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RESEARCH ARTICLE

Morphology and evolution of bioluminescent organs in the glowbellies (Percomorpha: Acropomatidae) with comments on the taxonomy and phylogeny of Acropomatiformes

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Abstract

Bioluminescent organs have evolved many times within teleost fishes and exhibit a wide range of complexity and anatomical derivation. Although some bioluminescent organs have been studied in detail, the morphology of the bacterial light organs in glowbellies (*Acropoma*) is largely unknown. This study describes the anatomy of the bioluminescent organs in Haneda's Glowbelly (*Acropoma hanedai*) and the Glowbelly (*Acropoma japonicum*) and places the evolution of this light-producing system in the context of a new phylogeny of glowbellies and their relatives. Gross and histological examination of the bioluminescent organs indicate that they are derived from perianal ectodermal tissue, likely originating from the developmental proctodeum, contrary to at least one prior suggestion that the bioluminescent organ in *Acropoma* is of endodermal intestinal derivation. Additionally, anterior bioluminescent organ development in both species is associated with lateral spreading of the bacteria-containing arms of the bioluminescent organ from an initial median structure. In the context of a 16-gene molecular phylogeny, the bioluminescent organ in *Acropoma* is shown to have evolved within the Acropomatidae in the ancestor of *Acropoma*. Further, ancestral-states reconstruction demonstrates that the bioluminescent organs in *Acropoma* evolved independently from the light organs in related howellid and epigonid taxa which have esophageal or intestinally derived bioluminescent organs. Across the acropomatiforms, our reconstructions indicate that bioluminescent organs evolved independently four or five times. Based on the inferred phylogeny of the order where *Acropoma* and *Doederleinia* were separated from other traditional acropomatids, the familial taxonomy of the Acropomatidae was modified such that the previously described Malakichthyidae and Synagropidae were recognized. We also morphologically diagnose and describe the family Lateolabracidae.

KEYWORDS

Acropoma, bioluminescence, deep sea, histology, Lateolabracidae, Malakichthyidae, perianal, *Photobacterium*, proctodeum, Synagropidae

1 | INTRODUCTION

Detailed consideration of unique anatomical structures in their phylogenetic context provides a means to understand the evolution of morphological complexity. Bioluminescent organs in fishes are particularly interesting because they necessarily exhibit complexity in their ability to emit light in a controlled manner and have evolved at least 27 times within teleost fishes (Davis, Holcroft, Wiley, Sparks, & Smith, 2014; Davis, Sparks, & Smith, 2016; Haddock, Moline, & Case, 2010). Given the large number of independent evolutionary origins of bioluminescence, the comparison of bioluminescent organs to putative homologous structures in related nonbioluminescent species allows insight into the anatomical origin of these specialized structures.

Bioluminescent organs in fishes are particularly diverse in their structure and anatomical derivation. Intrinsic bioluminescent organs that produce light directly may be evolutionarily and developmentally

derived from integumentary, intestinal, muscle, or hepatopancreatic tissues (Ghedotti, Barton, Simons, & Davis, 2015; Johnston & Herring, 1985; Wassersug & Johnson, 1976), whereas bioluminescent organs that emit light via symbiotic bacteria have a more limited range of developmental origin, typically being restricted to structures contacting or closely associated with the external environment. Lineages of fishes that use their intrinsic or bacterially mediated bioluminescent organs for communication and sexual selection also have significantly increased rates of speciation relative to other lineages of bioluminescent fishes that primarily use light for camouflage (Davis et al., 2014, 2016). Symbiotic bioluminescence has evolved more frequently in teleost fishes than intrinsic bioluminescence, 17 of the estimated 27 times (Davis et al., 2016). Bacterial bioluminescent organs are derived from in-folding of a wide range of ectodermal or endodermal epithelial tissues contiguous with the external surface or the digestive tract (Chakrabarty et al., 2011; Davis et al., 2016; Johnson & Rosenblatt, 1988; Thacker & Roje, 2009).

The light organs of the members of the genus *Acropoma* have a structure that is somewhat typical of bacterial bioluminescent organs, but previous work has only generally described and figured these organs (Haneda, 1950; Matsubara, 1953; Thacker & Roje, 2009). Haneda (1950, figures 1 and 2) figured the extent of the light organs in *A. japonicum* and *A. hanedai* and noted that they are compartmentalized, are embedded in the transparent ventral body-wall muscle tissue through which light travels to provide camouflaging ventral counter illumination, have a medial cavity or duct, and connect to the exterior in the region of the anus. The left and right arms of the organs were depicted as connecting across the midline at the most anterior point and separate across the midline at the most posterior point in *A. japonicum*, with the inverse true in *A. hanedai* in which the bioluminescent organs also extend much further anterior and posterior (Haneda, 1950). Thacker and Roje (2009), figure 2F published a histological section of the bioluminescent organ of an unidentified species of *Acropoma* and noted that the organ had a folded epithelium rather than being composed of tubules.

The genus *Acropoma* is diagnosed, in part, by the presence of a bioluminescent organ that is presumed to provide camouflage via ventral counter illumination through transparent body-wall musculature. The organ varies in extent within the genus with some species having shorter organs as in *A. japonicum* (e.g., *A. argentistigma*, *A. lecorneti*) and other species with longer bioluminescent organs as in *A. hanedai* (e.g., *A. boholensis*, *A. neglectum*; Okamoto & Golani, 2018). However, only the general presence and extent of the organ has been documented for other species in the genus (Fourmanoir, 1988; Okamoto, 2014; Okamoto & Golani, 2018; Yamanoue & Matsuura, 2002).

Knowing which fish groups are most closely related to *Acropoma* is critical for exploring the evolution of their bioluminescent organ. Until recently, the phylogeny of the percomorph fishes, the crown group of ~17,000 fish species, was poorly known. Recent large-scale studies have begun the process of clarifying the relationships of these fishes including a novel placement for species of *Acropoma* among several deep-sea or reef percomorph groups (Davis et al., 2016; Near et al., 2013, 2015; Sanciangco, Carpenter, & Betancur-R, 2016; Thacker et al., 2015). This hypothesis differs from their traditional treatment as a "lower percoid" group that was allied with taxa ranging from the cardinalfishes in the Apogonidae to the sea basses in the Serranidae (e.g., Jordan & Richardson, 1910; Katayama, 1959; Schultz, 1940).

All molecular or molecular and morphological combined studies that have included multiple genera of acropomatids have recovered the family as polyphyletic (Betancur-R, Broughton, et al., 2013; Davis et al., 2016; Mirande, 2017; Near et al., 2013, 2015; Rabosky et al., 2018; Sanciangco et al., 2016; Smith & Craig, 2007; Thacker et al., 2015) except for Lautredou et al. (2013). The polyphyly of the Acropomatidae is consistent with morphological studies that have noted, "I know of no synapomorphy that unites the acropomatids, and further work will be necessary to test their monophyly" (Johnson, 1984, p. 464) or Schwarzhans and Prokofiev (2017) who have highlighted the group's uncertain monophyly and suggested that it may contain multiple independent clades.

Despite the lack of evidence for the monophyly of the family and the nearly universal polyphyly of the traditional Acropomatidae, molecular studies have recovered all traditional acropomatids together in a larger group with many other families that has either been referred to as the Acropomatiformes (Davis et al., 2016; Smith, Stern, Girard, & Davis, 2016) or Pempheriformes (Betancur-R et al., 2017; Rabosky et al., 2018; Sanciangco et al., 2016). The composition of this acropomatiform clade has varied across studies (Bentancur-R, Broughton, et al., 2013; Davis et al., 2016; Near et al., 2015; Rabosky et al., 2018; Sanciangco et al., 2016; Smith & Craig, 2007; Smith & Wheeler, 2006; Thacker et al., 2015; Tsunashima et al., 2016), and the relationships among component acropomatiform families have differed tremendously. Six of these studies have included *Acropoma*, and it has been recovered as sister to Ostracoberycidae (Davis et al., 2016; Near et al., 2015; Thacker et al., 2015), Howellidae + Ostracoberycidae (Near et al., 2013; Sanciangco et al., 2016), or Symphysanodontidae (Rabosky et al., 2018), but these sister-group relationships for *Acropoma* have either lacked support or have been poorly supported in all of these studies (bootstrap support across all studies was <70%). Therefore, a focused examination of acropomatiform phylogeny is necessary to understand the evolution of the bioluminescent organ in *Acropoma*.

