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Investigations into the ancestry of the Grape-eye Seabass (*Hemilutjanus macrophthalmos*) reveal novel limits and relationships for the Acropomatiformes (Teleostei: Percomorpha)

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For 175 years, an unremarkable bass, the Grape-eye Seabass (*Hemilutjanus macrophthalmos*), has been known from coastal waters in the Eastern Pacific. To date, its phylogenetic placement and classification have been ignored. A preliminary osteological examination of *Hemilutjanus* hinted that it may have affinities with the Acropomatiformes. To test this hypothesis, we conducted a phylogenetic analysis using UCE and Sanger sequence data to study the placement of *Hemilutjanus* and the limits and relationships of the Acropomatiformes. We show that *Hemilutjanus* is a malakichthyid, and our results corroborate earlier studies that have resolved a polyphyletic Polyprionidae; accordingly, we describe Stereolepididae, new family, for *Stereolepis*. With these revisions, the Acropomatiformes is now composed of the: Acropomatidae; Banjosidae; Bathyclupeidae; Champsodontidae; Creediidae; Dinolestidae; Epigonidae; Glaucosomatidae; Hemerocoetidae; Howellidae; Lateolabracidae; Malakichthyidae; Ostracoberycidae; Pempheridae; Pentacerotidae; Polyprionidae; Scombropidae; Stereolepididae, new family; Symphysanodontidae; Synagropidae; and *Schuettea*. Finally, using our new hypothesis, we demonstrate that acropomatiforms repeatedly evolved bioluminescence and transitioned between shallow waters and the deep sea.

Keywords: Bioluminescence, Deep sea, Phylogeny, Taxonomy, UCE.

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Durante más de 175 años el Serranido ojo de uva (*Hemilutjanus macrophthalmos*), un pez parecido a la lubina común, se conoce de las zonas costeras del Pacífico Oriental. Al día de hoy la posición filogenética de esta especie se desconoce. Un estudio preliminar de *Hemilutjanus* basado en caracteres osteológicos sugirió que esta especie puede tener afinidades con el orden Acropomatiformes. Para investigar la posición filogenética de *Hemilutjanus* y los límites y relaciones dentro del orden Acropomatiformes realizamos análisis filogenéticos utilizando datos de secuencias Sanger y de UCEs. Demostramos que *Hemilutjanus* es un malakichthyid y nuestros resultados recobran Polyprionidae como una familia polifilética corroboran así estudios anteriores. En consecuencia, diagnosticamos y describimos una nueva familia de peces, Stereolepididae, que incluye ambas especies del genero *Stereolepis*. Con esta revisión, ahora el orden Acropomatiformes se compone de las familias: Acropomatidae; Banjosidae; Bathyclupeidae; Champsodontidae; Creediidae; Dinolestidae; Epigonidae; Glaucosomatidae; Hemerocoetidae; Howellidae; Lateolabracidae; Malakichthyidae; Ostracoberycidae; Pempheridae; Pentacerotidae; Polyprionidae; Scombropidae; Stereolepididae, nueva familia; Symphysanodontidae; Synagropidae; y *Schuettea*. Finalmente, utilizando nuestra hipótesis filogenética, demostramos que bioluminiscencia ha evolucionado varias veces dentro de los miembros de Acropomatiformes y tambien demostramos múltiples transiciones entre aguas someras y zonas profundas del océano dentro de este grupo.

Palabras clave: Aguas profundas, Bioluminiscencia, Filogenia, Taxonomia, UCE.

INTRODUCTION

In 1846, Johann Jakob von Tschudi described a grouper-like fish, *Plectropoma macrophthalmos* (von Tschudi, 1846), from multiple coastal locations in the tropical Eastern Pacific near Lima, Peru (Fig. 1). Since its original description, this species has been collected from Antofasta, Chile, in the south, to the Galápagos Islands in the north, typically among rock outcroppings at depths ranging from 10 to 55 m (Grove, Lavenberg, 1997; Froese, Pauly, 2021). Following von Tschudi's work, Bleeker (1876) reclassified this species in his Lutjanini, an assemblage that included species currently classified in groups as varied as the Arripidae, Banjosidae, Haemulidae, and Lutjanidae. Because of similarities between members of Bleeker's Lutjanini and *Plectropoma macrophthalmos* and dissimilarities between this species and sea basses and groupers, Bleeker described a new genus, *Hemilutjanus*, for *P. macrophthalmos*. Most subsequent authors in the late 19th and early 20th century followed Bleeker's generic assignment but continued to follow von Tschudi's (1846) placement of *Hemilutjanus macrophthalmos* by aligning this species with the Epinephelidae or Serranidae (Jordan, Eigenmann, 1890; Boulenger, 1895; Jordan, 1923; Hildebrand, 1946). Jordan, Eigenmann (1890:344) went so far as to state, "the name selected by Dr. Bleeker for this genus is peculiarly unfortunate, for besides the lack of euphony in the name, the genus has neither resemblance to nor affinity with the genus *Lutjanus*". Most systematic ichthyologists have not discussed

Hemilutjanus macrophthalmos, and most large-scale classifications published in the last 75 years have made little or no specific mention of the somewhat nondescript species from the Eastern Pacific Ocean (*e.g.*, Katayama, 1959; Greenwood *et al.*, 1966; Gosline, 1971; Nelson, 1976, 1984, 1994). Johnson (1983), on the basis of an alcohol-preserved specimen and radiograph, formally excluded *Hemilutjanus* from his "Serranidae" because it clearly lacked his diagnostic "serranid" features (hereafter any family name in quotes refers to a non-monophyletic assemblage that has been or continues to be used in the literature; for the "Serranidae", this is an assemblage composed of the Acanthistiidae, Anthiadidae, Epinephelidae, Niphonidae, and Serranidae used by many authors [*e.g.*, Nelson, 2006] unless otherwise noted). Later synopses, reviews, and field guides to coastal fishes in the tropical Eastern Pacific followed Johnson (1983) and treated *Hemilutjanus* as *incertae sedis* in the Percoidei (*e.g.*, Johnson, 1984; Grove, Lavenberg,

