Introduction

The lateral line (LL) system of shallow water taxa is well-known, but descriptions of the LL systems of deep-sea fishes are scattered and incomplete (reviewed in Webb, 2014). The little data that is available provides evidence for two morphological strategies: **1**) Widened canals with large canal neuromasts (Fig. 1A-B; Garman, 1899; Jakubowski, 1974; Marshall, 1996), 2) Reduced canals with superficial neuromasts that in the place of canal neuromasts (Fig. 1C-D; Marshall, 1996; Pietsch, 2009). These are likely two sensitivity to water flows in the

hydrodynamically quiet deep sea.

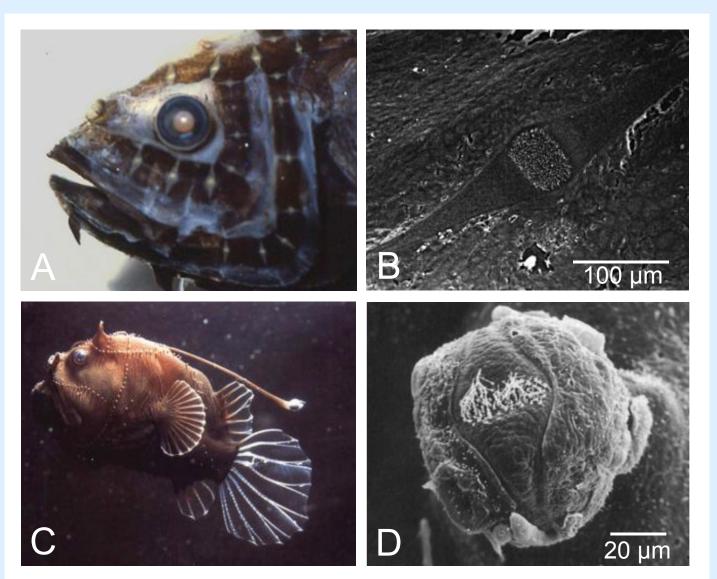


Figure 1: Deep-sea species with widened canals or reduced canals with superficial neuromasts (SN). A) A melamphaid (Poromitra sp.) with skin over widened LL canals removed revealing large neuromasts. B) SEM of a canal neuromast in *Poromitra capito*. C) The anglerfish, alternative strategies for enhancing *Phrynichthys wedli* with SN's on papillae. D) SEM of SN in *Phrynichtys wedli*. (B-D from Marshall, 1996).

However, some deep-water taxa appear to have a reduction of both LL canals and in the number of neuromasts (Fig. 2C; Handrick, 1901, the only mention of LL morphology in hatchetfishes), which is proposed as a **third** strategy among deep-sea fishes. Handrick (1901) reported a few, small neuromasts on the head of Argyropelecus hemigymnus. Marshall (1954) indicated superficial neuromasts are small in hatchetfishes and that the LL system is not as developed as in myctophids. Few descriptions of the LL system are available for any other stomiiform fishes (i.e. Yamanaka et al, 2010; Marshall1954). Osteology of hatchetfishes (*Argyropelecus:* Sternoptychidae) and bristlemouths (*Cyclothone:* Gonostomatidae) do reveal extreme bone reduction, with no obvious cranial LL canals (Fig. 2 A-B).