In this study, we seek to clarify the detailed anatomical structure and likely embryological derivation of the bioluminescent organ in *Acropoma japonicum* and *A. hanedai*. In addition, we address the hypothesis that the bioluminescent organs in species of *Acropoma* represent an independent evolution of a bioluminescent organ by comparing the anatomical structure of the described bioluminescent organs and the phylogenetic relationships of bioluminescent acropomatiforms and allies using a DNA-sequence data set.

2 | MATERIALS AND METHODS

2.1 | Morphological examination

The relative paucity of deep-sea specimens in museum collections limited the number of specimens available to be dissected and/or sampled histologically. We conducted dissections using museum-cataloged specimens that were previously formaldehyde-fixed and ethanol-preserved from the Field Museum of Natural History

(FMNH), Chicago, IL and the University of Minnesota Bell Museum of Natural History (JFBM), St. Paul, MN. Gross examination in the coelom was facilitated by making a right ventral parasaggital cut into the coelom from immediately anterior to the anus and continuing anteriorly to the isthmus, angling dorsolaterally in the vicinity of the pelvic girdle. The body wall was reflected to allow examination of the ventral body wall. Gross examination of the right bioluminescent organ or the median bioluminescent organ embedded in the body wall muscle was conducted by removing the overlying skin and then separating muscle masses using fine forceps to reveal the bioluminescent organ. Once identified, microdissection forceps were used to follow the organ by spreading muscle tissue and removing enough of the overlying muscle to allow viewing. We examined and photographed specimens using a Leica MZ 12.5 stereomicroscope (Leica Microsystems, RRID: SCR_008960) with an attached Q Imaging MicroPublisher 5.0 RTV photodocumentation system (Q Capture Software, RRID: SCR_014432). For the related acropomatiform specimens examined (i.e., species not classified in *Acropoma*), coelomic dissection and a simple cut through the ventral body wall were used to determine if previously undocumented bioluminescent organs were present. We conducted gross dissection and examination of ethanol-preserved museum specimens (see Specimens Examined section) at Regis University, Denver, CO.

2.2 | Histological analysis

We prepared histological samples from museum-cataloged specimens that were previously formaldehyde-fixed and ethanol-preserved from JFBM. We prepared histological samples via dissection of approximately 0.5–1 cm^3 from the ventral body wall approximately 2 cm anterior to the anus, around the anus, and approximately 2 cm posterior to the anus from a 127 mm standard length (SL) individual of *Acropoma japonicum* (JFBM 48680) and a 120 mm SL individual of *A. hanedai* (JFBM 48733). Additionally, we prepared a whole 43 mm SL individual of *A. japonicum* (JFBM 48680) and a whole 51 mm SL individual of *A. hanedai* (JFBM 48733) for sectioning.

We decalcified acropomatid samples in a 20% formic acid, 1.9% formaldehyde solution for 5 days (samples removed from larger specimens) to 2 weeks (whole small individuals) followed by dehydration in an ethanol series to 100% and clearing in xylene. We sectioned specimens embedded in paraffin every 10 μm using a rotary microtome and mounted the sections on slides (Humason, 1979). The Masson's trichrome (MT) staining protocol (Bancroft & Stevens, 1982; Sheehan & Hrapchak, 1980) was used to assist in differentiating collagen-containing tissues. We conducted all histological procedures at Regis University, Denver, CO. We examined and photographed slide-mounted sections using a Leica DM 2500 compound microscope (Leica Microsystems, RRID:SCR_008960) with an attached Q Imaging MicroPublisher 5.0 RTV photodocumentation system (Q Capture Software, RRID:SCR_014432).

2.3 | Specimens examined

All work used preserved and cataloged museum specimens, did not involve live animals or euthanasia of animals, and complied with the laws of the United States (where it was performed). Museum abbreviations follow Sabaj (2016). Asterisks follow catalog numbers for specimens used in histological sectioning. Numbers in parentheses are the number of specimens examined in the lot. Specimens in the listed lots were examined and, when not previously dissected, were dissected to permit examination. **Acropomatidae:** *Acropoma hanedai* FMNH 120390 (3), JFBM 48681 (10), JFBM 48733 (9), JFBM 48743 (4); *Acropoma japonicum* FMNH 120943 (2), JFBM 48680 (6), JFBM 48707 (8); *Doederleinia berycoides* FMNH 57378 (1), FMNH 120946 (2). **Epigonidae:** *Epigonus occidentalis* FMNH 67460 (4); "*Epigonus*" *pandionis* FMNH 67481 (2), FMNH 121740 (2). **Howellidae:** *Howella simplex* JFBM 48686 (2). **Lateolabracidae:** *Lateolabrax japonicus* FMNH 55546 (2). **Malakichthyidae:** *Malakichthys griseus* FMNH 120948 (3); *Malakichthys wakiyae* JFBM 48682 (4); *Neoscombrops pseudomicrolepis* FMNH 65090 (2). **Pempheridae:** *Parapriacanthus ransonneti* FMNH 119258 (4); *Pempheris schomburgki* FMNH 93774 (3). **Synagropidae:** *Parascombrops phillippinensis* JFBM 48684 (3); *Parascombrops spinosus* FMNH 46426 (2); *Synagrops bellus* FMNH 65100 (2); *Synagrops japonicus* JFBM 48705 (4).

2.4 | Taxon sampling for phylogenetic analysis

The resulting hypotheses of percomorph relationships were rooted using the mugiliform, *Agonostomus*, following the results of Wainwright et al. (2012), Betancur-R, Broughton, et al. (2013), and Near et al. (2012) that consistently found this order outside of the crown percomorph clade that includes the Acropomatiformes. Six additional nonacropomatiform outgroups were included in the analysis from the Centrarchidae, Drepanidae, Gerreidae, Labridae, Percidae, and Serranidae (Supporting Information Table 1). Forty ingroup terminals were analyzed, including representatives of all putative acropomatiform (=pempheriform) families (sensu Betancur-R et al., 2017) except the Champsodontidae and Leptoscopidae (Supporting Information Table 1). These 40 ingroup taxa include the Dinolestidae following Smith and Craig (2007) and Scombropidae following Tsunashima et al. (2016) in contrast with Betancur-R et al. (2017) who included the Dinolestidae in their Eupercaria (*incertae sedis*) and Scombropidae in their Scombriformes. The taxa included in the analysis were chosen to resolve the limits and relationships of the Acropomatidae and to include bioluminescent taxa or representatives of groups exhibiting bioluminescence.

