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Evidence of a dorsal pharynx in the marine polychaete *Capitella teleta* (Polychaeta: Capitellidae)

MICHAEL J. BOYLE & ELAINE C. SEAVER[1]
Pacific Biosciences Research Center, University of Hawaii, Kewalo Marine Laboratory, 41 Ahui Street, Honolulu, Hawaii 96813,USA. E-mail: boylem@hawaii.edu, seaver@hawaii.edu
[1]Corresponding author

Abstract

Observations from compound, confocal, and scanning electron microscopy reveal that the buccal organ in *Capitella teleta* Blake, Grassle & Eckelbarger, 2009 should be classified as a dorsal pharynx. This buccal organ is an eversible proboscis that has the following characters: (1) dorsal ciliated pad, (2) well-developed pharyngeal retractor muscles, (3) pharyngeal gland-like structures, (4) cuticular fold surrounding the dorsal ciliated pad, and (5) unciliated buccal cavity and anterior ventral epithelium. All of these features are characteristic of dorsal pharyngeal organs present in oligochaetes and one terrestrial polychaete. Our observations in *C. teleta* confirm the presence of a dorsal pharynx in larvae, juveniles, and adults. *C. teleta* is a subsurface deposit feeder and a dorsal pharynx may have evolved independently in Capitellidae through selection of feeding mode in benthic marine habitats. Our results represent the first detailed description of a dorsal pharynx in a marine polychaete.

Key words: Pharyngeal**,** foregut, proboscis, buccal organ, eversible, deposit feeder, annelid, capitellid

Introduction

Polychaete annelids have successfully colonized nearly every benthic marine habitat. Such evolutionary success likely stems from their ability to access and process different food resources with a diversity of feeding structures and gut architectures (Dales 1962; Fauchald & Jumars 1979; Penry & Jumars 1990; Rouse & Pleijel 2001). Indeed, it has been said that the evolution of polychaetes is mirrored by the evolution of their feeding methods (Dales 1967). Most polychaete feeding methods include a structurally differentiated foregut, which is the anterior region of the digestive tract consisting of the buccal cavity, pharynx and esophagus (Tzetlin & Purschke 2005). If a foregut region can be everted through the mouth, it is called a proboscis, and the proboscis may or may not contain a muscular pharynx, jaws, ciliated and/or unciliated cuticular regions. Adult structures of the buccal cavity and eversible foregut regions are collectively referred to as a buccal organ (Rouse 2000; Rouse & Pleijel 2001; Tzetlin & Purschke 2005).

The symmetry, composition, and structural arrangement of different foregut tissues (e.g., muscles, epithelia, cilia) are used to classify buccal organ types. In accordance with current terminology and descriptions (Saulnier-Michel 1992; Rouse & Pleijel 2001; Purschke 2002, 2003; Tzetlin & Purschke 2005), annelid buccal organs are classified by six general plans of organization. These are: (1) axial non-muscular proboscis, (2) axial muscular proboscis (pharynx), (3) ventral

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proboscis, (4) ventral muscular proboscis (pharynx), (5) dorsolateral ciliary folds, and (6) dorsal pharynx. A buccal organ is absent or occluded in many polychaete species (Rouse & Pleijel 2001). An eversible dorsal pharynx is typical of oligochaetes (Jamieson 1992), and only has been described in one polychaete, the terrestrial species *Hrabeiella periglandulata* (Purschke 2003). The dorsal pharynx type of buccal organ is characterized by a number of distinct features. It has a conspicuously thickened dorsal foregut wall constructed of muscular, glandular and epithelial tissues (Jamieson 1992; Purschke 2003). Additionally, the dorsal epithelium of the pharynx forms a ciliated pad that faces the foregut canal, and it is surrounded by an unciliated cuticle. An unciliated cuticle lines both the buccal cavity and much of the ventral epithelium.

Historically, there have been two general trends in the study polychaete feeding structures. Several workers have emphasized the ecology of polychaete feeding structures by assigning functional categories to worms with similar feeding behaviors (Dales 1967; Fauchald & Jumars 1979; Rouse & Pleijel 2001). Such feeding categories (e.g., filter-feeders, carnivores, deposit-feeders) can often be recognized by distinguishing one buccal organ type from another, or its absence. More than one buccal organ may be found within a single category, and it is important to consider the overall complement of structures used by an individual species or family during a particular feeding method. Other work has emphasized the phylogenetic value of feeding structures, among other characters, in an effort to help resolve inter-relationships among polychaete families (Dales 1962; Purschke and Tzetlin 1996; Purschke 2002).