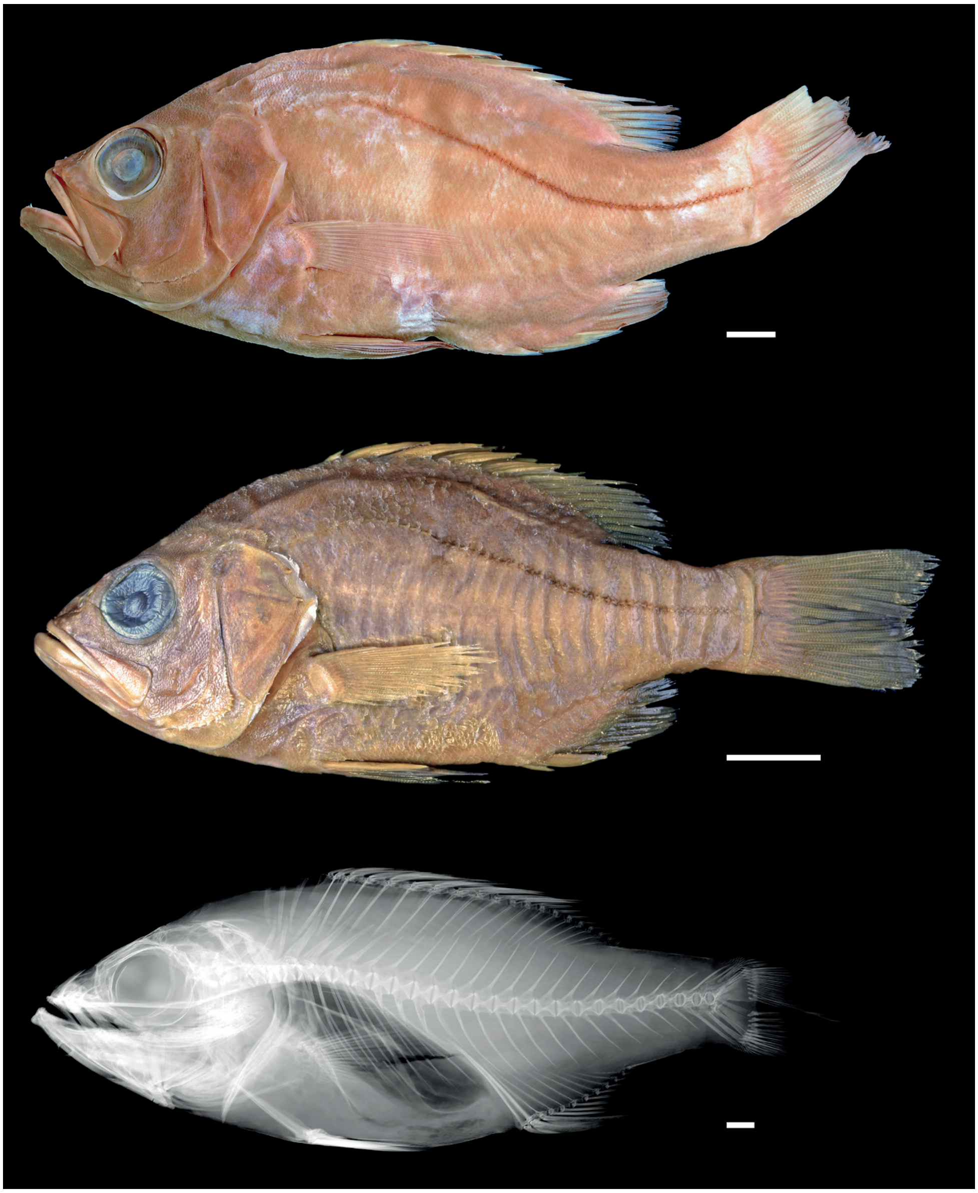

FIGURE 1 | Images of preserved and radiographed specimens of *Hemilutjanus macrophthalmos*: USNM 77623 (upper); SIO 12-3086 (middle); LACM 44038 (lower). Scale bars = 10 mm.

1997; McCosker, Rosenblatt, 2010). In 2016, Nelson *et al.* returned *Hemilutjanus* to the Epinephelidae (their Epinephelinae) without discussion. Most recently, Parenti, Randall (2020) separated *Hemilutjanus* from their "Serranidae" and described a new "closely related" family, Hemilutjanidae, for this species in their annotated checklist of fishes of the family "Serranidae". This monotypic Hemilutjanidae was classified by van der Laan *et al.* (2021) as a member of their "Perciformes *sedis mutabilis*", a group that includes the traditional "Serranidae" as well as families as phylogenetically divergent as the Apogonidae, Centrogenyidae, Lutjanidae, and Moronidae (see Smith, Craig, 2007; Near *et al*., 2013; and Betancur-R *et al*., 2017 for family-level placement in molecular phylogenies). Despite *Hemilutjanus macrophthalmos* being known to science for 175 years, the closest relative of the Grape-eye Seabass remains obscure, with the publication by Parenti, Randall (2020) recognizing the species as a monotypic family and effectively declaring that it is not a "serranid" but that its placement among percomorphs remains unknown.