2.5 | Acquisition of nucleotide sequences for phylogenetic analysis

Fish tissues were preserved in 70–95% ethanol prior to extraction of DNA. Genomic DNA was extracted from muscle or fin clips using a DNeasy Tissue Extraction Kit (Qiagen, RRID:SCR_008539) or the Maxwell® RSC Whole Blood DNA Kit (Promega, RRID:SCR_006724) following the manufacturers' extraction protocols (except the replacement of the blood DNA kit's lysis buffer with Promega's tissue lysis buffer). For high-throughput sequencing, Qiagen extractions were dried down with a DNA SpeedVac Concentrator (Thermo Fisher Scientific, RRID:SCR_008452) to a 102 μL volume and Promega extractions were eluted into a 102 μL volume. For high-throughput

sequencing, 2 μL of the raw extracts were quantified using a Qubit fluorometer (Life Technologies, RRID:SCR_008817) using the dsDNA BR Assay Kit. Quantified samples were sent to Arbor Biosciences (formerly MYcroarray, Ann Arbor, MI) for library preparation (e.g., DNA shearing, size selection, cleanup), target capture and enrichment, sequencing using an Illumina HiSeq 2,500 (Illumina HiSeq 2500 System, RRID:SCR_016383), and demultiplexing of samples. Raw fastq files from Arbor Biosciences were processed using PHYLUCE 1.5 (Faircloth, 2015). With PHYLUCE, we trimmed reads to remove adapter contamination and low-quality bases using Trimmomatic (Bolger, Lohse, & Usadel, 2014; Trimmomatic RRID:SCR_011848) in a parallel wrapper (https://github.com/faircloth-lab/illumiprocessor). Sequence data from ribosomal and transfer RNA and protein-coding gene fragments were extracted from these Illumina sequence runs. To capture these data, the cleaned reads were compared to existing sequences of close allies for the 16S rRNA, 28S rRNA, tRNA-Val, and protein-coding genes using the "map to reference" functionality in Geneious v8.1.8 (Kearse et al., 2012; Geneious, RRID:SCR_010519) with low-sensitivity and two to five (typically three) iterations to collect homologous DNA-sequence regions. In addition to high-throughput sequencing, PCR was used to amplify seven gene fragments (tRNA-Valine and 5' 16S, 16S, COI, 28S, GlyT, HH3, and RAG1; Supporting Information Table 1). For PCR, double-stranded amplifications were performed in a 25 μL volume containing one Ready-To-Go PCR bead (GE Healthcare, RRID:SCR_00004), 1.25 μL of each primer (10 pmol), and 2–5 μL of undiluted DNA extract. Primers and primer sources are listed in Table 1. Amplifications for all novel fragments except GlyT and RAG1 were performed using the following temperature profile: initial denaturation for 360 sec at 94 °C; 36 cycles of denaturation for 60 s at 94 °C, annealing for 60 s at 46–49 °C (see Table 1 for primary annealing temperature for each locus), and extension for 75 s at 72 °C; with a final terminal extension for 360 s at 72 °C. For GlyT and RAG1, the following temperature profile was used: initial denaturation for 180 s at 94 °C; 10 cycles of denaturation for 45 s at 94 °C, annealing for 45 s at 56–57 °C (see Table 1 for core annealing temperature for each locus), and extension for 75 s at 72 °C; 30 cycles of denaturation for 45 s at 94 °C, annealing for 30 s at 53–56 °C (see Table 1 for secondary annealing temperature for each locus), and extension for 75 s at 72 °C; with a final terminal extension for 360 s at 72 °C. The double-stranded amplification products were desalted and concentrated using AMPure (Beckman Coulter, RRID:SCR_008940). Both strands of the purified PCR fragments were used as templates and amplified for sequencing using the amplification primers and a Prism Dye Terminator Reaction Kit v1.1 (Applied Biosystems, RRID:SCR_005039) with minor modifications to the manufacturer's protocols. The sequencing reactions were cleaned and desalted using cleanSEQ (Beckman Coulter, RRID:SCR_008940). The nucleotides were sequenced and the base pairs were called on a 3,730 automated DNA sequencer (Applied Biosystems, RRID:SCR_005039) or by Beckman Coulter Genomics (Danvers, MA). Contigs for high-throughput and Sanger sequencing were built in Geneious v8.1.8. Sequences were edited in Geneious and collated into fasta text files. The novel sequences were submitted to GenBank (NCBI GenBank via FTP, RRID:SCR_010535) and assigned accession numbers MH807833–MH807928, MH813010–MH813021, MH813289–MH813294, and MH813440–MH813446. All extractions, DNA quantifications for high-throughput sequencing, and PCR

TABLE 1 Primers, primer reference, and PCR conditions for each amplicon sequenced using Sanger sequencing in the current study

Primer name and sequence		Primary annealing temperature (°C)
tRNA-Val and 5′ 16S (Feller & Hedges, 1998; Titus, 1992)		
12SL13-L	5′-TTAGAAGAGGCAAGTCGTAACATGGTA-3′	48
TitusI-H	5′-GGTGGCTGCTTTTAGGCC-3′	48
16S (Kocher et al., 1989; Palumbi, 1996)		
16S ar-L	5′-CGCCTGTTTATCAAAAACAT-3′	48
16S br-H	5′-CCGGTCTGAACTCAGATCACGT-3′	48
COI (Folmer, Black, Hoeh, Lutz, & Vrijenhoek, 1994).		
LCO1490	5′-GGTCAACAAATCATAAAGATATTGG-3′	46
HCO2198	5′-TAAACTTCAGGGTGACCAAAAAATCA-3′	46
28S (Hillis & Dixon, 1991)		
28SV	5′-AAGGTAGCCAAATGCCTCGTCATC-3′	48
28SJJ	5′-AGGTTAGTTTTACCCTACT-3′	48
GlyT (Li, Ortí, Zhang, & Lu, 2007)		
Glyt_F559	5′-GGACTGTCMAAGATGACCACMT-3′	57/55
Glyt_R1562	5′-CCCAAGAGGTTCTTGTTRAAGAT-3′	57/55
HH3 (Colgan et al., 1998)		
H3a-L	5′-ATGGCTCGTACCAAGCAGACVGC-3′	48
H3b-H	5′-ATATCCTTRGGCATRATRGTGAC-3′	48
RAG1 (López, Chen, & Ortí, 2004)		
RAG1-OF2	5′-CTGAGCTGCAGTCAGTACCATAAGATGT-3′	56/54
RAG1-OR2	5′-CTGAGTCCTTGTGAGCTTCCATRAAYTT-3′	56/54

amplifications were conducted at the University of Kansas, Lawrence, KS or the Field Museum of Natural History, Chicago, IL.

2.6 | Character sampling

A total of 11,520 aligned nucleotides from 13 nuclear and three mitochondrial loci were collected. The molecular terminals analyzed in this study and GenBank accession numbers corresponding to the gene fragments sequenced are listed in Supporting Information Table 1. For these analyses, the 94 novel DNA sequences were combined with 436 previously published DNA sequences from the following sources: (Alfaro et al., 2018; Betancur-R, Broughton et al., 2013; Betancur-R, Li, Munroe, Ballesteros, & Ortí, 2013; Bossu, Beaulieu, Ceas, & Near, 2013; Cawthorn, Steinman, & Witthuhn, 2011; Chang et al., 2017; Chen, Ruiz-Carus, & Ortí, 2007; Davis et al., 2016; Dunlap et al., 2007; Durand et al., 2012; Holcroft & Wiley, 2008; Kenchington, Baillie, Kenchington, & Bentzen, 2017; Kimmerling et al., 2018; Li et al., 2014; Li, Ortí, & Zhao, 2010; Near et al., 2011, 2012, 2013, 2015; Near & Keck, 2013; Rabosky et al., 2018; Sanciangco et al., 2016; Satoh, 2018; Satoh, Miya, Mabuchi, & Nishida, 2016; Smith et al., 2016; Smith, Smith, & Wheeler, 2009; Smith & Craig, 2007; Smith & Wheeler, 2004, 2006; Sparks & Smith, 2004; Thacker et al., 2015; Tsunashima et al., 2016; Wainwright et al., 2012; Yagishita et al., 2009; Yamanoue et al., 2007; and 21 unpublished studies). The matrix was 70.4% complete at the amplicon level.