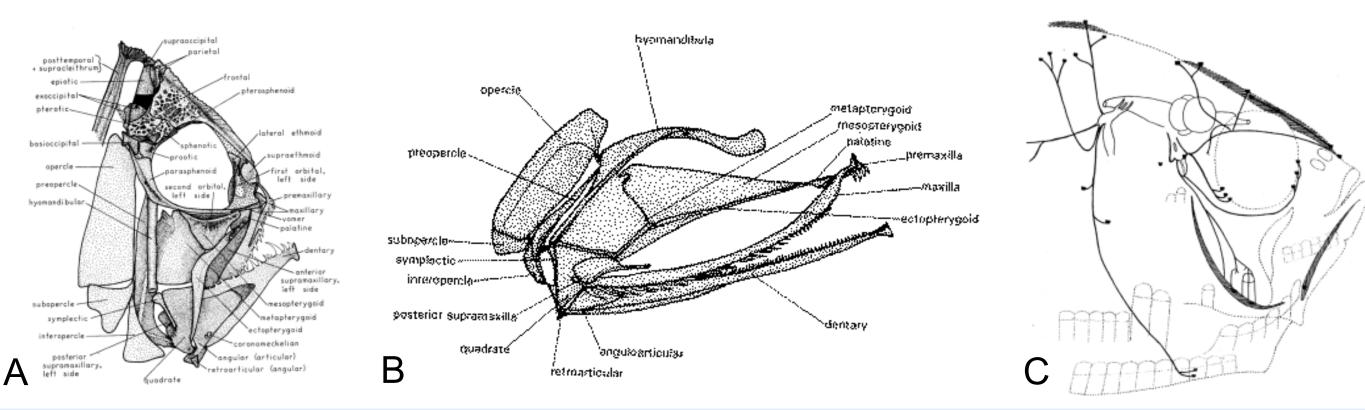


Figure 2: Osteology of A) Argyropelecus aculeatus (from Weitzman, 1974) and B) Cyclothone acclinidens reveals extreme bone reduction, including bones associated with LL canals, and show no obvious canals (from Harold, 1998). C) Innervation of LL organs in Argyropelecus hemigynus shows few, small neuromasts on the head (Handrick, 1901).

This study provides the first descriptions of the LL system of representatives of two prominent stomiiform taxa (Argyropelecus and *Cyclothone*) to explore a potential alternative strategy for the evolution of the LL system in the deep sea.

Methods

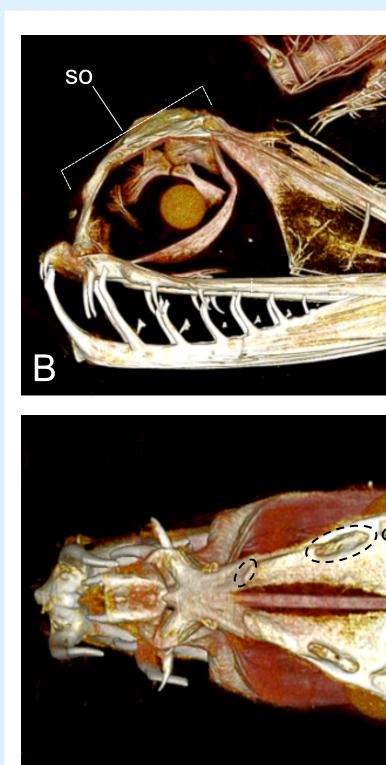
LL morphology was examined using clearing and staining (Pothoff, 1984) and/or µCT to determine presence or absence of cranial LL canals in Aristostomias tittmanni, Argyropelecus aculeatus, A. lynchnus, and *Cyclothone* spp. Meyer's hematoxylin was used to stain *Cyclothone* spp. to identify the location of superficial neuromasts. Scanning electron microscopy (SEM) was used to examine skin for the presence of superficial neuromasts in Argyropelecus spp., Cyclothone spp., and Bathophilus filifer. Specimens used were from the Webb Lab and Seibel Lab collections (identified by ANM) and the Ichthyology Department at the Museum of Comparative Zoology, Harvard University.

The Lateral Line System of Deep-Sea Fishes: Preliminary Observations on Stomiiform Fishes Ashley N. Marranzino¹ and Jacqueline F. Webb^{1,2}

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A Stomiid with LL Canals

Figure 3: LL canals in Aristostomias. A) Aristostomias sp. (from Morrow, 1964, FNWA). B-E are µCT images of *A. tittmanni* (MCZ163949). B) lateral view indicating supraorbital (so) LL canal confirming the description by Fink (1985). C) Dorsal view (same individual as in B shows bilateral supraorbital canal in the frontal bone (outlined by dashed circles). D) Rostral view shows bilateral supraorbital canals in the frontal bones, with a pore indicated by white arrow. E) µCT slice of the head shows (at the level of the orbits) the supraorbital (so). No other definitive LL canals were visualized.