Capitella teleta Blake, Grassle & Eckelbarger, 2009 has been morphologically described and given its current species designation by Blake et al. (2009). *C. teleta* was provisionally known as *Capitella* sp. I, and is one member of a complex of genetically distinct sibling species (Grassle & Grassle 1976; Blake et al. 2009) in the family Capitellidae Grube, 1862. This marine polychaete is a subsurface deposit feeder that extracts sediment organics from muddy sands with an eversible proboscis (Eisig 1887; Fauchald & Jumars 1979). For sand-swallowing deposit feeders in Capitellidae, Arenicolidae, and Maldanidae, the buccal organ is commonly an axial non-muscular proboscis (Eisig 1887; Wells 1952, 1954; Dales 1962; Saulnier-Michel 1992; Purschke & Tzetlin 1996; Rouse & Pleijel 2001). Within Maldanidae and Arenicolidae, some species possess a ventral muscular pharynx, other species have dorsolateral ciliary folds, and still others may have a combination of both; however, all members of Capitellidae are described as having an axial non-muscular proboscis (Eisig 1887; Michel 1967; Purschke & Tzetlin 1996). Interestingly, *C. teleta* does not conform to any of these generalizations.

Here we describe, for the first time in detail, the existence of a dorsal pharynx in a marine polychaete. Through the use of compound, confocal and scanning electron microscopy, we show the major diagnostic characters as evidence of this type of buccal organ in larval, juvenile, and adult stages of *C. teleta*. From this evidence, we discuss ecological and evolutionary implications of the presence of a dorsal pharynx, which may indicate an interesting feeding adaptation for the *Capitella* sibling-species complex.

Materials and methods

Animals. A laboratory colony of *C. teleta* was maintained in 20-μm filtered seawater (FSW) at 19°C and fed organically rich mud following the original culture conditions established for members of the *Capitella* sibling-species complex (Grassle & Grassle 1976). Adult worms were periodically inspected for brooded larvae, which were subsequently collected into 0.2 μm FSW and raised until late larval or juvenile stages. Culturing and handling of adult animals and the isolation of embryos and larvae followed published methods (Seaver et al. 2005). A detailed protocol is available upon request.

Confocal microscopy. For molecular analyses of foregut structure, late-stage larvae and juvenile worms were relaxed in 1:1 0.37 M $MgCl_2$:FSW, fixed in 3.7% formaldehyde/FSW for 30 minutes, and washed in phosphate-buffered saline, 0.1% Triton X-100 (PBT). Labeling of microtubules was performed by first blocking in PBT with 10% normal goat serum (NGS) for 1 hour, followed by consecutive overnight treatments at 4°C with primary 1:200 anti-acetylated tubulin (Sigma) and secondary 1:300 Alexa Fluor® 647 (Molecular Probes) antibodies. To label DNA, animals were incubated in RNase A at 1.0 mg/ml PBT for 1 hr at 37 °C, followed by treatment with propidium iodide (Sigma) at 5 μg/ml PBT for 2 hours at room temperature (RT). To label musculature, the same animals were treated with phallacidin (BODIPY FL phallacidin, Molecular Probes) at 2.0 U/ml PBT for 2 hours during the propidium iodide incubation. Labeled specimens were rinsed in PBT and mounted in glycerol (80% glycerol / 10% 10X PBS / 10% diH20). Visualization and confocal imaging was performed with a Zeiss Axioplan 2 LSM510 confocal microscope.

Scanning electron microscopy. Adult worms were placed in non-coated plastic dishes in FSW overnight to empty their guts. Worms were relaxed in 1:1 0.37 M $MgCl_2$/FSW for 20 minutes, and pre-fixed for 1 hour in 3.2 % paraformaldehyde/FSW. For sectioning, worms were fixed with 4% glutaraldehyde in 0.1M sodium cacodylate with 0.35M sucrose (pH 7.6) for 2 hours at RT. While in glutaraldehyde, anterior thoracic regions were placed on wax and sagittally bisected with a scalpel along the midline. Sagittal sections were washed in 0.1M cacodylate buffer with 0.44M sucrose, postfixed with 1% osmium tetroxide in 0.1M cacodylate buffer for 1 hour at RT, dehydrated through a graded ethanol series and dried in a critical point dryer (CPD). Dried specimens were mounted on aluminum pin stubs with copper tape, sputter-coated with gold palladium and imaged with an Hitachi S-800 Field Emission Scanning Electron Microscope. Fixation, sectioning and SEM imaging were conducted at the Biological Electron Microscope Facility at the University of Hawai‘i at Manoa (UH).

Compound light microscopy. Foregut anatomy in larvae and juvenile worms was analyzed with a Zeiss Axioskop 2 compound, light microscope. DIC Micrographs were captured with a stem-mounted, 4.0 megapixel Nikon Coolpix 4500 digital camera. Digital images generated from all three microscopy methods were analyzed and edited in Adobe Photoshop CS3. Digital figure plates and the adult schematic were produced in Adobe Illustrator CS3.

Results and discussion

Capitella teleta is a subsurface deposit feeder. The mouth opens on the ventral surface posterior to the prostomium, adjacent to the junction of the peristomium and first chaetiger. Beginning at the mouth, the alimentary canal consists of a foregut (buccal cavity, pharynx, esophagus), midgut and hindgut with a terminal anus (Fig. 1). Together, the buccal cavity and pharynx form an eversible buccal organ, which we describe here as a dorsal pharynx.