2.7 | Phylogenetic analysis

Partitioned likelihood and Bayesian analysis were used to analyze the molecular data. For these analyses, each of the 16 gene fragments (tRNA-Valine and 5′ 16S, 16S, COI, 28S, ENC1, GlyT, HH3, MYH6, PLAGL2, Ptr, RAG1, SH3PX3, SIDKEY, SREB2, TBR, and ZIC1) was aligned individually in MAFFT v7.017 (Katoh, Misawa, Kuma, & Miyata, 2002; MAFFT, RRID:SCR_011811) using default values. The individual gene fragments were broken into 41 partitions. One partition was designated for the mitochondrial (tRNA-Valine and 5′ 16S, and 16S) amplicons, and one partition was designated for the nuclear (28S) ribosomal DNA amplicon. Thirty-nine partitions covered the three codon positions in each of the 13 protein-coding genes. The separate partitions were submitted to PartitionFinder (Lanfear, Frandsen, Wright, Senfeld, & Calcott, 2016) which selected 31 partition subsets using the AICc and rcluster search method. The preferred molecular models were used in the subsequent phylogenetic analyses (Supporting Information Table 2). The data set was coded, concatenated, examined, and analyzed (ancestral-state reconstructions) in Mesquite v3.2 (Maddison & Maddison, 2017). The maximum-likelihood analysis was conducted in IQ-Tree v1.6.3 (Chernomor, von Haeseler, & Minh, 2016; Nguyen, Schmidt, von Haeseler, & Minh, 2014). The tree with the best likelihood score from 10 independent runs where the numbers of iterations without improvement was increased from the default of 100–500 (–nstop 500) was selected as the preferred hypothesis and is referred to as the optimal maximum-likelihood phylogeny. A nonparametric maximum-likelihood bootstrap analysis was conducted for 100 random pseudoreplicates to assess nodal support for the optimal phylogeny. The Bayesian analysis was conducted in MrBayes 3.2.6 (Ronquist et al., 2012; MrBayes, RRID: SCR_012067). The parameters and tree topologies from four independent Bayesian analyses converged on a stationary distribution and were combined (40 million generations with the initial 16 million generations removed as burnin). A 50% majority-rule tree was generated from the posterior tree distribution (24,000 trees) that were further subsampled down to 100 trees for individual ancestral-states reconstructions (Supporting Information Figure S2).

3 | RESULTS

3.1 | Gross examination

The bioluminescent organ is not directly visible by external examination, but characteristics of the ventral body wall and anus that are associated with the organ are visible. The ventral body wall in which the bioluminescent organ is embedded is cloudy and more translucent than the reflective and pink tinted more dorsal body wall in fresh specimens of both *Acropoma japonicum* and *A. hanedai*. The skin of the ventral body wall has scattered obvious dark chromatophores in both species that are less numerous in *A. japonicum* than *A. hanedai*. In preserved specimens, the dorsal and ventral regions of the body wall are opaque and do not noticeably differ in translucence in either species. A laterally visible dark pigment line separates the ventral translucent musculature from more dorsal musculature in both fresh and alcohol-preserved *A. hanedai* and is not visible in *A. japonicum*. The anus in *A. japonicum* has only a few scattered dark chromatophores, is surrounded by a less obvious scaled pouch, and is located close to the pelvic fins at a vertical approximately under the base of the third spine in the spinous dorsal fin. The anus in *A. hanedai* is darkly pigmented, is within a dark pigmented fleshy pouch, and is located approximately midway between the pelvic-fin origin and the anal-fin origin at a vertical approximately at the posterior margin of the spinous dorsal fin. In the species examined that are not in *Acropoma*, the anus was immediately anterior to the anal-fin and lacked a surrounding pouch. In both species of *Acropoma*, the urogenital opening is posterior to and outside of the pouch surrounding the anus.

The bioluminescent organ is not directly visible by examination from within the coelom in *Acropoma*, and, other than the more anterior termination of the intestine, the species of *Acropoma* do not significantly differ from the other species examined except *Parapriacanthus ransonneti* in which pyloric ceca and the posteriormost intestine show evidence of being bioluminescent as discussed in the literature (Haneda & Johnson, 1958). All examined species have a posterior intestine that extends posteriorly from an anterior bend approximately straight to the anus. This is regardless of the position of the anus. Therefore, in *Acropoma* where the anus is more anterior than in all the examined species outside *Acropoma*, there is no obvious indication in the coelom of secondary anterior displacement of the terminal intestine. In both species of *Acropoma*, the terminal intestine within the coelom remains narrow and lacks any visible expansion toward or direct connection to the lateral arms of the bioluminescent organ. The peritoneum has many black chromatophores and, when removed from along the ventral coelom in *A. japonicum* and *A. hanedai*, reveals a whitish

opalescent layer in the ventral coelom dorsal to the bioluminescent organ.

Dissection into the body-wall musculature of preserved specimens allows direct examination of the bioluminescent organ. In both species of *Acropoma*, the organ is an opaque tan to beige and has thin, easily damaged walls. Anteriorly, the swollen, bacteria-filled left and right components are joined at the midline in all individuals of *A. japonicum* and *A. hanedai* examined (Figure 1a,b). In specimens of *A. hanedai* greater that 120 mm SL, the swollen anteriormost left and right sides of the bioluminescent organ are slightly separated. Thin dorsal and ventral sheets of tissue bound a lumen connecting the left and right swollen arms of the bioluminescent organ anterior to the anus in both species of *Acropoma* and connects the lateral arms posterior to the anus but anterior to the anal-fin origin in *A. hanedai*. The sheet of tissue contains a lumen that is barely visible as being continuous with the space contained by the pouch around the anus. This connection is only anterior to the anus in *A. japonicum* and both anterior and posterior to the anus in *A. hanedai*. The posteriormost bioluminescent organ is particularly distinctive in *A. hanedai*. On the left and right sides of the anterior anal-fin base, the bacteria-containing arms of the bioluminescent organ loop forming a posterior bend resulting in dorsal and ventral components. The left and right ventral components connect medially in front of the anal fin via a relatively thinner bacteria-containing connection (approximately half the width and height of the left and right ventral arms; Figure 1c).