Phylogenetic studies over the last 50 years have improved our understanding of the limits and relationships of percomorph fishes (reviewed or discussed in Johnson, 1984, 1993; Nelson, 1989; Stiassny *et al*., 2005; Chakrabarty, 2010; Smith, 2010; Nelson *et al*., 2016; Betancur-R *et al*., 2017). Explicit analyses in the last 30 years have begun to resolve the relationships among percomorph fishes (*e.g*., Johnson, Patterson, 1993; Wiley *et al*., 2000; Chen *et al*., 2003; Miya *et al*., 2003; Springer, Orrell, 2004; Dettaï, Lecointre, 2005; Smith, Wheeler, 2006; Smith, Craig, 2007). The last decade has seen continued improvements in our understanding of percomorph relationships through even larger datasets (*e.g*., Near *et al*., 2012a, 2013; Wainwright *et al*., 2012; Betancur-R *et al*., 2013a; Davis *et al*., 2016; Mirande, 2016; Sanciangco *et al*., 2016; Smith *et al*., 2016; Alfaro *et al*., 2018; Rabosky *et al*., 2018). One of the major findings of these large-scale percomorph analyses and the complementary focused morphological and/or molecular analyses of the traditional "Serranidae" and relatives (Imamura, Yabe, 2002; Smith, Wheeler, 2004; Smith, 2005; Craig, Hastings, 2007; Smith, Craig, 2007; Smith *et al*., 2009, 2018; Lautredou *et al*., 2013) is that the "Serranidae", where most scientists have classified *Hemilutjanus*, is not monophyletic and that the overwhelming majority of "serranids", but not all, have been resolved among the mail-cheeked fishes (for discussion, see Imamura, Yabe (2002); Dettaï, Lecointre (2004); Smith, Wheeler (2004); Smith (2005); Smith, Craig (2007); Lautredou *et al.* (2013)). Most of the groups traditionally allied with the "Serranidae" *sensu* Katayama (1959) that have been subsequently removed from this "serranid" and mail-cheeked-fish assemblage because they lacked Johnson's (1983) and Smith's (2005) synapomorphies have been placed in a new order, the Acropomatiformes (*i.e*., Acropomatidae, Lateolabracidae, Malakichthyidae, Polyprionidae, Synagropidae; Smith, Wheeler, 2006; Smith, Craig, 2007; Betancur-R *et al*., 2013a; Near *et al*., 2013, 2015; Thacker *et al*., 2015; Davis *et al*., 2016; Mirande, 2016; Sanciangco *et al*., 2016; Ghedotti *et al*., 2018; Rabosky *et al*., 2018; Satoh, 2018; van der Laan *et al*., 2021; Fig. 2).

The newly recognized Acropomatiformes is a percomorph order that was first recovered as a clade, but not formally named, in Smith, Wheeler (2006) with *Dinolestes*, *Howella*, *Lateolabrax*, *Malakichthys*, *Pentaceros*, *Polyprion*, and *Stereolepis*. The composition of this clade and the relationships of the families within it have expanded and varied across subsequent molecular studies that did or did not specifically reference this assemblage (Smith, Wheeler, 2006; Smith, Craig, 2007; Betancur-R *et al*., 2013a, 2017; Near *et al*., 2013, 2015; Thacker *et al*., 2015; Davis *et al*., 2016; Mirande, 2016; Sanciangco *et al*., 2016; Ghedotti *et al*., 2018; Rabosky *et al*., 2018; Satoh, 2018; Fig. 2; Tab. 1). Adding some complication, this clade has had alternative names including: Acropomatiformes, "Clade R", Pempheriformes, and "unnamed clade" of former trachinoids (Betancur-R *et al*., 2013a; Near *et al*., 2015; Thacker *et al*., 2015; Davis *et al*., 2016; Sanciangco *et al*., 2016; Ghedotti *et al*., 2018; Rabosky *et al*., 2018; Fig. 2; Tab. 1). Rabosky *et al.* (2018) used the name Pempheriformes for this clade when their phylogeny resolved Pempheridae outside of this clade. Across the most relevant molecular phylogenies (Fig. 2), the consensus is that this order includes 17 to 23 families, 50 to 60 genera, and approximately 300 species. Based on the species typically recovered in this clade, it is clear that the Acropomatiformes includes both shallow- and deep-water fishes that are distributed across all tropical, subtropical, and temperate latitudes. Interestingly, they are not well represented in the tropical and temperate Eastern Pacific (Schwarzhans, Prokofiev, 2017) where only eight species classified in five genera and four families (*Bathysphyraenops* and *Howella* [Howellidae], *Florenciella* [Epigonidae], *Pentaceros* [Pentacerotidae], and *Stereolepis* [Polyprionidae]) are found; these species all live in deeper waters except *Stereolepis* (Froese, Pauly, 2021). All previous phylogenetic hypotheses and classifications of this newly recognized order have included *Polyprion, Stereolepis,* Acropomatidae, Banjosidae, Epigonidae, Howellidae, Lateolabracidae, and Pentacerotidae, when included in a given analysis, but they have also variously included or excluded the Bathyclupeidae, Champsodontidae, Creediidae, Dinolestidae, Glaucosomatidae, Hemerocoetidae, Leptoscopidae, Malakichthyidae, Ostracoberycidae, Pempheridae, Scombropidae, Symphysanodontidae, and Synagropidae (Fig. 2; Tab. 1). Thus, the limits, relationships, and classification of this order still need extensive phylogenetic study.

Given that recent results have placed many former "serranids" either among the mail-cheeked fishes or the acropomatiforms, this study was designed to look at the placement of the enigmatic *Hemilutjanus* with a particular focus on acropomatiforms. This placement seemed most likely given that *Hemilutjanus* lacks the characteristic third opercular spine, suborbital stay, extensive head spination, and the expected distal insertion condition of the epaxial musculature on the dorsal-fin pterygiophores that are common to the "serranids" allied with the mail-cheeked fishes (Johnson, 1983; Mooi, Gill, 1995; Smith, 2005; current study). Therefore, we conducted a genome-scale molecular analysis with several goals associated with the phylogenetic placement of *Hemilutjanus macrophthalmos*. First, we tested whether *Hemilutjanus* was most closely related to the traditional "Serranidae" as suggested by von Tschudi (1846) and Parenti, Randall (2020), the members of Bleeker's (1876) Lutjanini (which includes several acropomatiforms), the modern Acropomatiformes, or a separate percomorph group altogether. Secondarily, we assessed the limits and relationships of the Acropomatiformes (including testing the monophyly of the "Acropomatidae" [viz. Acropomatidae, Malakichthyidae, and Synagropidae]) using genome-scale DNA-sequence data with the goal of resolving the limits of the order and clarifying the conflicting familial interrelationships by including dramatically more sequence data and representatives of all putative families. Finally, we will use our resulting hypothesis to trace the evolution of bioluminescence and the invasions of the deep sea among the acropomatiforms.