Adult buccal organ—SEM description

The adult buccal organ is distinguished by an assemblage of muscular, epithelial and glandular tissues that are restricted to the dorsal side of the foregut (Fig. 2). A complex network of muscle fibers is attached to the dorsal surface of the pharyngeal epithelium, and forms two groups of retractors (Fig. 2A–B, D). One group extends posteriorly to attachment sites on the worm’s dorsal body wall (not shown). Another group extends posteriorly and branches into bilaterally symmetric left and right sets that attach to the lateral body wall (Fig. 2D). Both groups of retractor muscles attach to the body within the fourth chaetiger. There is an incomplete muscular septum positioned between chaetigers four and five. This septum is present in Capitellidae and Arenicolidae (Purschke and Tzetlin 1996), and likely separates the anterior part of the body cavity into a hydrostatic compartment to facilitate proboscis eversion. There appears to be a set of anterior retractors (not shown); however, there are no obvious protractor muscles. No obvious retractor muscles attach to the ventral wall of the pharyngeal canal. The epithelium of the dorsal ciliated pad is 23–25 µm thick, generally uniform, and extends from the posterior of chaetiger one to the anterior of chaetiger three (Fig. 2A–B, F–G). The cilia of the pad are 5–6 µm long and motile (Fig. 2G). In its retracted position, the anterior, posterior and lateral sides of the pad curve dorsally (Fig. 2A–B), and the lumen side of its epithelium is surrounded by a fold of unciliated cuticle (Fig. 2A, C). Lateral walls of the pharyngeal canal are unciliated. Except for occasional ciliary tufts within the mouth opening (Fig. 2C), the buccal cavity is lined with unciliated cuticle that is continuous with the epidermis. Directly opposite the dorsal ciliated pad, there is an abrupt transition on the ventral-posterior surface of the pharyngeal canal where the cuticle meets a ciliated epithelium (Fig. 2D, F). In the dorsal-anterior region of the pharynx, there are several lobate gland-like structures (Fig. 2D–E). Visceral musculature of the gut tube surrounding the pharynx and buccal cavity is composed of a network of orthogonal muscle fibers (not shown).

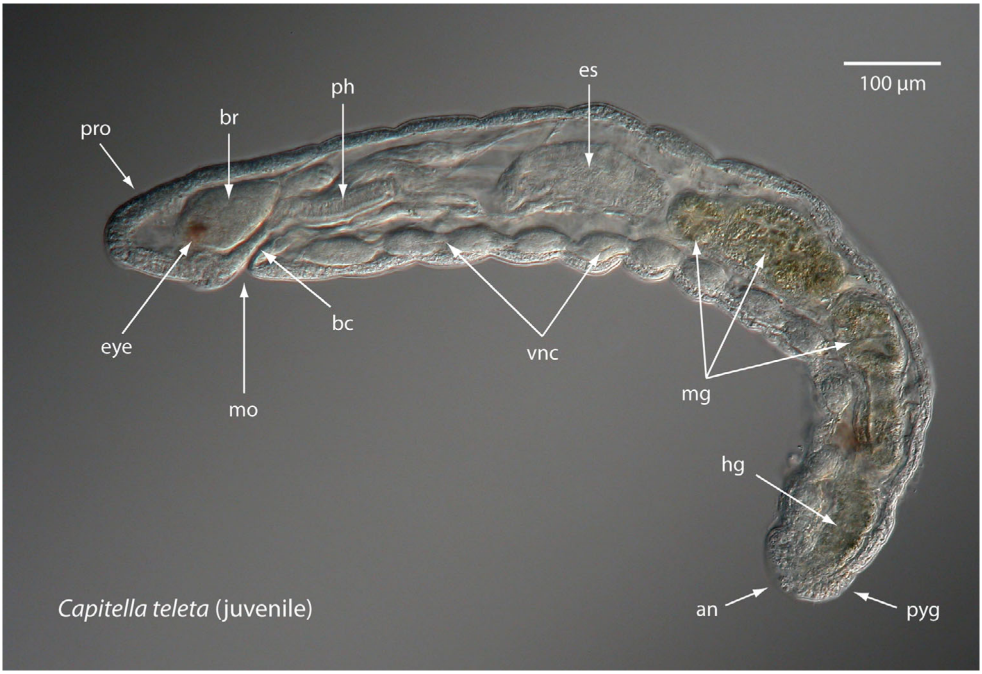

FIGURE 1. Juvenile specimen of *Capitella teleta*. DIC micrograph in lateral view with anterior to the left and ventral down. From anterior to posterior, the alimentary canal consists of a mouth, buccal cavity, pharynx, esophagus, midgut, hindgut, and posterior terminal anus (not in focus). Abbreviations: an, anus; bc, buccal cavity; br, brain; es, esophagus; hg, hindgut; mg, midgut; mo, mouth; ph, pharynx; pr, prostomium; pyg, pygidium; vnc, ventral nerve cord.