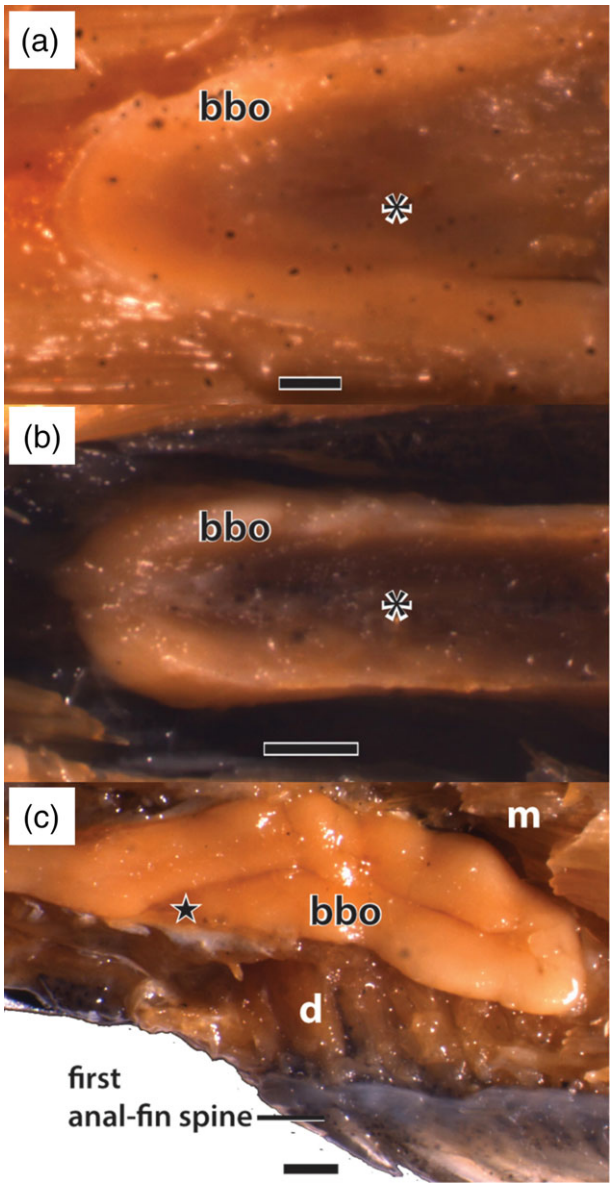

FIGURE 1 (a) Dorsal view of anteriormost bioluminescent organ in *Acropoma japonicum* (JFBM 48680, 113 mm SL) dorsal to the pelvic girdle demonstrating a short connection of bacteria-containing arms anteriorly. The overlying dark peritoneum was removed. (b) Ventral view of anteriormost bioluminescent organ in *A. hanedai* (JFBM 48733, 108 mm SL) demonstrating the continuity of the bacteria-containing arms anteriorly. The overlying muscle, urohyal bone, and skin were removed. (c) Left lateral view of left arm of posteriormost bioluminescent organ in *A. hanedai* (JFBM 48733, 108 mm SL) in the region ventral to the orbit demonstrating the folded left bioluminescent organ lateral to the anterior anal-fin radials. The overlying muscle and skin were removed. The star indicates where the left bioluminescent organ connects across the midline to the right. Asterisk (*) indicates tissue surrounding the lumen connecting left and right component of bioluminescent organ; bbo = bacterial bioluminescent organ; d = depressor analis muscle; m = hypaxial skeletal muscle. Scale bars = 1 mm

3.2 | Bioluminescent-organ structure and histology

The bioluminescent organ of *Acropoma japonicum* is composed of compartmentalized left and right arms that unite anteriorly, are connected by a medial lumen anterior to the anus, and remain separated posteriorly (Figure 2). These arms form the bioluminescent component of the bioluminescent organ and were referred to as the filiform body, U-shaped tube, or glandular organ by Haneda (1950). The bioluminescent component of the bioluminescent organ is separated into folded chambers or lobules and lined by a simple cuboidal epithelium where the cells often become somewhat compressed apically to basally. The lobules are filled with bacterial cells and open toward the center medial surface of the bioluminescent arms where there is substantial connective tissue. Small winding vessels lined by a simple cuboidal epithelium lead from the lateral bioluminescent arms to the medially connecting lumen. The medially connecting lumen of the bioluminescent organ is lined by simple cuboidal epithelium anteriorly and laterally and a stratified cuboidal epithelium medially that becomes and is continuous with the stratified epidermis of the skin via the pouch around the anus (Figure 2e). The bioluminescent arms are dorsoventrally elongate except for the anteriormost point where they are united into a single, approximately circular, structure. There is no connecting medial lumen posterior to the anal region (Figure 2f). The bioluminescent arms and the connecting lumen are surrounded by collagen-rich connective tissue that is notably vascularized around the bioluminescent arms but does not have a muscular layer, indicating that it is unlikely that the bacteria are rapidly ejected by the organ.

The bioluminescent organ of *Acropoma hanedai* also is composed of compartmentalized left and right bacteria-containing arms connected by a medial lumen that extends from ventral to the eye in the region of the isthmus to the middle anal fin. In the 51 mm SL individual, the anteriormost bacteria-containing arms are united into a single median structure. The posteriormost lateral arms of the

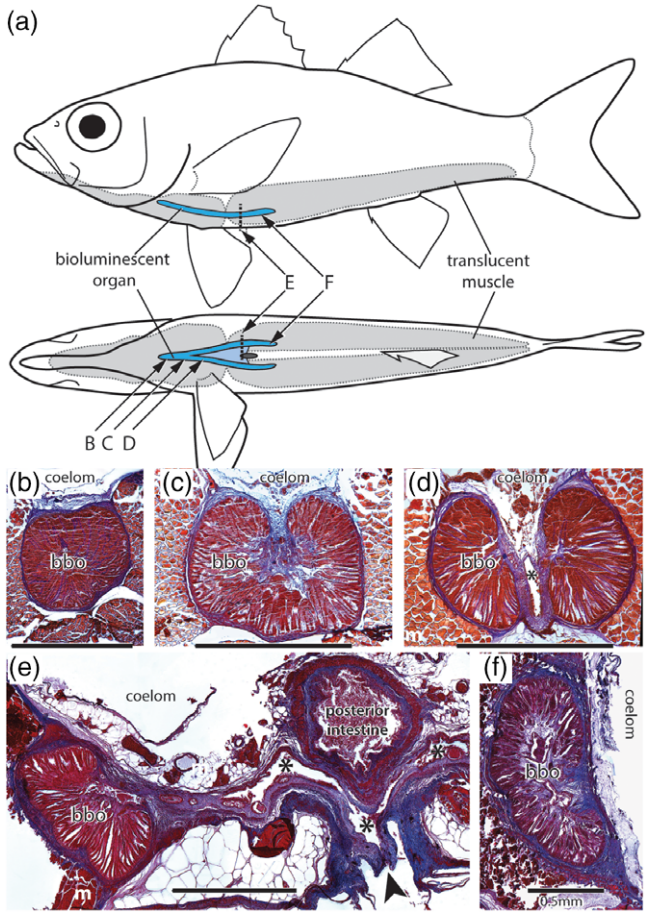

FIGURE 2 The ventral bioluminescent organ in *Acropoma japonicum* (JFBM 48680). All sections from 43 mm SL individual stained with MT. All scale bars are 1 mm unless otherwise indicated. (a) Diagrammatic illustration of the bioluminescent organ in *A. japonicum*. Left lateral view top. Ventral view bottom. Gray shading indicates transparent muscle. Letters indicate location of sections depicted in b–f. (b–d) Cross sections of anterior bacterial bioluminescent organ. Asterisk (*) indicates lumen connecting left and right component of bioluminescent organ; bbo = bacterial bioluminescent organ. (e) Cross-section of left lateral bioluminescent arm of the bioluminescent organ with connecting lumen immediately anterior to the anus. Note the connection of the lumen with the external opening. Arrow head = external opening of pouch surrounding anus; m = skeletal muscle. (f) Cross-section of left lateral ventral bioluminescent organ posterior to the anus. Note the absence of an associated lumen

bioluminescent organ lie lateral to the anal-fin skeleton, loop ventrally, and extend anteriorly in contact with the more dorsal bacteria-containing arm until immediately anterior to the anal-fin skeleton where the left and right ventral lateral arms connect across the midline (Figure 3). The bioluminescent component is histologically similar to *A. japonicum* except that the connecting lumen of the bioluminescent organ connects to the external environment via the pouch both anterior and posterior to the anus, not just anteriorly, and the bioluminescent arms are about as wide as tall or somewhat laterally elongate (Figure 3c) except lateral to the anal-fin skeleton where they are particularly dorsoventrally elongated (Figure 3d–f). As in *A. japonicum*, the bioluminescent arms and the connecting lumen in *A. hanedai* are surrounded by collagen-rich connective tissue that is notably vascularized around the bioluminescent arms (Figure 3g). Despite the visual transparency of the ventral body-wall musculature as compared to the more dorsal musculature in fresh specimens, the ventral body-wall musculature did not differ histologically under MT staining from the more dorsal musculature in either species of *Acropoma* (Figure 3c).