TABLE 1 | Analysis summary data, taxonomic inclusion information, and classification information of acropomatiform families and genera in current and prior phylogenetic studies that included broad acropomatiform sampling.

	Smith, Wheeler (2006)	Smith, Craig (2007)	Betancur-R *et al.* (2013b)	Near *et al.* (2013)	Near *et al.* (2015)	Thacker *et al.* (2015)	Davis *et al.* (2016)	Mirande (2016)	Sanciangco *et al.* (2016) and Betancur R *et al.* (2017)	Rabosky *et al.* (2018)	Satoh (2018)	Ghedotti *et al.* (2018)	Current Study
STUDY SUMMARY DATA													
Acropomatiform species included in analysis	8	12	15	16	18	22	17	41	33	60	24	40	31
Acropomatiform families or *incertae sedis* genera included in analysis	8	10	10	12	12	11	13	19	18	19	13	19	21
Data analyzed	3 mtDNA and 2 nuclear loci	3 mtDNA and 2 nuclear loci	1 mtDNA and 20 nuclear loci	10 nuclear loci	10 nuclear loci	10 nuclear loci	1 mtDNA and 10 nuclear loci	274 morphological characters, 15 mtDNA loci, and 29 nuclear loci	1 mtDNA and 20 nuclear loci	6 mtDNA and 21 nuclear loci	37 mtDNA loci	3 mtDNA and 13 nuclear loci	2 mtDNA and 455 nuclear loci
Alignment length in bps	4.721	4.036	20.853	8.577	8.577	8.577	9.114	30.970	~21,000	24.143	13.439	11.520	273.579
Extent of missing data	<30% missing data	<30% missing data	>50% missing data	<30% missing data	<30% missing data	<30% missing data	<30% missing data	>50% missing data	>50% missing data	>50% missing data	<30% missing data	<30% missing data	<30% missing data
TAXON INCLUSION AND/OR PLACEMENT													
Acropomatidae			Present	Present	Present	Present	Present	Present	Present	Present	Present	Present	Present
Banjosidae				Present	Present	Present	Present	Present	Present	Present	Present	Present	Present
Bathyclupeidae							Present	Present	Present	Classified as Eupercaria, but in Acropomatiformes in phylogeny	Present	Present	Present
Champsodontidae	In Ophidiiformes in phylogeny			Present	Present			In Labriformes in phylogeny	Present	Classified as Eupercaria, but in Syngnathiformes in phylogeny			Present
Creediidae			in Sygnathiformes in phylogeny	Present	Present	Present		In Acanthuriformes in phylogeny	Present	Present	Present	Present	Present
Dinolestidae	Present	Present						In Acanthuriformes in phylogeny	Classified as Eupercaria, but not in phylogeny	Classified as Eupercaria, but in Acropomatiformes in phylogeny		Present	Present
Epigonidae		Present	Present				Present	Present	Present	Present	Present	Present	Present
Glaucosomatidae			Present	Present	Present	Present	Present	Present	Present	Classified as Acropomatiformes, but in Acanthuriformes in phylogeny	Present	Present	Present
Hemilutjanus													Present
Hemerocoetidae				Present	Present	Present	Present	In Acanthuriformes in phylogeny	Present	Present	Present	Present	Present

TABLE 1 | (Continued)

	Smith, Wheeler (2006)	Smith, Craig (2007)	Betancur-R *et al.* (2013b)	Near *et al.* (2013)	Near *et al.* (2015)	Thacker *et al.* (2015)	Davis *et al.* (2016)	Mirande (2016)	Sanciangco *et al.* (2016) and Betancur R *et al.* (2017)	Rabosky *et al.* (2018)	Satoh (2018)	Ghedotti *et al.* (2018)	Current Study
Howellidae	Present	Present	Present	Present	Present	Present	Present	Present	Present	Present	Present	Present	Present
Lateolabracidae	Present	Present	Present					Present	Present	Present	Present	Present	Present
Malakichthys or *Verilus*	Present	Present		Present	Present	Present	Present	In Acropomatiformes and Centrarchiformes in phylogeny	Present	Present		Present	Present
Ostracoberycidae		In Uranoscopiformes in phylogeny		Present	Present	Present	Present	Present	Present	Classified as Acropomatiformes, but not in phylogeny		Present	Present
Pempheridae			Present	Present	Present	Present	Present	Present	Present	Classified as Acropomatiformes, but in Acanthuriformes in phylogeny	Present	Present	Present
Pentacerotidae	Present	Present		Present	Present	Present	Present	Present	Present	Present	Present	Present	Present
Polyprionidae	Present	Present	Present					Present	Present	Present	Present	Present	Present
Schuettea													Present
Scombropidae								Present	Classified as Scombriformes, but not in phylogeny	Classified as Scombriformes, but in Acrpomatiformes in phylogeny		Present	Present
Stereolepididae	Present	Present	Present	Present	Present	Present	Present		Present	Present	Present	Present	Present
Symphysanodontidae								Present	Present	Classified as Eupercaria, but in Acropomatiformes in phylogeny		Present	Present
Synagropidae		In Sygnathiformes in phylogeny	Present				Present	Present	Present	Present		Present	Present
Non-acropomatiform families, if any, included in the acropomatiform classification presented									Leptoscopidae	Leptoscopidae		Leptoscopidae	

