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INTRODUCTION

Bioluminescent organs in fishes that produce ventral camouflage against a background of downwelling light are very common, yet their anatomy often is poorly understood (Hastings, 1971; Young & Roper, 1976). Camouflage via ventral bioluminescence has evolved at least seven times within a wide range of teleosts (Haddock et al., 2010; Davis et al., 2014, 2016) and they vary greatly in the anatomical structures that form them (Haygood et al., 1994; Chakrabarty et al., 2011; Ghedotti et al., 2015, 2018).

The luminous roughies (genus *Aulotrachichthys*) have a light organ in the region of the anus that houses lumiescent bacteria in the genus *Photobacterium*. Kuwabara (1955) and Haneda (1957) discuss the anatomy and function of the bioluminescent organ in *A. prosthemius* noting that it contained *Photobacterium* in **lobules in an area around the anus** (Fig. 1) and a light conducting structure they called the **"unknown" structure** or the **filiform body** respectively.

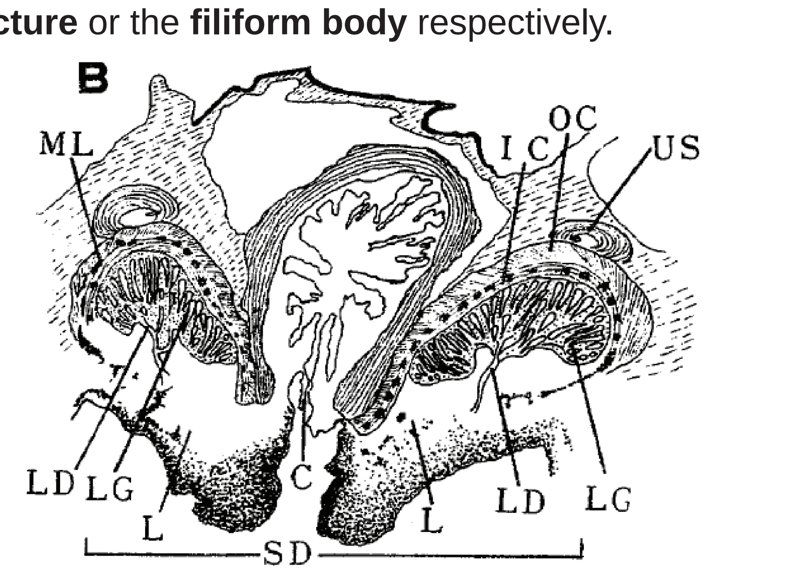

Figure 1. Kuwabara's (1955: Fig. 2B) depiction of the *A. prosthemius* bioluminescent organ. C=anus, IC=inner capsule, L=lens, LD=luminous duct, LG=luminous gland, ML=chromatophore, OC=outer capsule, SD=scaleless depression, US=unknown structure.

We seek to determine more specifically the **structure of the bioluminescent organ in *A. prosthemius*** and determine **if *Paratrachichthys*, a closely related genus, is similarly bioluminescent.** We also generate a **phylogeny to better understand the evolution of bioluminescence** in the Family Trachichthyidae.

METHODS

All specimens were obtained from the Bell Museum of Natural History (JFBM) or the Field Museum of Natural History (FMNH).

GROSS EXAMINATION. We conducted gross dissections of ethanol-preserved specimens of *Aulotrachichthys prosthemius*, *Paratrachichthys fernandezianus*, *Anoplogaster cornuta*, *Hoplostethus atlanticus*, and *Diretmus argenteus*.

HISTOLOGY. Paraffin sections were prepared by dehydration in an ethanol series followed by xylene clearing, embedding in paraffin, sectioning on a rotary microtome at 10 μm, and mounting sections on slides. We stained using Masson's trichrome (MT) and hematoxylin-eosin staining protocols. Slides were examined and photographed using a Leica DM 2500 compound microscope and attached imaging system.

PHYLOGENY. We explored the distribution of bioluminescence using published DNA-sequence (Near et al., 2013; Betancur et al., 2017) and morphological data (Kotlyar, 1992; Moore, 1993) to generate a phylogeny using maximum-likelihood methods.