Comparison of the sectioned whole small individuals and dissected small individuals of *Acropoma japonicum* and *A. hanedai* with the sectioned and grossly dissected large individuals demonstrate some variation due to development. In the smaller individuals of both species, the anteriormost bioluminescent arms form a more extensive median structure without a medial lumen (Figures 1a–c and 3b) than

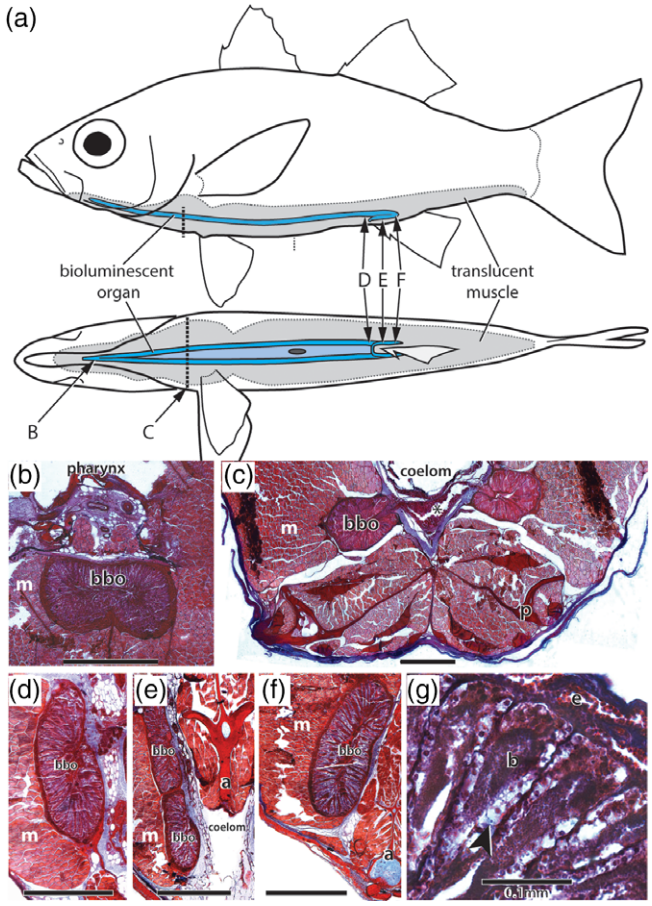

FIGURE 3 The ventral bioluminescent organ in *Acropoma hanedai* (JFBM 48733). All sections from 51 mm SL individual stained with MT. All scale bars are 1 mm unless otherwise indicated. (a) Diagrammatic illustration of the bioluminescent organ in *A. hanedai*. Left lateral view top. Ventral view bottom. Gray shading indicates transparent muscle. Letters indicate location of sections depicted in b–f. (b) Cross-section of anterior bacterial bioluminescent organ. bbo = bacterial bioluminescent organ; m = skeletal muscle. (c) Cross-section of ventral body wall immediately anterior to pelvic - and pectoral - fin origins. Note the connection of left and right arms of the bioluminescent organ by a lumen. Asterisk (*) = lumen connecting left and right arms of bioluminescent organ; p = bone of pelvic girdle. (d–f) Cross-sections of left lateral ventral bioluminescent organ in region of anterior anal fin. A = proximal anal-fin radial. (g) Cross-section of bacterial bioluminescent organ in C showing close-up of lobules. Arrow head = cuboidal epithelial cell; b = bacteria (*Photobacterium* sp.); e = erythrocytes

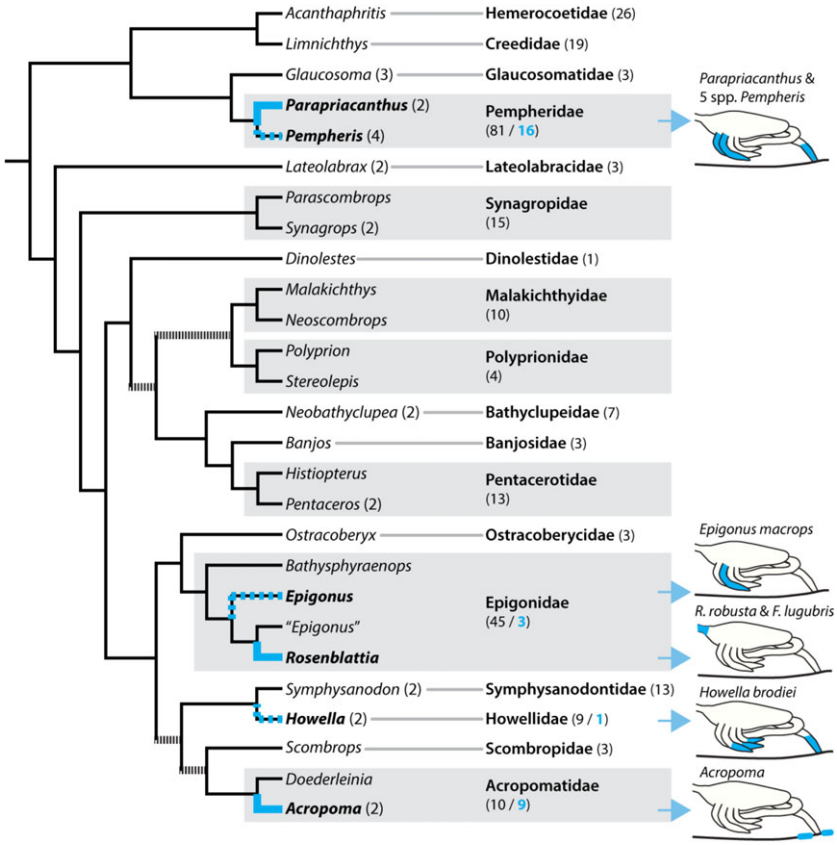

FIGURE 4 Evolutionary relationships among representative acropomatiform genera based on a maximum likelihood analysis of 16 gene fragments (13 nuclear and 3 mitochondrial) in a data set that is 70% complete at the amplicon/gene level that produced a species-level phylogeny visible in Supporting Information Figure S1. Numbers in parentheses after genera are numbers of species included in the analysis if greater than 1. Dashed lines indicate nodes present in the maximum likelihood analysis optimal tree that were not present in the 50% majority-rule Bayesian tree (Supporting Information Figure S2). Blue lines indicate bioluminescent genera. Numbers under family names are the number of species in each family (Eschmeyer, Fricke, & van Laan, 2018) followed by a blue number for the number of bioluminescent species if greater than 0. The diagrams at right are left lateral views of generalized post-pharyngeal digestive tracts and ventral body wall (anterior at left) for bioluminescent taxa with anatomical areas where bacterial bioluminescent organs originate indicated in blue (esophagus, pyloric cecum, posterior intestine, and/or proctodeum)

in larger individuals, indicating a lateral separation of the anterior left and right arms as development proceeds.

3.3 | Phylogenetic analysis

The phylogenetic relationships of the Acropomatiformes (Figure 4; Supporting Information Figures S1–S2) are somewhat consistent with those reported in prior analyses that included six or more acropomatiform families, including the polyphyly of the fishes previously classified in the family Acropomatidae (Davis et al., 2016; Near et al., 2013, 2015; Rabosky et al., 2018; Sanciangco et al., 2016; Thacker et al., 2015). As Davis et al. (2016), Sanciangco et al. (2016), and Rabosky et al. (2018) found, we recovered the traditional Acropomatidae in three independent clades in both our optimal maximum-likelihood analysis and all 100 examined Bayesian trees (Supporting Information Figures S1–S2). Because there are no known morphological synapomorphies for the traditional acropomatids and this study along with nine of the 10 published studies using DNA-sequence data have recovered the traditional acropomatids as polyphyletic, it is time to correct the taxonomy of the acropomatid fishes. As such, we recognize the family Acropomatidae as currently containing two genera, *Acropoma* and *Doederleinia*. We recognize the genera *Apogonops*, *Malakichthys*, *Neoscombrops*, and *Verilus* in the Malakichthyidae (Jordan & Richardson, 1910, p. 422) based on our phylogeny and the evidence provided by Yamanoue (2016) and Schwarzhans and Prokofiev (2017). Finally, we recognize the genera *Caraibops*, *Kaperangus*, *Parascombrops*, and *Synagrops* in the Synagropidae (Smith, 1961, p. 374) based on our phylogeny and the evidence provided by Schwarzhans and Prokofiev (2017). In recent classifications (e.g., Betancur-R et al., 2017), our Malakichthyidae and Synagropidae were recognized provisionally as independent clades in a nonmonophyletic Acropomatidae.