Sternoptychidae: Argyropelecus

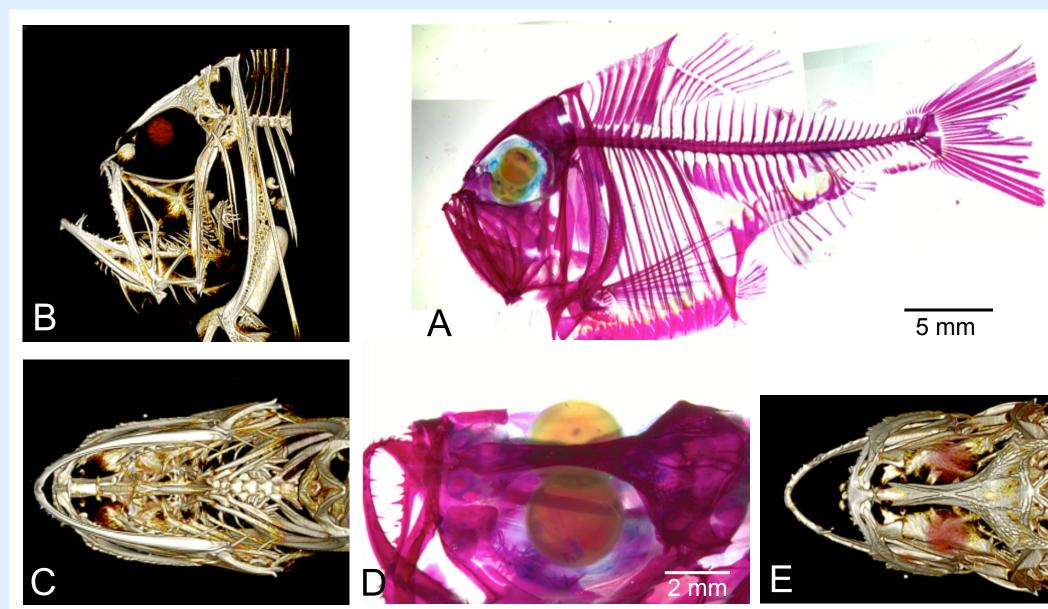
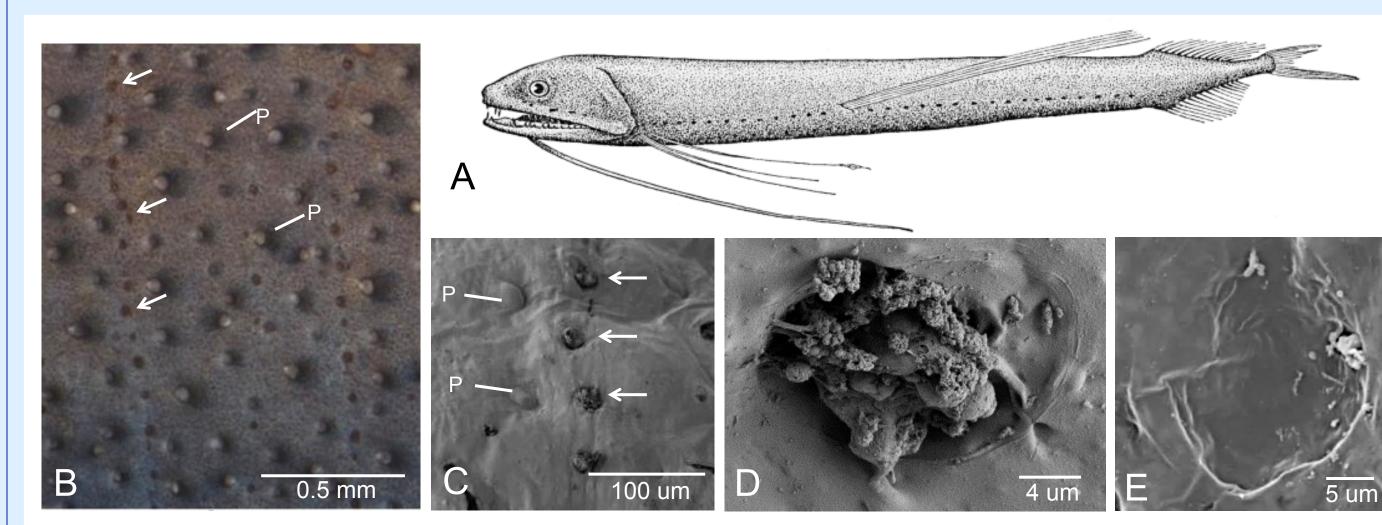


Figure 5: Putative superficial neuromasts on head and body of Argyropelecus affinis (specimen from Seibel Lab). A) Dorso-lateral view shows the dorsal ridge formed by the frontal bones between the orbits. B) close up of black box in A reveals putative superficial neuromasts that appear as opaque white bumps on the surface of the skin in fixed specimens, and are arranged in rows on the head and body. C-D) putative superficial neuromasts around the nares (C) and below the eye (D). E) Schematic representation of locations of putative superficial neuromasts (red dots, not to scale, homologies uncertain) based on one specimen of A. affinis, superimposed on image of A. affinis from Schultz (1961). The location of some of the neuromasts in E correspond to the locations of those illustrated by Handrich (1901) shown in Figure 2C. Similar structures have been noted in the same locations in another individual of A. affinis (Seibel Lab specimen) and several individuals of *A. aculeatus* (MCZ specimens).