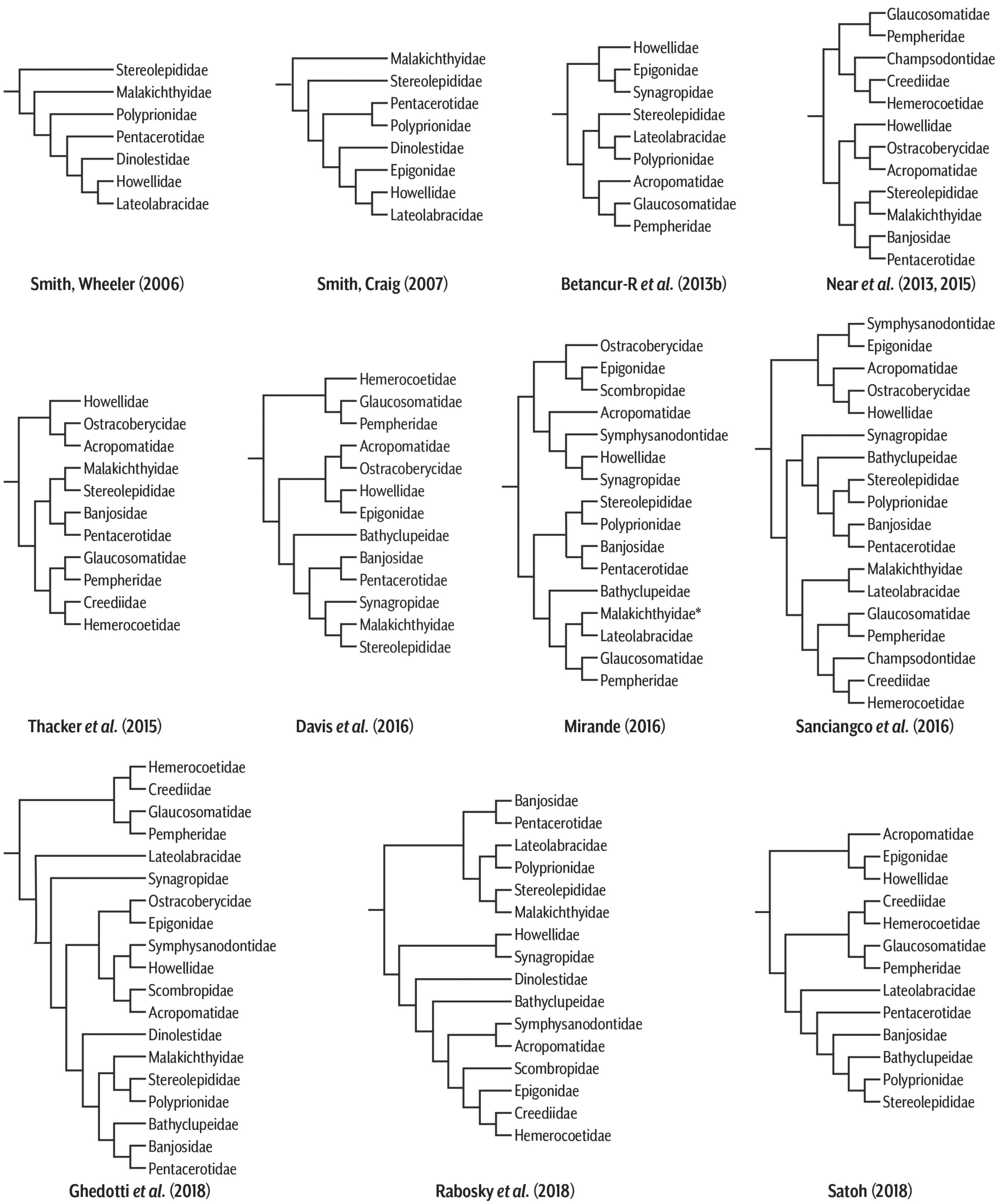

FIGURE 2 | Hypotheses of relationships among the Acropomatiformes based on the following studies: Smith, Wheeler (2006); Smith, Craig (2007); Betancur-R *et al*. (2013b); Near *et al*. (2013, 2015); Thacker *et al*. (2015); Davis *et al*. (2016); Mirande (2016); Sanciangco *et al*. (2016); Ghedotti *et al*. (2018); Rabosky *et al*. (2018); Satoh (2018). The asterisk in Mirande refers to the polyphyly of Malakichthyidae, where some members of the family were resolved outside of the Acropomatiformes.

MATERIAL AND METHODS

Classification. Throughout this study, we will use the name Acropomatiformes for the clade being investigated following Davis *et al.* (2016), Ghedotti *et al.* (2018), and van der Laan *et al.* (2021). This name was preferred over the occasionally used Pempheriformes for several reasons. First, the initial higher-level grouping of many of the families in this clade using comparative data was Katayama (1959); he included the modern Acropomatidae, Lateolabracidae, Malakichthyidae, Niphonidae, Ostracoberycidae, Polyprionidae, Sinipercidae, and Synagropidae in his "*Acropoma*-stem" clade in his phylogeny of serranid fishes. Second, the most taxon-rich analysis to date of the Acropomatiformes found Pempheridae outside of the "Pempheriformes", making the placement of that taxon less stable (Rabosky *et al*., 2018; Tab. 1). Additionally, the limits of the Pempheriformes have dramatically expanded (from two to 17 families) across closely related studies over a five-year period (*e.g*., Betancur-R *et al*., 2013a, 2017; Sanciangco *et al*., 2016); whereas, the composition of the Acropomatiformes has been more stable at the family level with only variation in the inclusion or exclusion of Leptoscopidae and Trichonotidae over the last five years (Davis *et al*., 2016; Ghedotti *et al*., 2018; van der Laan *et al*., 2021). All ordinal-level names and composition, unless modified or noted herein, will follow the classification used by Davis *et al.* (2016), and all genus- and species-level taxonomy will follow Fricke *et al.* (2021) unless modified herein. Finally, when making comparisons to Mirande (2016: appendix S5), we will refer to that study as a molecular phylogeny despite the study globally incorporating morphological data. This was done because his evidence used for acropomatiform limits and intrarelationships, the focus of our study, was almost exclusively DNA-sequence data.