Our analyses recovered the following family level clades in the Acropomatiformes: Acropomatidae, Banjosidae, Bathyclupeidae, Creediidae, Dinolestidae, Epigonidae, Glaucosomatidae, Hemerocoetidae, Howellidae, *Lateolabrax*, Malakichthyidae, Ostracoberycidae, Pempheridae, Pentacerotidae, Polyprionidae, Scombropidae, Symphysanodontidae, and Synagropidae. Our analysis did not include Champsodontidae or Leptoscopidae which Betancur-R et al. (2017) also placed in this order.

The included members of the genus *Acropoma* were recovered as a clade sister to the nonbioluminescent acropomatid genus *Doederleinia*. Unlike previous studies, our likelihood analyses recovered the

Scombropidae sister to the Acropomatidae, although most of the earlier studies (e.g., Near et al., 2013, 2015; Sanciangco et al., 2016) did not include this family in their analyses. As with other analyses (e.g., Davis et al., 2016; Sanciangco et al., 2016) that did not include Scombropidae, we recovered the Acropomatidae (sensu stricto) in close relationship with the Epigonidae, Howellidae, Ostracoberycidae, and Symphysanodontidae. Our Bayesian analysis recovered Acropomatidae in a polytomy with Epigonidae+Ostracoberycidae, Howellidae+Symphysanodontidae, and Scombropidae. In both analyses, this clade was recovered sister to a clade composed of the Banjosidae, Bathyclupeidae, Dinolestidae, Malakichthyidae, Pentacerotidae, and Polyprionidae. While this clade has been recovered in previous analyses (Near et al., 2015; Thacker et al., 2015), it was never recovered sister to the clade that includes the Acropomatidae, Epigonidae, Howellidae, Ostracoberycidae, Scombropidae, and Symphysanodontidae. Sister to these large "acropomatoid" and "pentacerotid" clades, our analysis recovered Synagropidae and *Lateolabrax* as subsequent sister groups. Finally, all of these taxa were recovered as the sister group to a clade composed of (Creediidae, Hemerocoetidae), (Glaucosomatidae, Pempheridae).

Our results pose a few problems for the prevailing taxonomy. First, we have the separation of *Lateolabrax* from any other family name bearing fish groups (see below). This necessitates the formal recognition of this genus at the family level (see Taxonomic Account below). Second, our results suggest that *Epigonus* is paraphyletic. *Epigonus telescopus*, the type for the genus in the *E. telescopus* species group with the bioluminescent species *E. macrops* (Okamoto, Bartsch, & Motomura, 2012), is sister to a clade composed of *E. pandionis* and *Rosenblattia robusta*. Rather than subsume *Rosenblattia* into *Epigonus* or recognize the *E. pandionis* species group in another genus, we recognize a tentative "*Epigonus*" clade for the *E. pandionis* species group until a larger phylogenetic study including more species of epigonids from all genera and species groups can be conducted.

Our revised study allows us to explore the phylogenetic distribution of bioluminescence among acropomatiform taxa. The bioluminescence-exhibiting taxa in our analysis *Acropoma*, *Howella brodiei*, *Rosenblattia robusta*, and Pempheridae are all sister to a nonbioluminescent taxon (Figure 4). All 11 pempherid species in the genus *Parapriacanthus* and at least five of the 73 species of *Pempheris* (*P. affinis*, *P. klunzingeri*, *P. multiradiata*, *P. ornata*, and *P. ypsilychus*, all found in the waters around Australia and New Zealand) have a pyloric-cecum derived bioluminescent organ, and all *Parapriacanthus* and two species of *Pempheris* also have a posterior intestinal bioluminescent organ (Koeda & Motomura, 2018; Mooi & Jubb, 1996). In the maximum-likelihood analysis, these sister-group relationships are supported by bootstrap-support values over 70% for *Acropoma* and over 95% for the other three (Supporting Information Figure S1). In the Bayesian analysis, these sister-group relationships are supported by support values over 95% for all four bioluminescent groups and their nonbioluminescent sister taxon (Supporting Information Figure S2). In addition, the bioluminescent *Epigonus macrops* is a member of the *E. telescopus* species group which contains four other nonbioluminescent species (Okamoto & Gon, 2018). *Rosenblattia robusta* likely is closely related to *Florenciella lugubris* (a species we were unable to include) as Prokofiev (2007a) suggests that the two species may be conspecific. The distribution of these well supported clades make it unlikely that any two of the bioluminescent taxa share a single evolutionary origin. Additionally, many of the organs housing bioluminescent bacteria are derived from differing anatomical structures. At least four unique evolutionary origins of bioluminescence are inferred to have occurred in the order, with at least one in the Pempheridae and at least three, but likely four, in the clade composed of Acropomatidae, Epigonidae, Howellidae, Scombropidae, and Symphysanodontidae (Figure 4). We found this evolutionary scenario in our maximum-likelihood phylogeny as well as all 100 examined Bayesian phylogenies that were sampled from across our postburnin distribution.

Although the family name Lateolabracidae has been used multiple times in prior works for species in the genus *Lateolabrax*, the family-group name Lateolabracidae is not currently available (van der Laan, Eschmeyer, & Fricke, 2014), so in the context of this acropomatiform phylogeny, we describe it herein.

4 | TAXONOMIC ACCOUNT

4.1 | Lateolabracidae Ghedotti, Davis, and Smith new fam.

ZooBank lsid:zoobank.org:act:6AC55712-ADCC-4F1B-AE6F-CF803F4A7E90.

Type genus: *Lateolabrax* Bleeker, 1855.

Species included: *Lateolabrax japonicus* (Cuvier, Cuvier, & Valenciennes, 1828), *Lateolabrax latus* Katayama, 1957, and *Lateolabrax lyiuy* (Basilewsky, 1855).

Diagnosis: Species in Lateolabracidae can be distinguished from all other acropomatiforms by a unique combination of 34–36 vertebrae and 12–14 dorsal spines. Species in Acropomatidae, Banjosidae, Bathyclupeidae, Dinolestidae, Epigonidae, Glaucosomatidae, Howellidae, Malakichthyidae, Ostracoberycidae, Pempheridae, Pentacerotidae, Polyprionidae, Scombropidae, Symphysanodontidae, and Synagropidae have 24–28 vertebrae, species in Leptoscopidae have 42–48 vertebrae, and species in the remaining families (Champsodontidae, Creediidae, and Hemerocoetidae) all have species that have overlapping or nearly overlapping vertebral counts with species of *Lateolabrax* (Table 2). Species in Acropomatidae, Banjosidae, Bathyclupeidae, Champsodontidae, Creediidae, Dinolestidae, Epigonidae, Glaucosomatidae, Hemerocoetidae, Howellidae, Leptoscopidae, Malakichthyidae, Ostracoberycidae, Pempheridae, Scombropidae, and Symphysanodontidae have 10 or fewer dorsal-fin spines, whereas species in Pentacerotidae, Polyprionidae, and Synagropidae have overlapping or nearly overlapping dorsal-fin spine counts (Table 2). Between these two characters, species in Lateolabracidae can be distinguished from all other acropomatiforms. These fishes can be further differentiated from other acropomatiforms by their dorsal-fin ray, anal-fin spine, and anal-fin ray counts (Table 2).