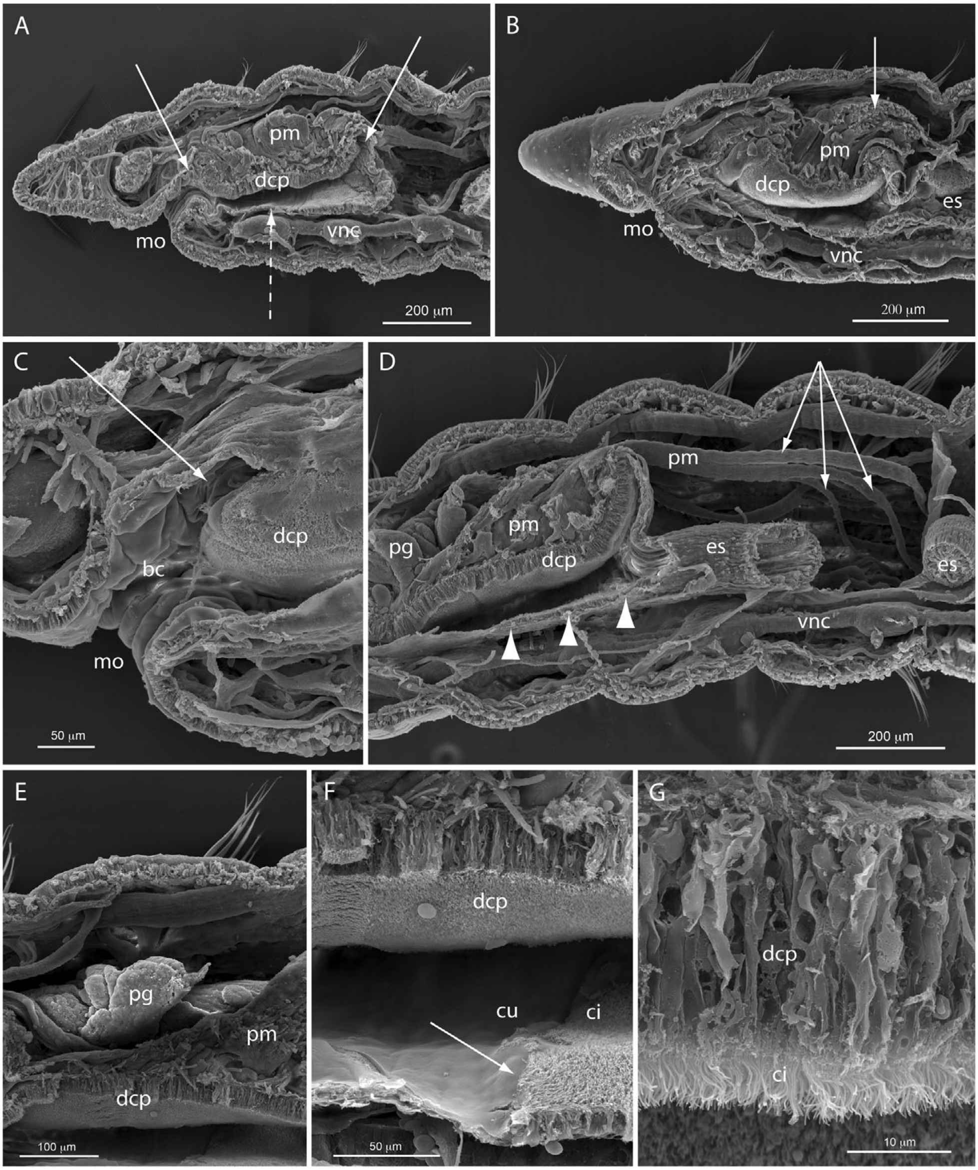

FIGURE 2. Details of foregut architecture in adults of *Capitella teleta*. Scanning electron micrographs (SEM) of sagittal dissections. Views are lateral with anterior to the left and ventral down. A, The pharynx primarily consists of a dorsal ciliated pad (dcp) attached to pharyngeal muscles (pm) that are located between the pad and the worm's dorsal body wall. Solid arrows mark the anterior and posterior margins of the pharynx. The floor of the pharyngeal canal (dashed arrow) is non-muscular, comparatively thin and overlies the ventral nerve cord (vnc). B, Most of the pharynx is visible. In its resting position, the ciliated pad curves dorsally and pharyngeal muscles (solid arrow) extend in a dorsal-posterior direction toward the dorsal side of the esophagus (es). C, The mouth (mo), buccal cavity (bc) and margins of the pharyngeal pad (arrow) are lined with unciliated cuticle. D, View of the posterior