RESULTS

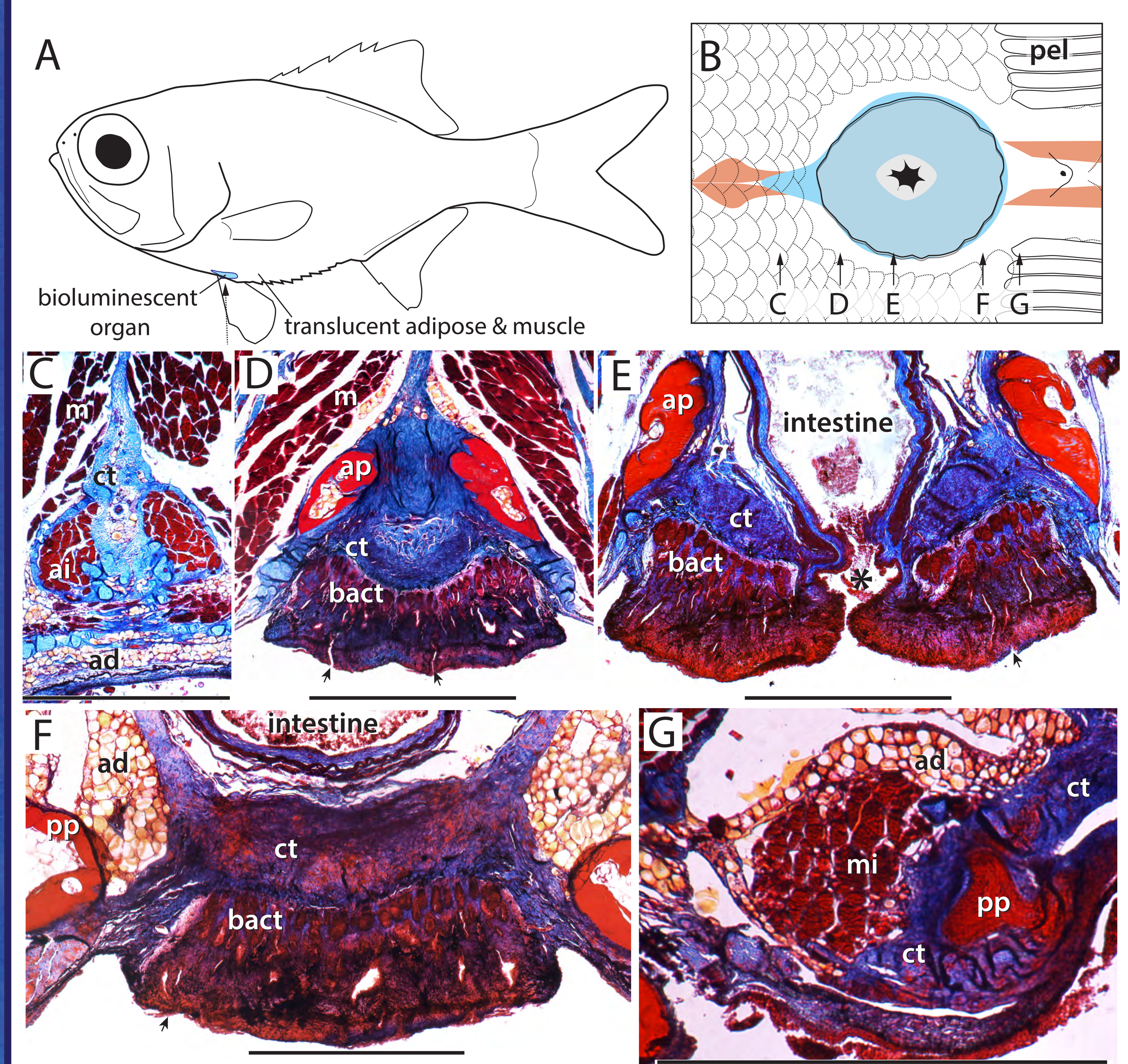

Figure 2. ***Paratrachichthys fernandezianus,*** FMNH 107298; MT. (**A**) Location of bioluminescent organ. **Arrow** indicates anus position. (**B**). Anal region with blue shading indicating bioluminescent organ position. Orange = infracarinalis muscles. Letters indicate approximate positions of subsequent cross section in (**C**)–(**G**). (**G**) Cross section of left anterior-most middle infracarinalis muscle. Scale bars indicate 1 mm.

ABBREVIATIONS: ✱ = anus; ➤ = external opening of duct from *Photobacterium* lobules; **ad** = adipose tissue; **ai** = anterior infracarinalis muscle; **ap** = anterior process of pelvic girdle; **bact** = *Photobacterium* containing lobules; **m** = hypaxial body-wall muscle; **mi** = middle infracarinalis muscle; **pel** = pelvic fin; **pp** = posterior process of pelvic girdle; **pfb** = posterior filiform body, transparent muscle; **ug** = urogenital opening.