5 | DISCUSSION

Histological examination of the bioluminescent organs in *Acropoma japonicum* and *A. hanedai* significantly expands upon the largely gross

TABLE 2 Selected meristic features that are useful in diagnosing the Lateolabracidae relative to other acropomatiforms

Family	Total vertebrae	Dorsal- fin spines	Dorsal-fin rays	Anal-fin spines	Anal-fin rays	Source(s)
Acropomatidae	25	8–9	10	3	7–9	Okamoto & Golani, 2018; Okamoto & Ida, 2002; Trnski & Leis, 2000
Banjosidae	25	10	12	3	7	Johnson, 1984
Bathyclupeidae	25	0	9	1	26–27	Johnson, 1984; Prokofiev, Gon, & Psomadakis, 2016
Champsodontidae	29–33	7	18–22	1	17–20	Watson, Matarese, & Stevens, 1984; Mooi & Johnson, 1997
Creediidae	37–57	0	18–40	0	11–17	Nelson, 1978; Watson, et al. 1984; Reader, Leis, & Rennis, 2000; Shibukawa, 2010
Dinolestidae	27	10	18–19	1	26–27	Johnson, 1984
Epigonidae	25	7–9	7–10	1–3	7–9	Suda & Tominaga, 1983; Johnson, 1984; Prokofiev, 2007a, 2007b; Okamoto & Gon, 2018
Glaucosomatidae	25	8	11	3	9	Johnson, 1984
Hemerocoetidae	32–50	2–6	13–23	0	15–29	Watson et al., 1984; Reader & Neira, 1998; Okiyama, 2000; Landeata, Neira, & Castro, 2003; Smith & Johnson, 2007
Howellidae	26	9	9	3	7	Johnson, 1984; Prokofiev, 2007c
Lateolabracidae	34–36	12–14	12–16	3	7–10	Johnson, 1984; Kang, Myoung, Kim, & Kim, 2012
Leptoscopidae	42–48	0	34–35	0	37	Watson et al., 1984; Neira, 1998
Malakichthyidae	25	10	9–11	3	7–9	Yamanoue & Matsuura, 2001, 2004; Yamanoue, 2016
Ostracoberycidae	25–26	9–10	8–10	3	7–8	Johnson, 1984
Pempheridae	25	4–7	7–12	3	17–45	Tominaga, 1968; Johnson, 1984
Pentacerotidae	24–27	4–15	8–29	2–6	6–17	Johnson, 1984; Kim, 2012
Polyprionidae	26–27	11–12	9–13	3	7–10	Johnson, 1984
Scombropidae	26	8–10	12–13	2	11–12	Johnson, 1984
Symphysanodontidae	25–28	9	10	3	7–8	Johnson, 1984; Anderson & Springer, 2005; Kimura, Johnson, Peristiwady, & Matsuura, 2017
Synagropidae	25	9–11	9–10	2–3	7–9	Ruiz-Carus, 2003; Ruiz-Carus, Matheson, & Vose, 2004; Schwarzhans & Prokofiev, 2017

description provided by Haneda (1950). The bacteria-containing bioluminescent arms of the organ are lined by a simple cuboidal epithelium that transitions to a stratified cuboidal epithelium in the medial lumen that connects the lateral arms. It is histologically clear that this medial lumen is contiguous with the space contained by the perianal pouch (Figure 2e). The cuboidal nature of the lining epithelium (as opposed to a columnar epithelium) and its continuity with the external environment outside of the anal sphincter indicate that the epithelium of the bioluminescent organ in *Acropoma* is of ectodermal developmental origin. Additionally, it is likely proctodeal because of the close association with the anus and the fact that the urogenital opening is outside the fleshy pouch. The proctodeum forms as a developmentally temporary chamber (a cloaca) into which both the urinary opening and the anus open (Baranowska Körberg et al., 2015; Pyati, Cooper, Davidson, Nechiporuk, & Kimelman, 2006). This extra-anal proctodeal derivation contradicts the depiction in a figure by Nealson and Hastings (1979, figure 7) of the bioluminescent organ in *Acropoma* having a direct connection to the posterior intestine. A less extensive but still perianal bacterial bioluminescent organ of likely ectodermal origin also is known in the distantly related aulopiform species *Chlorophthalmus albatrossis* (Somiya, 1977).

We generally confirm the differences between *Acropoma japonicum* and *A. hanedai* as described by Haneda (1950) but can draw additional conclusions based on the size variation of the specimens examined. In both species, the smaller individuals have a unitary anterior bioluminescent organ without separate bacteria-filled arms (Figures 2b and 3b–c), whereas there is some separation in large individuals of *A. hanedai* and large individuals have a much more limited anterior connection in *A. japonicum*. This indicates that increased separation of the lateral arms occurs anteriorly in both species during growth between 40 and 120 mm SL, increasing the amount of medial lumen anteriorly and separating the light-producing portions as the body width increases. The anterior position of the anus and the anterior–posterior extent of the bioluminescent organ did not differ among sizes, indicating that these characteristics develop before individuals reach 40 mm SL. In fishes with an anteriorly positioned anus, migration of the anus to an anterior position may occur at a relatively large size as in *Aphredoderus sayanus*, 15–44 mm SL (Mansueti, 1963), or at a smaller size in as in *Paratrachichthys* and *Aulotrachichthys*, 6.5–7.8 and 3.9–4.9 mm SL, respectively (Jordan & Bruce, 1993). An anteriorly positioned anus is present in larvae of *Acropoma* that are as small as 4.6 mm SL (Johnson, 1984; Trnski & Leis, 2000), suggesting a timing of anus migration similar to or earlier than in *Aulotrachichthys*.

The phylogenetic relationships of *Acropoma* indicate a close relationship to the genus *Doederleinia* (recognized and retained in the family Acropomatidae) and the Epigonidae, Howellidae, Ostracoberycidae, Scombropidae, and Symphysanodontidae (Figure 4). Most of the 83 species in this clade have not been identified as bioluminescent, but this group does include four identified bioluminescent species in addition to the species in *Acropoma*. The howellid *Howella brodiei* and the epigonids *Epigonus macrops*, *Florenciella lugubris*, and *Rosenblattia robusta* are bioluminescent or putatively bioluminescent (Herring,

1992; Mayer, 1974; Mead & DeFalla, 1965). However, their bioluminescent organs are clearly derived from the endodermal components of the digestive tract, either an intestinal pyloric cecum as in *Howella brodiei* and *Epigonus macrops*, the posterior intestine in *Howella brodiei*, or lateral enlargements of the esophagus as in *Florenciella lugubris* and *Rosenblattia robusta* (Herring, 1992; Mayer, 1974) and are not derived from the ectodermal perianal region as in *Acropoma* (Figure 4). The pempherid species in the genus *Parapriacanthus* and at least five of the 73 species of *Pempheris* have a pyloric-cecum derived bioluminescent organ, and most of these species also have a posterior intestinal bioluminescent organ (Koeda & Motomura, 2018; Mooi & Jubb, 1996; Pinheiro, Bernardi, & Rocha, 2016). However, the relatively distant phylogenetic relationship of the Pempheridae to *Acropoma* in combination with the ectodermal origin of the light organ in *Acropoma* strongly suggests that the two structures evolved independently. Therefore, it is likely that a novel bacterial bioluminescent organ evolved in the ancestor of *Acropoma* independently of the bioluminescent organs in howellids, epigonids, and pempherids and that bioluminescence evolved at least four times involving at least four different anatomical regions in the acropomatiform clade.

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AUTHOR CONTRIBUTIONS

Michael J. Ghedotti was the primary author of the paper, constructed Figures 1–4, worked on the taxonomic update, conducted the gross dissections, and conducted the histological sectioning with JNG and RWB.

Josephine N. Gruber conducted paraffin histological sectioning with MJG and RWB, formatted most of the photographs for Figures 2–3, and consulted with the other authors in the writing of the manuscript.

Ryan W. Barton conducted paraffin histological sectioning with MJG and JNG and consulted with the other authors in the writing of the manuscript.

Matthew P. Davis extracted DNA, collected and provided DNA sequence data for the phylogenetic analyses, worked on the taxonomic update, and conducted the phylogenetic analyses with WLS, and helped edit the paper.

W. Leo Smith extracted DNA, collected and provided DNA sequence data for the phylogenetic analyses, worked on the taxonomic update, and conducted the phylogenetic analyses with MPD, wrote portions of the paper, constructed Tables 1–2, constructed all supplemental figures and tables, and helped write and edit the paper.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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