Taxon sampling. All analyses were rooted with the ophidiid *Chilara taylori* and included either 54 or 57 species from approximately 40 percomorph families (Tab. 1; Tab. **S1**). The analyses included representatives of 12 percomorph orders and the families historically allied with *Hemilutjanus* in previous classifications (*e.g*., Acanthistiidae, Anthiadidae, Arripidae, Banjosidae, Epinephelidae, Haemulidae, Lutjanidae, Serranidae). The "core" 54-taxon analysis included all previously recognized acropomatiform families except the Hemerocoetidae and Symphysanodontidae, and the 57-taxon analysis included all previously recognized acropomatiform families. Our analytical focus was on the placement of *Hemilutjanus*, but our taxon sampling also allowed us to test the monophyly and relationships of the "Acropomatidae", "Serranidae", and Acropomatiformes with genome-scale data. Institutional abbreviations for anatomical and tissue vouchers follow Sabaj (2020).

Acquisition of new nucleotide sequence data. Fish tissues were preserved in 70–95% ethanol or stored cryogenically prior to the extraction of DNA. Genomic DNA was extracted from muscle or fin clips using either a DNeasy Tissue Extraction Kit (Qiagen) or the Maxwell® RSC Whole Blood DNA Kit (Promega) following the manufacturers' extraction protocols (except the replacement of the blood DNA kit's lysis buffer with Promega's tissue lysis buffer).

For Sanger sequence data, polymerase chain reaction (PCR) was used to amplify seven gene fragments (16S, COI, ENC1, GlyT, HH3, PLAGL2, and RAG1). Sanger molecular protocols for amplifying and cleaning these markers can be found in Grande *et al.* (2013) and Smith, Busby (2014). 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). The sequencing reactions were cleaned and desalted using cleanSEQ (Beckman Coulter). The nucleotides were sequenced and called on a 3730 or 3730xl automated DNA sequencer (Applied Biosystems) or by Beckman Coulter Genomics (Danvers, MA).

For high-throughput sequencing, Promega extractions were eluted into a 102 µL volume or the first and second Qiagen elutions were combined and dried down with a DNA SpeedVac Concentrator (Thermo Fisher) to a 102 µL volume. Two microliters of the raw or concentrated extracts were quantified using a Qubit fluorometer (Life Technologies) using the dsDNA BR Assay Kit. Quantified samples (100 µL volume) were sent to Arbor Biosciences (Ann Arbor, MI) for library preparation (*e.g.*, DNA shearing, size selection, cleanup), target capture (using the 500 UCE actinopterygian loci probe set; Faircloth *et al.* (2013)), enrichment, sequencing using an Illumina HiSeq 2500 or NovaSeq 6000, and demultiplexing of samples.

Character sampling. New Sanger sequence data were collected by us or received from Beckman Coulter, and the resulting contigs were built and edited in Geneious v8.1.8 (Kearse *et al*., 2012). These edited Sanger sequences were combined with homologous data captured from high-throughput sequencing and sequence data available on BOLD, DRYAD (Rabosky *et al*., 2018), or GenBank (Tab. 1; Tab. **S1**), as well as previously published SREB2 and TBR data. To capture high-throughput sequence data homologous with these "Sanger data", the cleaned reads from Arbor Biosciences or previously published cleaned reads were compared to existing sequences of close taxonomic allies for the 16S, COI, ENC1, GlyT, HH3, PLAGL2, RAG1, SREB2, and TBR loci using the "map to reference" function in Geneious v8.1.8 (Kearse *et al*., 2012) set to low-sensitivity and three iterations. Previously reported DNA-sequence data were taken from GenBank based on the following published studies: Pondella *et al*., 2003; Smith, Wheeler, 2004, 2006; Sparks, Smith, 2004a, 2004b; Sparks *et al*., 2005; Thacker, Hardman, 2005; Chen *et al*., 2007; Li *et al*., 2007, 2010, 2011; Mahon, 2007; Smith, Craig, 2007; Yamanoue *et al*., 2007; Holcroft, Wiley, 2008; Rocha *et al*., 2008; Yagishita *et al*., 2009; Near *et al*., 2011, 2012a, 2012b, 2013, 2015; Liang *et al*., 2012; Victor, 2012; Wainwright *et al*., 2012; Wang *et al*., 2012; Betancur-R *et al*., 2013a,b; Near, Keck, 2013; Ellingson *et al*., 2014; Li *et al*., 2014; Mabuchi *et al*., 2014; Thacker *et al*., 2015; Chang *et al*., 2016; Dahruddin *et al*., 2016; Sanciangco *et al*., 2016; Satoh *et al*., 2016; Smith *et al*., 2016; Tsunashima *et al*., 2016; Kenchington *et al*., 2017; Kimmerling *et al*., 2017; Ghedotti *et al*., 2018; Satoh, 2018 (Tab. 1; Tab. **S1**). Additionally, DNA-sequence data were taken from publicly available, but unpublished, data from BOLD and GenBank (Tab. 1; Tab. **S1**). The DNA-sequence data for these nine "Sanger" loci were aligned individually in MAFFT 7.130b (Katoh, Standley, 2013) using default settings. The resulting alignment of this matrix was 6.400 base pairs (bps), which was 90% complete at the locus level and 81% complete at the base-pair level. Novel sequences were submitted to GenBank and assigned accession numbers ON328326–ON328327, ON365542–ON365555, and ON365668–ON365669.