pharynx and esophagus region. Pharyngeal retractor muscles (arrows) extend posteriorly toward attachment sites along the body wall. There is a ciliated epithelium on the ventral-posterior floor of the pharyngeal canal that extends into the esophagus (arrowheads, see A and F). E, Pharyngeal gland-like structures (pg) are located on the dorsal-anterior side of the pharyngeal pad, and anterior to most pharyngeal musculature; F, Magnified view of the pharyngeal canal in E. There is a clear demarcation (arrow) on the ventral-posterior floor of the pharyngeal canal where the anterior unciliated cuticle (cu) meets a posterior ciliated epithelium (ci); G, Close-up view of the columnar epithelium and ciliation of the dorsal ciliated pad. Abbreviations: bc, buccal cavity; cu, cuticle; ci, cilia; dcp, dorsal ciliated pad; es, esophagus; mo, mouth; pg, pharyngeal gland-like structure; pm, pharyngeal muscle; vnc, ventral nerve cord.

A disproportionately thickened dorsal wall of the pharynx is considered to be typical of oligochaetes (Jamieson 1981; Jamieson 1992; Purschke 1999, 2003), and has been used as a conspicuous character to distinguish oligochaetes from polychaetes (Jamieson 1992). Several features of gross foregut anatomy in oligochaetes and the terrestrial polychaete *Hrabeiella periglandulata* are strikingly similar, and both of their foregut plans have a structural organization that is classified as a “dorsal pharynx.” In *H. periglandulata*, the only polychaete species previously described to have this pharyngeal type, the dorsal pharynx is composed of prominent protractor and retractor muscles attached to a dorsal ciliary pad, and there are four pairs of pharyngeal glands (Purschke 2003). Additionally, pharyngeal cilia are restricted to the dorsal pad, a fold of unciliated cuticle surrounds the pad, the buccal cavity is lined with cuticle, and there is a distinct unciliated-ciliated transition on the floor directly opposite the dorsal pad (Purschke 2003). By comparison, there is strong correspondence between the basic foregut structure in oligochaetes and *H. periglandulata* and the foregut structure we observe in *C. teleta*. What is most obvious in each of these annelids is the highly asymmetric organization of the pharynx. Hugo Eisig (1887) meticulously described major organ systems for several capitellids, and his drawings of *Capitella* clearly show multiple features of a dorsal pharynx. Eisig thought it was interesting that the proboscis retractor muscles are strongly developed (Eisig 1887). Although we cannot directly compare biochemical or ultrastructural foregut features reported for oligochaetes and *H. periglandulata* (Jamieson 1981; Jamieson 1992; Purschke 2003), the cellular and morphological characters that we have described clearly support the organization of a dorsal pharynx in *C. teleta*.

Juvenile buccal organ—cellular and morphological description

To determine whether there is a transition in pharyngeal type among different life history stages in *C. teleta*, we also examined the morphology of the foregut in recently metamorphosed juveniles and late larval stages. In *C. teleta*, feeding commences in juveniles following metamorphosis. In juveniles, a muscular pharynx is positioned within the dorsal wall of the foregut canal, posterior to an unciliated buccal cavity (Fig. 3). Molecular markers for cilia (tubulin), cell nuclei (DNA) and muscle fibers (actin) show that the pharynx is primarily composed of a dorsal ciliated pad with a well-developed system of pharyngeal retractor muscles (Fig. 3A, D–F). Pharyngeal muscles are attached to the dorsal side of the pad, and extend from the pad in both dorsal-posterior and lateral-posterior directions (Fig. 3A, D). A pair of relatively thin muscle fibers connects the anterior end of the pad to the worm’s dorsal body-wall musculature, and may function as accessory retractors (Fig. 3A, D). The dorsal ciliated pad is approximately 90 µm by 72 µm (L x W), and is surrounded by an unciliated cuticular fold (Fig. 3B–C). The dorsal ciliated pad is composed of a columnar epithelium, which is conspicuously thicker than the ventral epithelium of the pharyngeal canal (Fig. 3A, B, F). Its ventral surface is lined with cilia (Fig. 3A, E), which are motile and make contact with the substrate when the pharynx is everted. The ventral epithelium directly overlies the ventral nerve cord, has few muscle fibers, and is ciliated toward its posterior end where it leads into the esophagus. There is a pair of pharyngeal gland-like structures on the dorsal-anterior side of the pharynx (Fig. 3B).

