be confused with those of the anterior mandibular protractor muscles, which are also attached to the lower lip (DALES, 1962; not shown on ÅKESSON's (1967a) figures). However, the latter are inserted in a midventral position, whereas the paired ventrolateral longitudinal muscle trunks are ventrolaterally attached.

Accessory peristomial fibres also branch off from the dorsolateral longitudinal muscle trunks and are attached to the body wall further forward at the level of peristomial subdivision.

Parougia eliasoni

Observations on this species were identical to those described for *Protodorvillea kefersteini*.

FIG. 2. — *Trilobodrilus* cf. *nipponicus*, cross sections showing body becoming increasingly narrow in anterior portion of second post-prostomial ring, at narrowest point (D) showing subdivision of ventrolateral longitudinal muscle bundle, the dorsal component of which may be homologous to accessory peristomial fibres in Dorvilleidae. Scale A-D = 10 µm. Nomarski differential interference contrast used on A-C. Abbreviations: a1 = aciculum of first setiger; a2 = aciculum of second setiger; a3 = aciculum of third setiger; amt = accessory mandibular teeth; ant = anterior peristomial ring (first post-prostomial ring); apf = accessory peristomial fibres; cc = circumesophageal connective; m = mandible; mpf = mid-peristomial furrow; ol = oesophageal lumen; pb = pharyngeal bulb; pl = pharyngeal lumen; pos = posterior peristomial ring (second post-prostomial ring); vc = ventral ciliation; vlm = ventrolateral muscle band; vnc = ventral nerve cord.



Ophryotrocha cf. hartmanni

The sectioned material of this species, although of a poorer quality, shows the presence of accessory peristomial fibres (Fig. 1D) attaching to the body wall at the level of the mid-peristomial furrow. As in the other dorvilleids that were examined, the accessory fibres branch off from the ventrolateral muscle bands in the posterior part of the second peristomial ring. The animal shown was fixed with the pharynx somewhat protruded; the accessory peristomial fibres are contracted and therefore the two posterior mandibular rods are visible. It was not possible to observe whether dorsal accessory fibres are present.

Ophryotrocha puerilis siberti

Observations on this species were as described for *O. cf. hartmanni*.

Trilobodrilus cf. nipponicus

From the middle of the second post-prostomial ring (Fig. 2A) to the furrow between the first and second rings (Fig. 2D) body width decreases from 54 mm to 38 mm. Observations on the possible presence of accessory peristomial fibres was hampered by the small size of the animals in question. Thus, in any given cross section each ventrolateral muscle band consists of 2-4 cells only. However, at the level of the furrow between the first two post-prostomial rings, the dorsalmost of these cells appears separated from the others. It was not possible to observe whether it was attached to the body wall at this point, but this cell is absent on more anterior sections, indicating that its rostral end must be very close to the furrow.

DISCUSSION

In the dorvilleid species studied, subdivision of the peristomium appears to be induced (at least in part) by the attachment of accessory muscle fibres with an origin in the longitudinal trunks. These observations correspond to those reported by ÅKESSON (1967a) for *Eunice kobeensis*, the only important difference being that the accessory fibres remain close to the main trunk throughout their entire length. In *Eunice* (as indicated on ÅKESSON's drawing) the ventral accessory peristomial fibres and the ventrolateral muscle bands appear to be clearly separated rostrally. This disparity may be due to differences in degree of muscle contraction.

Recently, ORENSANZ (1990) has suggested that a number of dorvilleid genera, among them *Ophryotrocha* should be placed in the family Iphitimidae. Doubtless a close relationship between Dorvilleidae and Iphitimidae exists. However, as the character studied in the present paper is most likely common to the entire order Eunicida, it probably has no bearing on inter-familial relationships. The question of whether ORENSANZ' rearrangement of genera is justified will be treated in a separate paper (EIBYE-JACOBSEN & KRISTENSEN, in press).

The accessory peristomial fibres and thus the subdivision of the peristomium in Dorvilleidae are very probably homologous to those in Eunicidae. Although corresponding anatomical studies have not yet been carried out on members of families such as Lumbrineridae and Oeonidae, and disregarding the aberrant conditions in Onuphidae, the presence of a secondary peristomial subdivision in association with a specific pattern of muscle attachment appears to be an autapomorphic character for the order Eunicida. Even though external signs of genuine peristomial subdivision are lacking in other polychaete groups, it would be preferable to test this hypothesis by carrying out corresponding studies on some of them. The sister group of Eunicida would be of special interest. Unfortunately, it is at the present time difficult to form an informed opinion as to which polychaete groups are likely candidates, as Eunicida is generally considered a somewhat isolated group (DALES, 1962; STORCH, 1968; FAUCHALD, 1977).

On the basis of the present study of *Trilobodrilus*, it is neither possible to conclude that accessory peristomial fibre(s) exist nor that the two anterior post-prostomial rings represent a subdivided peristomium. The results are too uncertain and the apparent presence of a muscle cell disassociated from the others of the ventrolateral longitudinal muscle band (Fig. 2D) may be due to an artifact. The fact that this cell has a dorsolateral position relative to the longitudinal muscle band (lateral in Dorvilleidae, ventrolateral in Eunicidae) should not be seen as a hindrance to considering the phenomenon (if it exists) as homologous. In all cases, the fibres that branch off are the most lateral ones and it is the orientation of the longitudinal muscle bands which varies. Ultrastructural studies must, however, be carried out before it can confidently be concluded that a homology does exist on this point between dinophilids and eunicidans.

ÅKESSON (1967a) and subsequently other authors have suggested that the function of the accessory peristomial fibres is to augment the operation of the complicated jaw apparatus present in members of the order Eunicida. No

actual mechanism for this has been proposed. In *Ougia subaequalis* (OUG, 1978) the pharynx may reach into setiger 13 with the maxillae placed in setiger 6 in the retracted state. In many other dorvilleids some of the anterior setigers also house parts of the pharyngeal apparatus. Thus, although the division of the peristomium may originally have had an explanation in accordance with ÅKESSON's hypothesis, it is difficult in light of their dimensions to credit the accessory peristomial fibres with an important role during pharyngeal protraction in all dorvilleid species.

Certainly, if it were later to be demonstrated that accessory peristomial fibres are present in dinophilids they must be regarded as rudiments or have some other function, as they are completely dwarfed by the strongly developed pharyngeal bulb (Fig. 2D).

ACKNOWLEDGMENTS

I wish to thank Wilfried WESTHEIDE (University of Osnabrück, Germany) for suggesting this line of investigation and for being a generous host during an extended visit to his institute. The assistance of the staff at the Station Biologique (Roscoff, France), especially that of Captain Alain MARON, during the collection of most of the animals used in this study is greatly appreciated. Kurt OCKELMANN (Marine Biological Laboratory, Helsingør, Denmark) kindly furnished the specimens of *Trilobodrilus*. Margit JENSEN (Zoological Museum, University of Copenhagen) is thanked for the use of her Zeiss Axiophot microscope (Carlsbergfondet grant no. 468). The Danish Natural Science Research Council provided post-doc funding for this project (grant no. 11-8808).

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