Arbor Biosciences generated DNA-sequence data using genomic extractions and the 500 UCE actinopterygian loci probe set (Faircloth *et al*., 2013). We processed the raw FASTQ files from Arbor Biosciences using the PHYLUCE 1.71 (Faircloth, 2016) workflow to retrieve UCE and flanking regions from newly sequenced specimens. Using a parallel wrapper (https://github.com/faircloth-lab/illumiprocessor), we trimmed reads to remove adapter contamination and low-quality bases using Trimmomatic (Bolger *et al*., 2014). The cleaned sequencing reads were submitted to GenBank and have been assigned BioProject PRJNA831283. We assembled cleaned reads from new and previously published samples (data from Alfaro *et al*., 2018; Friedman *et al*., 2019; Girard *et al*., 2020; Tab. 1; Tab. **S1**) using a python script (assemblo_abyss.py) with PHYLUCE and SPAdes v3.14.1 (Prjibelski *et al*., 2020) under the default settings. To identify assembled, orthologous contigs for the UCE loci, we aligned species-specific contig assemblies to a FASTA file of all enrichment baits using match_contigs_to_probes. This PHYLUCE program implements a matching process using LASTZ (Harris, 2007) and ensures that UCE matches are at least 80% identical over 80% of their length to avoid contamination and paralogy. Further, this program assesses and removes apparent duplicate contigs and contigs hit by baits targeting more than one locus. As noted by Faircloth (2016), the program then creates a relational database containing several tables that map the contig names generated by the assembler to the names of each corresponding locus across all selected taxa. Next, we extracted the contigs corresponding to non-duplicate conserved loci into a monolithic FASTA-formatted file (all UCEs for all species) using get_fastas_from_match_counts. We then aligned the sequence data for UCEs containing more than four taxa using seqcap_align that parallelizes MAFFT 7.130b (Katoh, Standley, 2013). The alignment was refined using GBlocks (Talavera, Castresana, 2007) using the default PHYLUCE settings. For a final PHYLIP-formatted data matrix, we concatenated the resulting alignments for all UCEs present for ≥ 75% of UCE taxa (*i.e*., loci with data for 40 or more of the 54 species with UCEs) using align_get_only_loci_with_min_taxa followed by align_concatenate_alignments. The resulting 75% complete "UCE matrix" was based on 457 UCEs or 273.579 bps that were present for the 54 species that had UCE data; this UCE matrix was 95% complete at the locus level (Tab. **S4**). Across all UCE loci, median sequence fragment length was 599 bps, with a range of 163–1.055 bps (Tab. 2; Tab. **S1**). The UCE and flanking region sequences were partitioned using the sliding-window site characteristics–entropy method (hereafter, SWSC-EN; Tagliacollo, Lanfear, 2018) to split each UCE locus into left and right flanking regions and the ultraconserved core (*i.e*., center segment) by rate of evolution.

The final concatenated molecular matrix or "expanded matrix" included 457 UCE loci and 9 Sanger-based loci that encompassed 279.979 aligned base pairs and 70.230 parsimony-informative characters. The resulting left, central, and right UCE segments from SWSC-EN were then used as input along with the independent 16S locus and the three independent codon positions for each of the eight protein-coding Sanger genes to PartitionFinder v2.1.1 (Lanfear *et al*., 2014, 2017; Stamatakis, 2014) for this software to find the best-fitting nucleotide substitution model for each data partition. PartitionFinder selected among models using AIC_c and the rclusterf search method with the setting -raxml (Lanfear *et al*., 2014). PartitionFinder designated 1.310 subsets with associated models for these regions. A list of the subsets of UCEs, partitions, and associated models can be found in Tabs. **S1, S2** and **S3**. The Sanger alignment can be found in Tabs. **S1** and **S4** and the expanded alignment can be found in Tabs. **S1** and **S5**.

TABLE 2 | Selected meristic and morphological features that are useful in diagnosing the families and *incertae sedis* genera of the Acropomatiformes. Data taken from specimens examined in the current study as well as Schultz (1940), Katayama (1952, 1959), Dick (1962, 1972), Fraser (1971), Fraser, Fourmanoir (1971), Suda, Tominaga (1983), Johnson (1984), Masuda *et al*. (1984), Rosa (1995), Quéro, Ozouf-Costaz (1991), Moser (1996), McKay (1997), Leis, Carson-Ewart (2000), Okamoto, Ida (2002), Heemstra, Yamanoue (2003), Landeata *et al*. (2003), Ruiz-Carus (2003), Yamanoue, Matsuura (2004), Anderson, Springer (2005), Richards (2005), Nelson (2006), Fahay (2007), Prokofiev (2007), Suntsov (2007), Gomon *et al*. (2008), Kang *et al*. (2012), Kim (2012), Yamanoue (2016), Kimura *et al*. (2017), Matsunuma, Motomura (2017), Schwarzhans, Prokofiev (2017), Okamoto, Golani (2018), Okamoto, Gon (2018), Bray (2019), Schwarzhans *et al*. (2020), and Hay *et al*. (2021).