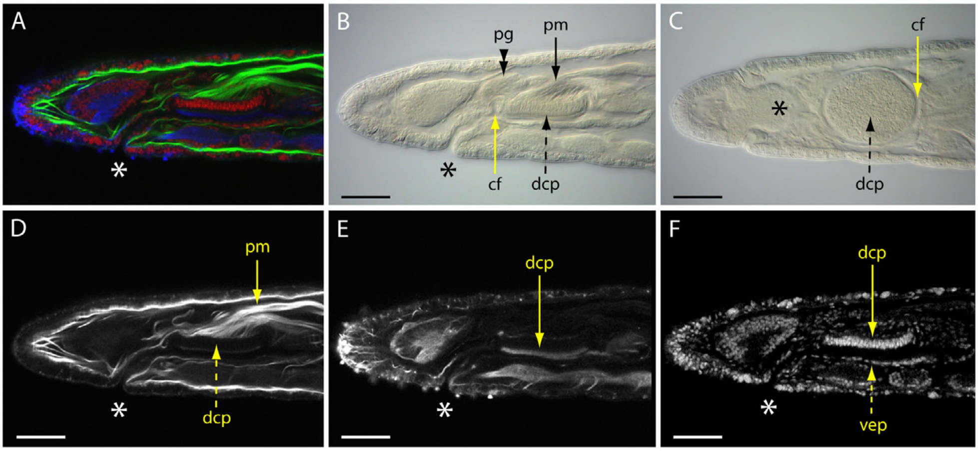

FIGURE 3. Foregut structure in the juvenile of *Capitella teleta*. A–B and D–F, lateral views with anterior to the left and ventral down; C, ventral view with anterior to the left. All panels (A–F) are images of the same animal. A, Triple-label confocal micrograph with fluorophores for F-actin (green, phallacidin), DNA (red, propidium iodide), and acetylated microtubules (blue, anti-acetylated tubulin), which identify the pharyngeal musculature, epithelium, and ciliation, respectively, among other anatomical features. B, DIC micrograph showing relative positions of the pharyngeal gland (double arrowhead), pharyngeal retractor muscles (black arrow), dorsal ciliated pad (dashed arrow) and cuticular fold surrounding the pad (yellow arrow). C, Ventral view of the foregut's dorsal ciliated pad (black dashed arrow) surrounded by a non-ciliated cuticular fold (yellow arrow). Note how the pad extends laterally across most of the worm's body. D, Single-channel (green, phallacidin) of the confocal image in A. Pharynx (proboscis) retractor muscles (yellow arrow) extend in a dorsal-posterior direction from the dorsal ciliated pad (yellow dashed arrow). E, Single-channel (blue, anti-acetylated tubulin) of the confocal image in A. There is a discrete band of cilia along the ventral side of the pharyngeal pad (yellow arrow). F, Single-channel (red, propidium iodide) of the confocal image in A. Nuclei in the dorsal pad (yellow arrow) show a thicker epithelium relative to cells along the foregut's ventral epithelium (yellow dashed arrow). Asterisk marks the position of the mouth. Scale bars = 50 µm. Abbreviations: cf, cuticular fold; dcp, dorsal ciliated pad; pg, pharyngeal gland-like structure; pm, pharyngeal muscle; vep, ventral epithelium.

Larval foregut—developmental description

A dorsal pharynx is also present in late-stage larvae of *C. teleta* (Fig. 4). In the dorsal wall of the anterior foregut canal, there is a thick pharyngeal epithelium that is ciliated on its ventral surface (Fig. 4A). The nuclei in this epithelium are elongate, suggesting that it has a columnar cell structure (Fig. 4B). In contrast, the ventral epithelium is comparatively thin, and the shape of the nuclei there indicate a simple squamous or cuboidal cell structure. In cross section, numerous actin-labeled muscle fibers are visible extending from the dorsal surface of the pharyngeal epithelium, and no ventral retractor fibers are observed (Fig. 4C, A).

In *C. teleta*, there is developmental continuity from larva to adult in the morphological presence of a dorsal pharynx. *C. teleta* is a brooder of relatively large yolky embryos, and active feeding does not occur until after larval settlement and metamorphosis. For species in which the stomodeum becomes a functional larval pharynx prior to metamorphosis (Anderson 1973), larval pharyngeal structures can be replaced by adult structures (Anderson 1959, 1973; Purschke and Tzetlin 1996), or additional pharyngeal structures may develop (Purschke 2002). However, during gut development in yolky polychaete embryos, the stomodeum typically develops directly into the adult pharyngeal epithelium (Anderson 1959; Åkesson 1967). During a recent study of gut development in *C. teleta* (Boyle and Seaver 2008), we recognized that an eversible buccal organ in feeding juvenile and adult worms is the direct product of foregut morphogenesis in larvae, and therefore the dorsal pharynx does not represent a transient developmental structure.