Stomiidae: Bathophilus



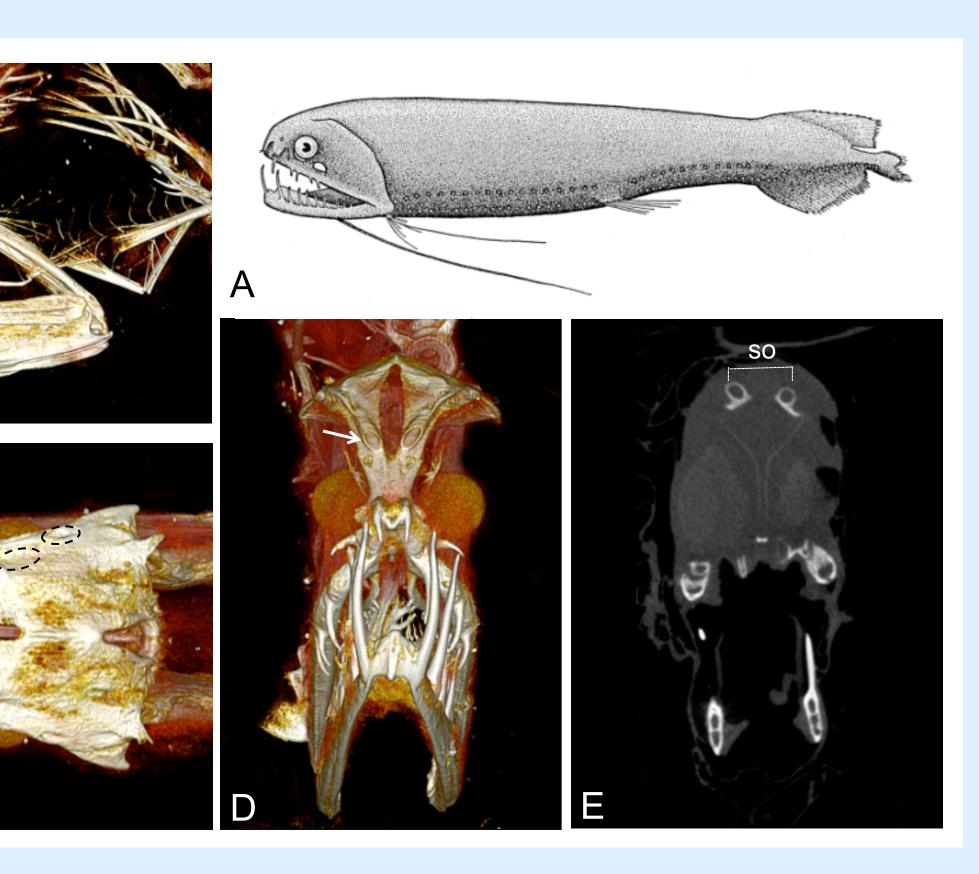
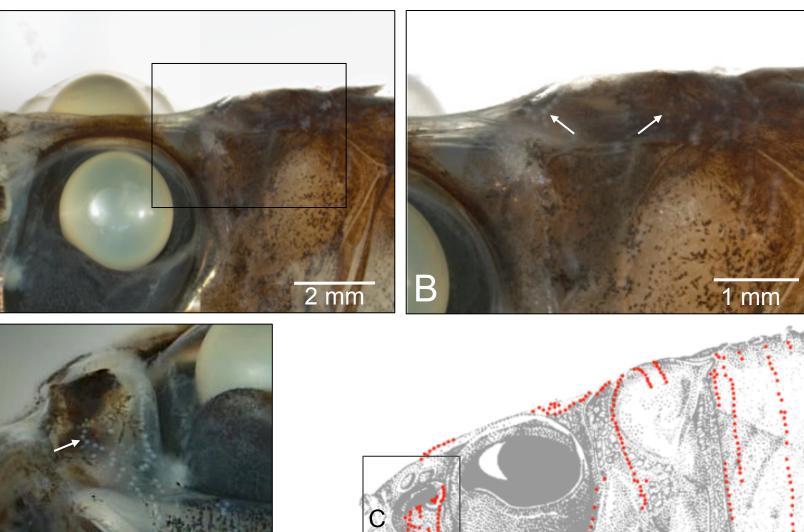
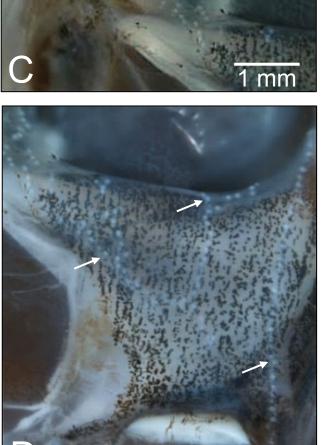