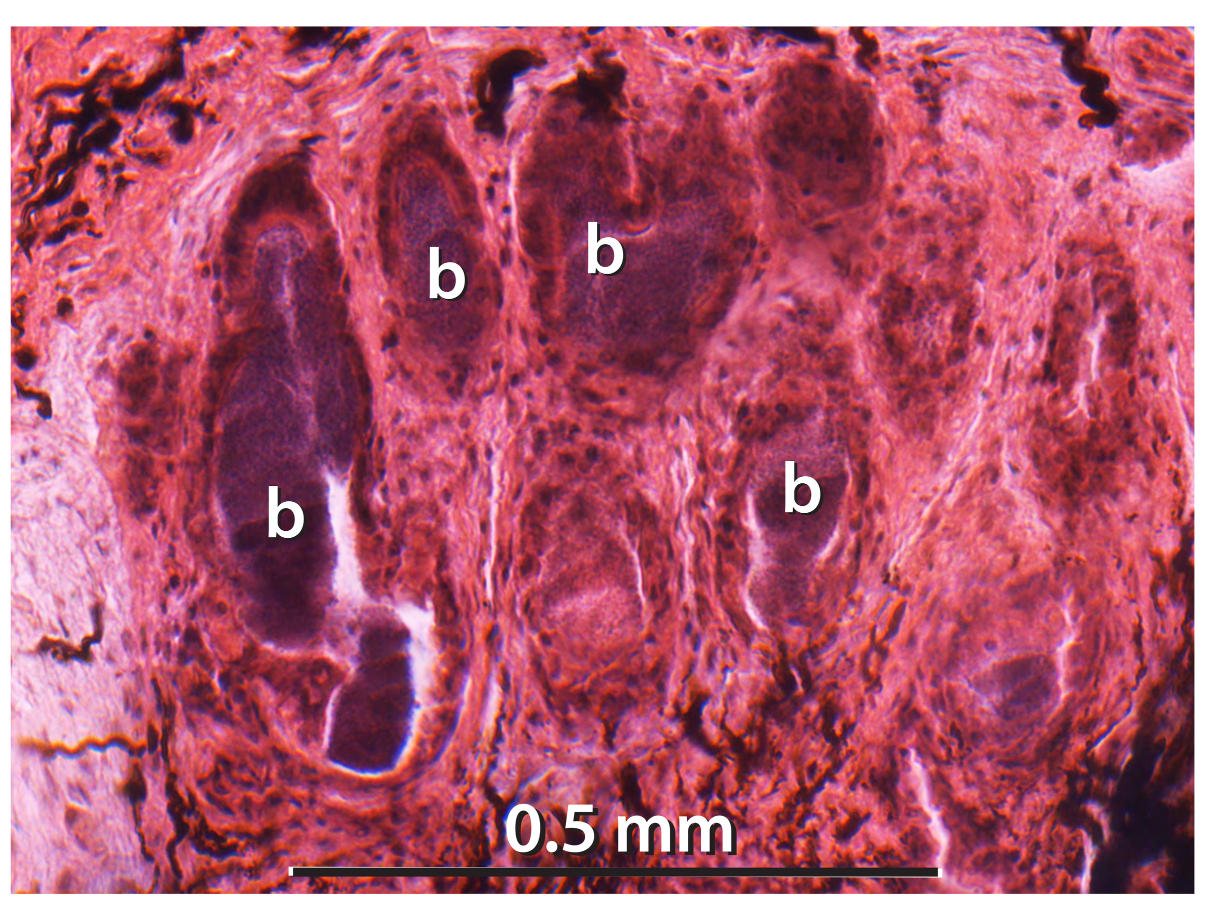

Figure 3. ***Paratrachichthys fernandezianus,*** FMNH 107298; H&E. *Photobacterium*-containing lobules from region posterior to anus. The H&E stain increases bacterial cell contrast.

ABBREVIATIONS: **b** = *Photobacterium* cells surrounded by a cuboidal epithelium.