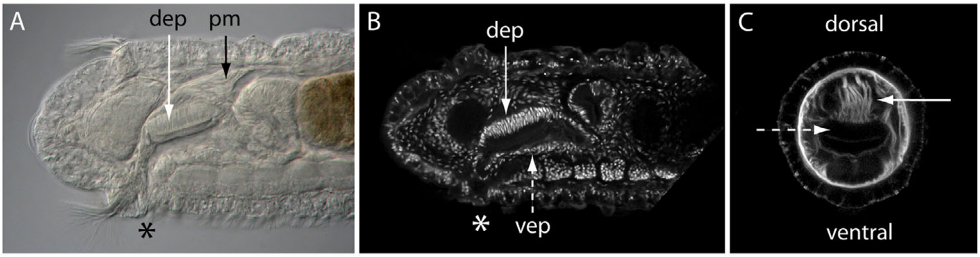

FIGURE 4. Foregut structure in late-stage larva of *Capitella teleta*. A–B, lateral views with anterior to the left and ventral down; C, anterior view. A, DIC micrograph showing a thick dorsal pharynx epithelium (white arrow) and associated pharyngeal retractor muscles (black arrow) in the late-stage metatrochophore larva. B, Single-slice confocal micrograph near the medial plane of the foregut. The DNA of cell nuclei is fluorescently labeled with propidium iodide and shows a difference in thickness between the foregut's dorsal pharyngeal epithelium (solid arrow) and the opposite thin-walled ventral epithelium (dashed arrow). C, Single-slice confocal micrograph. The view is an anterior, optical transverse section through the pharynx. Dorsal pharyngeal retractor muscles (arrow) are labeled with a phallacidin-conjugated dye for F-actin, and extend from the dorsal body wall to the dorsal pharyngeal epithelium (dashed arrow). Asterisk marks the position of the stomodeum in panels A & B. Abbreviations: dep, dorsal pharyngeal epithelium; pm, pharyngeal retractor muscles; vep, ventral epithelium.

Ecological considerations

Polychaete foregut structure is directly related to feeding biology (Purschke 1988), and a dorsal pharynx in *C. teleta* may be a unique feeding adaptation of the *Capitella* sibling species complex. Eisig (1887) stated that in *Capitella*, the proboscis is not used as a digging tool, nor is it everted and retracted in a rhythmic cycle as in other capitellids. Our observations of *C. teleta* behavior are consistent with Eisig's observations. We often see periodic, singular proboscis eversion movements in laboratory cultures. It was also found that *C. teleta* selectively ingests the smallest sediment particles, regardless of the worm's body size or the degree of sediment contamination (Horng & Taghon 1999). Fauchald and Jumars (1979) reported that capitellid guts "nearly always contain algal fragments" suggesting some degree of selective feeding. Regarding the *Capitella* sibling species in particular, "the complexity of feeding modes and selectivity of these species may have been underestimated" (Fauchald & Jumars 1979). The structure of a dorsal pharynx in oligochaetes is considered to be an adaptation for ingestion of decaying plant material and detritus in terrestrial environments, or environments not saturated with water (discussed in Purschke 1999; Tzetlin & Purschke 2005). However, there are descriptions of a dorsal pharyngeal pad in both terrestrial (lumbricids) and marine (naids, enchytraids) oligochaetes (Jamieson 1992). Furthermore, '*Capitella capitata*' is typically found in submerged marine sediments where they are known as both opportunistic species and indicators of polluted, unpredictable and organic-rich sulphidic environments (Grassle & Grassle 1974; Grassle & Grassle 1976; Pearson & Rosenberg 1978; Levin et al., 1996).

Several studies report both *Capitella* and oligochaete species feeding within the same subsurface marine deposits (Trueblood et al. 1994; Thiel & Watling 1998; Snelgrove et al. 2001). Both *Capitella* and oligochaete populations appear to increase in algal-enriched sediments (Norkko & Bonsdorff 1996; Thiel & Watling 1998; Lopes et al. 2000), both prefer muddy sites to sandy environments (Snelgrove et al. 2001), and both are considered contamination-tolerant taxa (Thompson and Lowe 2004). These two annelid groups seem to share the ability to consistently exploit subsurface nutrients in relatively dynamic environments, and it would be interesting to determine whether the shared presence of a dorsal pharynx confers some feeding advantage in a particular benthic habitat. Other opportunistic species in these environments often include tube-dwelling spionid polychaetes (Grassle & Grassle 1974; Levin et al. 1996) that possess either axial or ventral buccal organs and accessory feeding palps, however these polychaetes are surface deposit feeders and therefore utilize a different feeding niche. These observations support a hypothesis whereby marine annelids with a dorsal pharynx are adapted to subsurface feeding in polluted or unpredictable environments.

Evolutionary considerations

The dorsal pharynx of *C. teleta* could have evolved independently in the lineage leading to Capitellidae. This might have occurred by reduction of certain structures and elaboration of others, and is therefore convergent with the dorsal pharynx in other marine and terrestrial annelids. Eisig (1887) noticed that the proboscis in *Capitella* is reduced in size compared with other capitellids, and assumed that reduction of the proboscis evolved faster than reduction of the strongly developed retractor muscles. The interpretation of a dorsal pharynx evolving independently in *Capitella* is partly supported by descriptions of a range of buccal organ types in maldanids, arenicolids, capitellids and other sand or mud-swallowing polychaete species (Dales 1967; Purschke & Tzetlin 1996; Fauchald & Rouse 1997; Rouse & Pleijel 2001; Tzetlin & Purschke 2005). Species within Capitellidae are generally characterized to have a simple axial proboscis (Eisig 1887; Michel 1967). Several species in Arenicolidae are described with a simple axial proboscis (Wells 1952, 1954), and species within Maldanidae have a simple axial proboscis (Dales 1962; Tzetlin 1991), a ventral proboscis (Orrhage 1973), or a combination of ventral and axial foregut structures (see Tzetlin 1991; see Tzetlin & Purschke 2005). Since a dorsal pharynx appears to be unique to Capitella within marine polychaetes, and analyses of morphological data (Rouse & Fauchald 1997) and molecular data (Struck et al. 2007) support a close group relationship among capitellids, arenicolids, and maldanids, convergence among *Capitella, Hrabeiella periglandulata,* and oligochaetes is the most parsimonious conclusion.