Figure 4: Cranial osteology of *Argyropelecus*. A) Cleared and stained A. lychnus (with gill arches removed) reveals no LL canals. μ CT images of A. aculeatus (MCZ 137835) in B) lateral and C) ventral views. Both indicate the absence of cranial LL canals. No tubular supraorbital canal is present, a bony ridge is formed by the frontal bones that meet between the orbits as illustrated in D (cleared and stained A. lychnus) and E (µCT of *A. aculeatus*).







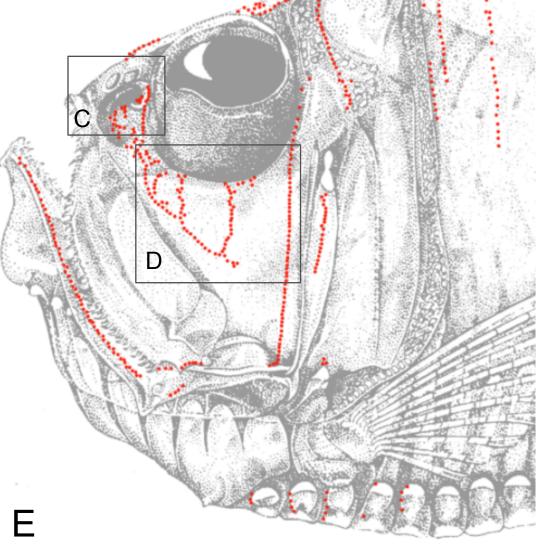


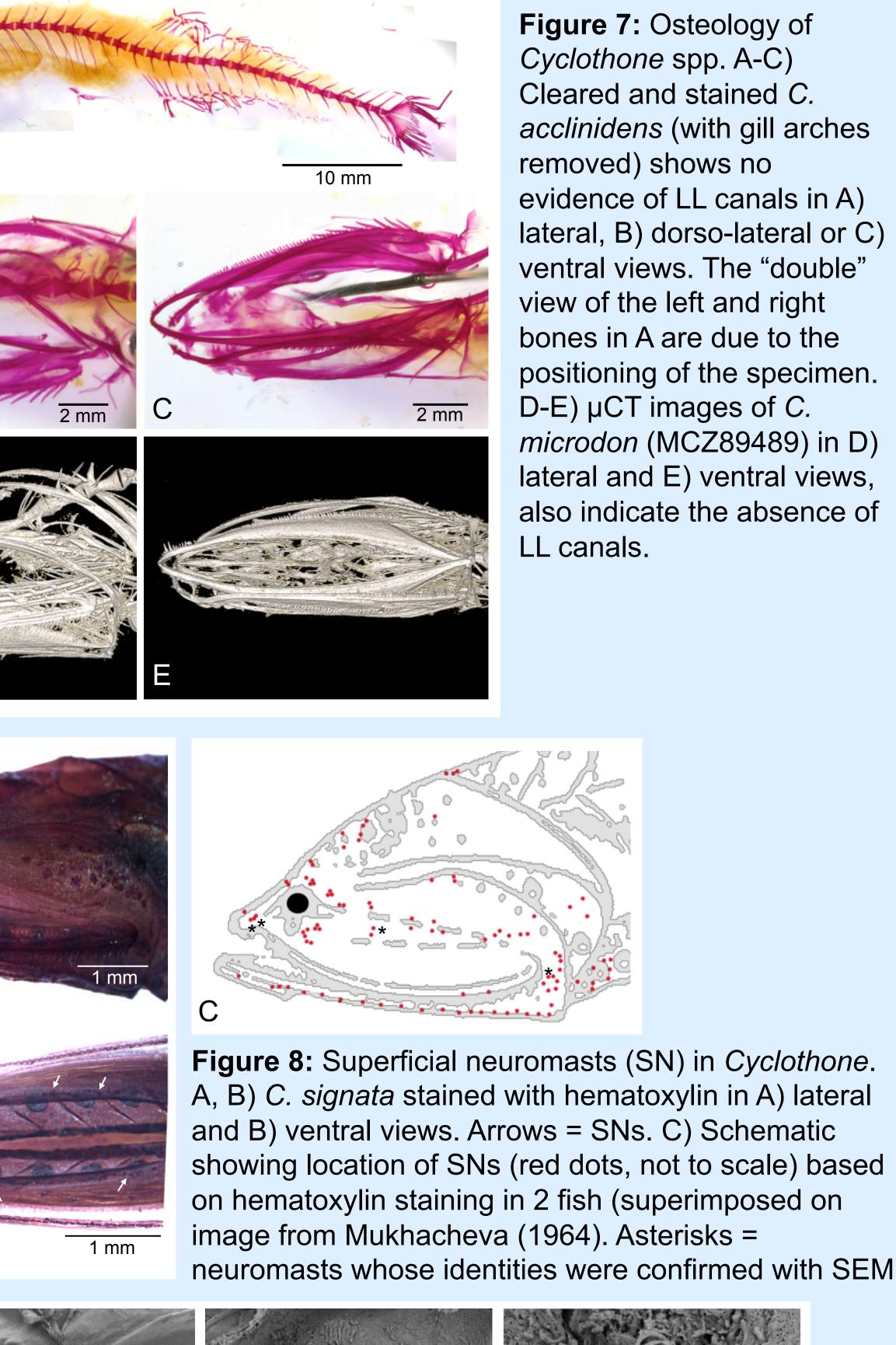
Figure 6: Skin of *Bathophilus* spp. A) Bathophilus sp. (Morrow and Gibbs, 1964, FWNA). B) Photograph of skin of *B. filifer,* which is covered by photophores (P) and vertical rows of unidentified organs (white arrows), thought to be neuromasts. C) SEM of skin showing photophores (P) and unidentified organs (white arrows). D-E) Close-up SEM's of unidentified organs covered in what was thought to be cupula or with a clean surface, with no hair cells visible, thus refuting their identity as neuromasts.



1) The presence of cranial LL canals in *Aristostomias* (as a representative stomiid) was confirmed. 2) Argyropelecus spp. and Cyclothone spp. do not have cranial LL canals. Putative SN's (white bumps) appear to be proliferated in Argyropelecus and Cyclothone, and occur in either dense lines or in less dense lines and clusters, respectively. SEM confirmed the identity of neuromasts in *Cyclothone*. This