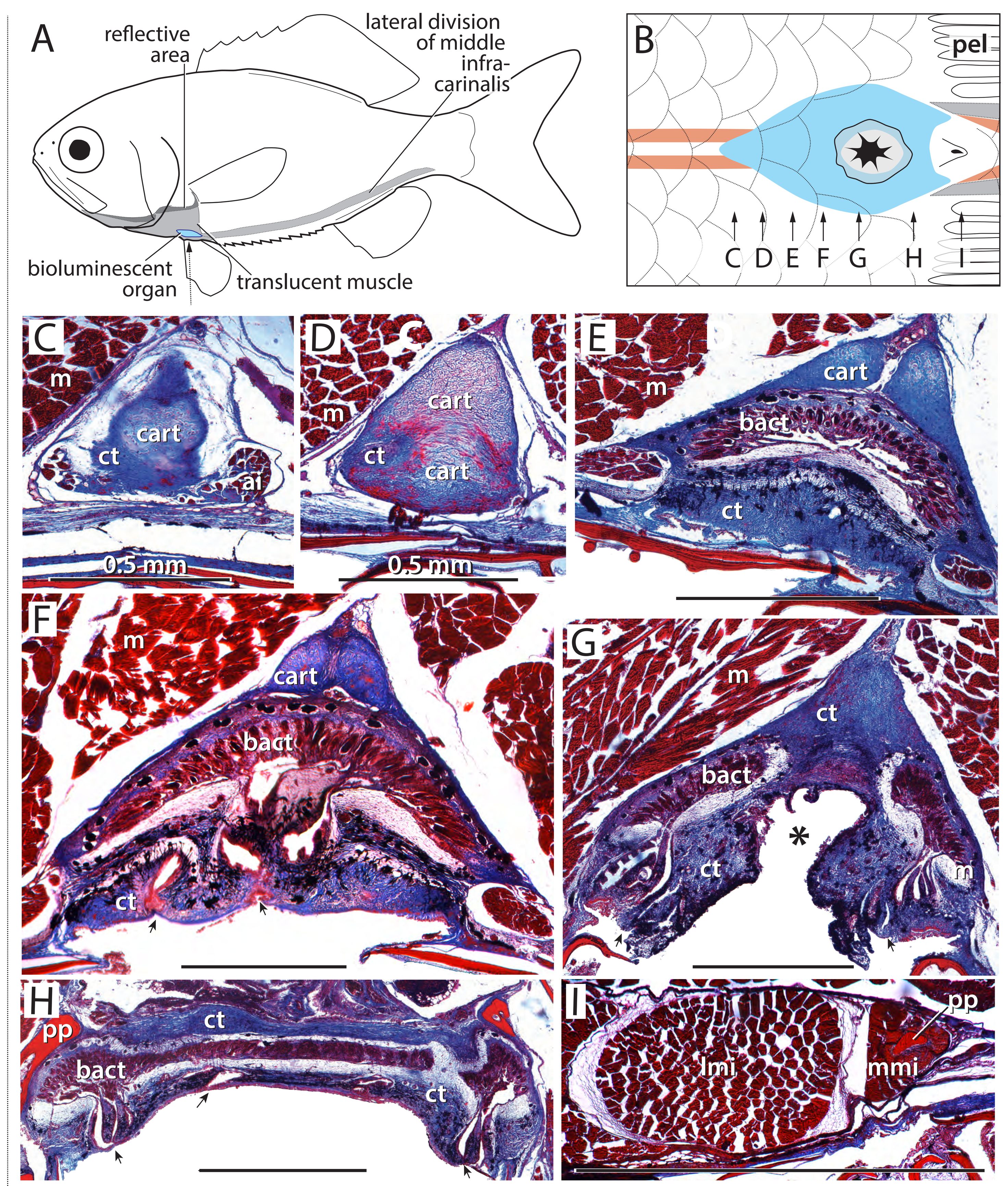

Figure 4. ***Aulotrachichthys prosthemius,*** JFBM 48165; MT. (**A**) Location of bioluminescent organ. **Arrow** indicates anus position. (**B**). Anal region with blue shading indicating bioluminescent organ position. Orange = infracarinalis muscles with original function. Gray with dashed border = lateral division of middle infracarinalis muscle. Letters indicate approximate positions of subsequent cross section in (**C**)–(**G**). (**G**) Cross section of left anterior-most middle infracarinalis muscle showing two divisions and posterior process of pelvic girdle.

ABBREVIATIONS: Same as Figure 2 with the following additions. **cart** = cartilage; **lmi** = lateral division of middle infracarinalis muscle (≈ "unknown" structure and filiform body of prior authors); **mmi** = medial division of middle infracarinalis muscle.