The other interpretation is that a dorsal pharynx was present in the last common ancestor of oligochaetes, terrestrial polychaetes, and capitellids. A complex dorsal pharynx may have evolved from the more simple dorsolateral ciliary folds, which is considered the plesiomorphic condition for Annelida (Purschke & Tzetlin 1996; Tzetlin & Purschke 2005). In their study of dorsolateral ciliary folds in polychaetes, Purschke & Tzetlin (1996) proposed that these “primitive feeding structures” could be homologous to the dorsal pharynx in oligochaetes. Interestingly, there are dorsolateral ciliary folds in some juvenile and adult capitellids (see Tzetlin & Purschke 2005), and if this represents an ancestral condition, the dorsal pharynx in *Capitella* could theoretically have evolved from these ancestral folds.

Prior to the description of a dorsal pharynx in the terrestrial polychaete, *H. periglandulata* (Purschke 2003), the dorsal pharynx was considered to be one of several distinctions between oligochaetes and polychaetes. With our observation, a dorsal pharynx is now described in two non-clitellate annelids. Furthermore, *C. teleta* shares several other features with oligochaetes and *H. periglandulata* (e.g., small prostomium lacking appendages, brain primarily behind prostomium, single circumesophageal connectives, ventral nerve cord with closely apposed connectives, reduced parapodia, pygidial cirri absent, hermaphroditism). Purschke (2003) thought a sister group relationship between *H. periglandulata* and Clitellata was conceivable, and Nielsen (1995) thought it would be useful to regard Capitellidae and Clitellata as sister groups. Currently, there is essentially no molecular support for either of the proposed sister groups, and there is not a strong argument for homology of foregut structure between *C. teleta* and either of the other annelids, especially since the loss of a dorsal pharynx would have to occur multiple times within the group of capitellid, arenicolid, and maldanid species. A broader sampling of cellular, molecular, and ultrastructural data is needed to assess any further possibility of homology.

In summary, we have presented evidence for the existence of a dorsal pharynx in the marine polychaete, *Capitella teleta*. This organ is a complex structure characterized by the following features: (1) dorsal ciliated pad, (2) well-developed pharyngeal retractor muscles, (3) pharyngeal gland-like structures, (4) cuticular fold surrounding the dorsal ciliated pad, and (5) unciliated buccal cavity and anterior ventral epithelium (Fig. 5). To date, the observation of a dorsal pharynx in *C. teleta* is unique within marine polychaetes and may have been overlooked. Although the phylogenetic implications are unclear, it is likely that this particular foregut structure evolved independently within Capitellidae. The dorsal pharynx in *C. teleta* is not a transient developmental character and may represent an adaptation for subsurface deposit feeding in polluted, organic-enriched, or unpredictable marine sediments. We hope our work contributes important cellular and morphological data for better understanding the evolutionary success of polychaete annelids.

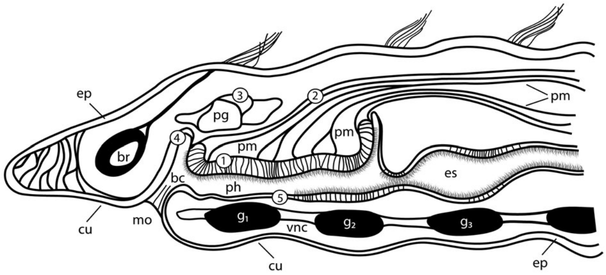

FIGURE 5. Diagnostic characters of the dorsal pharynx in *Capitella teleta*. Lateral schematic view with anterior to the left and ventral down. A ciliated epithelial pad (1), pharyngeal musculature (2), and gland-like structures (3) are all positioned dorsally with respect to the alimentary canal. Unciliated cuticle covers a fold of tissue surrounding the pharynx (4), and forms the lining of the mouth, buccal cavity, and ventral-anterior pharyngeal canal (5). Drawn from sagittal dissections. Abbreviations: bc, buccal cavity; br, brain; cu, cuticle; ep, epidermis; es, esophagus; g, ganglia; mo, mouth; pg, pharyngeal gland-like structure; ph, pharynx; pm, pharyngeal muscle; vnc, ventral nerve cord.

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