first description of the LL system in these fishes demonstrates that they do not exhibit the third hypothesized strategy for LL evolution in the deep sea. 3) The skin of *Bathophilus* is covered with photophores and what were thought to be SN's in vertical rows. However, SEM demonstrates that these structures are not neuromasts and their identity is still in question.

Acknowledgements: We thank Dr. Chris Kenaley for CT imaging and to Ben Sevey for reconstructing the CT images. We thank Dr. Nathan Bird for his help and advice on specimen preparation. We thank Louis Kerr, Everett Crisman, and Mike Platek for their SEM expertise and Dr. Brad Seibel for specimens and Karsten Hartel (Museum of Comparative Zoology, Harvard) for specimen loans. Funded by NSF Graduate Research Fellowship to ANM.

Gonostomatidae: Cyclothone



Cyclothone spp. A-C) Cleared and stained *C*. acclinidens (with gill arches removed) shows no evidence of LL canals in A) lateral, B) dorso-lateral or C) ventral views. The "double" view of the left and right bones in A are due to the positioning of the specimen. D-E) µCT images of C. *microdon* (MCZ89489) in D) lateral and E) ventral views, also indicate the absence of LL canals.

Figure 9: SEM's of Cyclothone braueri. A) Lateral view of region above upper jaw. Arrow denotes a neuromast. B) Enlargement of neuromast in A, which appears to have a diamond shape. C) Enlargement of B showing hair cells (double arrow = orientation).