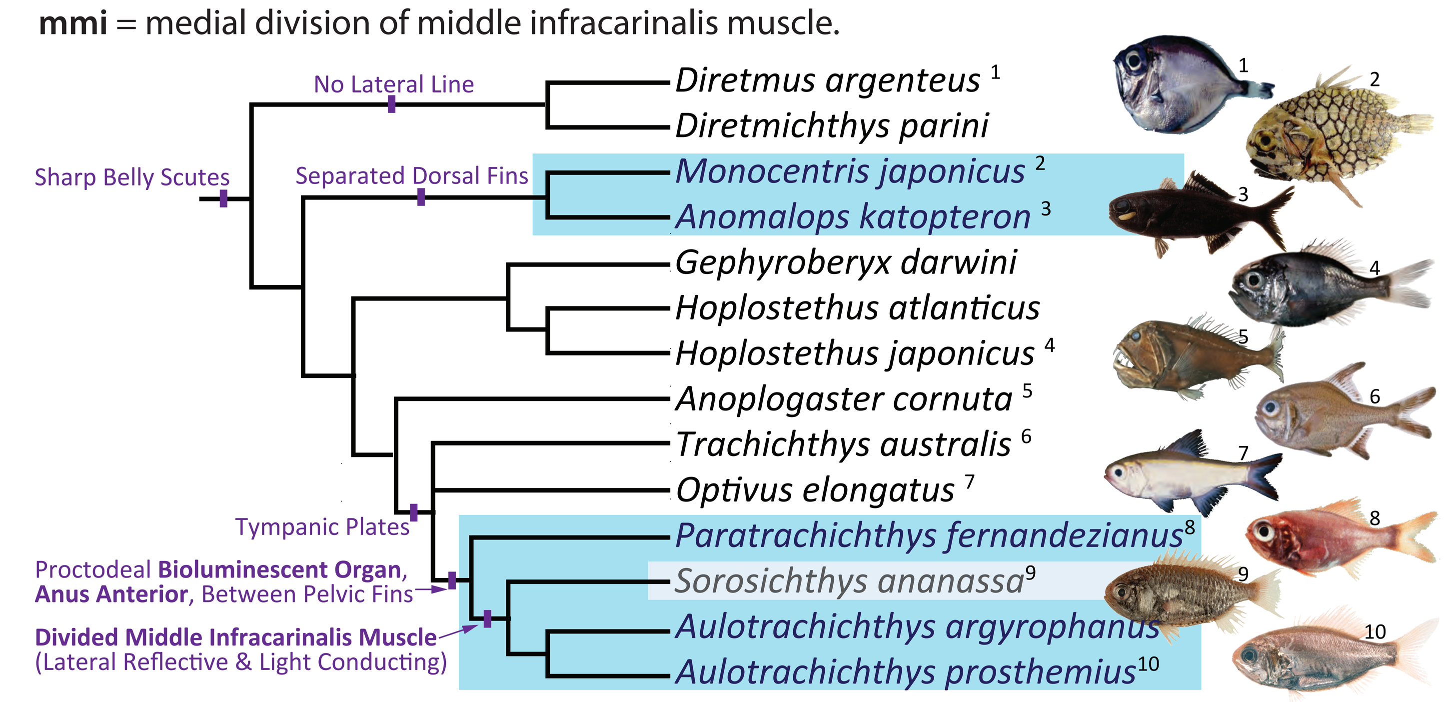

Figure 5. Phylogeny of trachichthyoids based on maximum-likelihood analysis of prior published DNA-sequence and anatomical data. Selected anatomical characters indicated. Blue indicates known bioluminescent taxa (*Sorosichthys* luminescence unknown).

CONCLUSIONS

- *Paratrachichthys,* like *Aulotrachichthys,* is bioluminescent with a bioluminescent organ (LO) with lobules containing *Photobacterium* lined by a simple cuboidal to squamous epithelium (Figs. 2-4).
- The light-producing components of the LO are proctodeum derived, not intestine derived *contra* Nealson & Hastings (1979), and are continuous with the perianal epidermis via a series of individual perianal ducts in *Paratrachichthys* and multiply joining ducts in *Aulotrachichthys* (Figs. 2E,4G).
- In *Paratrachichthys* the LO is immediately under the swolen anal rim on which the ducts from the bacterial lobules form openings (Fig. 2D-F). In *Aulotrachichthys* the LO is is more proximal within the body wall (with a smaller anal rim) and the bacterial-lobule ducts unite and form fewer openings around the anal rim (Fig. 4F-H).
- The LO has an anterodorsal cartilage cap in *Aulotrachichthys* and the LO is connected to the infracarinalis muscles in both genera (Figs. 2C, 4C-F). In *Aulotrachichthys* the middle infracarinalis muscle forms two divisions. The lateral division forms the reflective "unknown" structure found in *Aulotrachichthys* and *Sorosichthys* (Figs. 2G, 4I, 5).
- The phylogeny and LO structure support a single evolutionary origin of the of *Aulotrachichthys* and *Paratrachichthys* LO in the ancestor of this clade (Fig. 5).
- The anterior anus and the reflective "unknown" structure in the rare *Sorosichthys ananassa* (known from 8 specimens) place this species in this LO clade and suggest it may luminesce (Fig. 5).

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