Taxon	Total vertebrae (Precaudal+Caudal)	Dorsal-fin spines	Dorsal-fin rays	Anal-fin spines	Anal-fin rays	Pectoral-fin rays	Lateral-line scales	Procurrent spur	Supramaxilla
Acropomatidae	25 (10+15)	8–9	10	3	6–9	15–18	41–47	Present	Present
Banjosidae	25 (11+14)	9–10	11–13	3	6–8	14–17	46–52	Present	Absent
Bathyclupeidae	25–32 (many combinations)	0–1	8–9	1	26–39	23–29	33–38	Present	Present
Champsodontidae	29–33 (11–13+18–20)	4–7	18–23	0	16–21	11–16	N/A	Absent	Absent
Creediidae	37–60 (many combinations)	0	12–43	0	18–41	8–17	34–60	Absent	Absent
Dinolestidae	27 (10+17)	10	18–19	1	26–27	16–17	63–70	Present	Present
Epigonidae	25 (10–11+14–15)	7–9	7–11	1–3	7–10	15–23	46–52	Present	Absent
Glaucosomatidae	25 (10+15)	8	11–14	3	9–12	15–16	44–52	Present	Present
Hemerocoetidae	25–50 (many combinations)	0–7	13–43	0	16–42	15–21	32–36	Absent	Absent
Howellidae	24–27 (10–11+14–16)	8–10	8–10	3	6–8	13–17	27–53	Absent	Absent
Lateolabracidae	34–36 (17–18+17–18)	12–14	12–16	3	7–10	14–18	71–86	Present	Present
Malakichthyidae: *Hemilutjanus*	25 (10+15)	10	10–11	3	9	16–18	64–66	Present	Present
Malakichthyidae: *Malakichthys*	25 (10+15)	10	9–11	3	7–9	12–15	42–53	Present	Present
Malakichthyidae: *Verilus*	25 (10+15)	10	10	2–3	7–8	14–17	37–69	Present	Present
Ostracoberycidae	25–26 (10+15–16)	9–10	8–10	3	7–9	14–15	47–55	Present	Absent
Pempheridae	25 (10+15)	4–7	7–13	3	17–45	14–19	45–82	Variable	Absent
Pentacerotidae	24–27 (12–13+11–14)	4–15	8–29	2–6	7–45	16–18	46–76	Variable	Absent

TABLE 2 | (Continued)

Taxon	Total vertebrae (Precaudal+Caudal)	Dorsal-fin spines	Dorsal-fin rays	Anal-fin spines	Anal-fin rays	Pectoral-fin rays	Lateral-line scales	Procurrent spur	Supramaxilla
Polyprionidae	26–27 (13+13–14)	11–12	11–13	3	8–10	17–18	84–98	Present	Present
Scombropidae	26 (10+16)	8–11	12–14	2–3	11–13	15–17	50–70	Present	Present
Stereolepididae	26 (12+14)	9–12	9–10	3	7–9	18–19	57–80	Present	Present
Symphysanodontidae	25–28 (10–11+15–17)	8–10	9–11	3–7	7–8	15–18	42–50	Variable	Absent
Synagropidae	25 (10+15)	9–11	8–10	2–3	6–9	15–18	28–33	Present	Present
Incertae sedis: *Schuettea*	24 (10+14)	5	28–31	3	28–32	14–18	46–50	Absent	Absent

Phylogenetic analyses. Concatenated maximum-likelihood and species-tree analyses were conducted on our "core" 54-taxon dataset that includes 54 percomorph terminals and both UCE and Sanger data. Additionally, we analyzed an "expanded" 57-taxon concatenated dataset that included three species that were only represented by 2–9 Sanger fragments. Both concatenated analyses used IQ-Tree v2.1.1 (Nguyen *et al*., 2015; Chernomor *et al*., 2016). These analyses began with ten independent runs of the software with the perturbation strength (-pers) set to 0.2 and using the 1.310-partition scheme from PartitionFinder. For each dataset, the optimal trees from each of the ten independent runs were submitted as starting trees with a final round of refinement with -pers set to 0.2 and a larger number of stop iterations (-nstop) set to 2.000, with more thorough nearest neighbor interchange branch swapping (-allnni), and the number of candidate trees (-nbest) to be maintained during the maximum-likelihood search set to 25. Support for the concatenated phylogenies for each analysis was assessed using IQ-Tree (-bo), and the results from 200 bootstrap replicates are summarized using majority-rule consensus trees. We recognize three levels of nodal support: ≥50% bootstrap support represents a supported node or clade, ≥70% bootstrap support represents a moderately well-supported node or clade, and ≥95% bootstrap support represents a well-supported or strongly supported node or clade.

In addition to the concatenated maximum-likelihood analyses above, each of the 457 UCE, 16S, and protein-coding "Sanger" loci described above were analyzed individually using RAxML v 8.2 (Stamatakis, 2014) using a GTRGAMMA substitution model for the core taxa (54 taxa that have UCE and Sanger data). The best likelihood result from five independent analyses for each UCE, 16S, and protein-coding locus were retained and combined with the results from each locus for subsequent analysis in ASTRAL-III (Zhang *et al*., 2018) to infer a species tree from the individual gene trees. Branch supports for this species-tree analysis represent support for the quadripartition across all loci or local posterior probability (LPP) for the nodes in the "species-tree analysis". As above, we recognize three levels of nodal support: ≥50% LPP support represents a supported clade, ≥70% LPP support represents a moderately well-supported clade, and ≥95% LPP support represents a well-supported or strongly supported clade.

Depth and bioluminescence data. We collected depth data for each clade from the institutions sharing their data on FishNet2 (2021). Following clade-level data downloading, we used the following procedure for data aggregation: 1) we removed all samples without depth data; 2) we removed all samples with depth listed as meter-wire-out; 3) we removed all unclear depth data; 4) we converted the data for all samples with a depth range of 0 to a number to only the non-zero number (*e.g.*, if the depth was listed as 0–2.500 m we converted the number to 2.500); 5) we converted all depth data to meters; 6) we calculated the mean depth for samples with a collection depth range and used this mean depth for the depth of these samples; 7) we removed samples that listed the depth of collection as 0; 8) finally, we removed outlier samples that were notably more extreme than other lots (typically 2–6 lots per clade). Once these cleaning procedures were completed, we calculated a mean depth value and standard deviation of depth for each family-level clade (along with median, minimum, and maximum values); we considered a fish clade as part of the deep sea if the mean + standard deviation extended beyond a depth of 200 m. We took the presence or absence of bioluminescence data from Ghedotti *et al.* (2018). We examined and analyzed the dataset (ancestral-state reconstructions) in Mesquite v3.5 (Maddison, Maddison, 2018). We examined ancestral-state reconstructions using parsimony and maximum likelihood.

Morphological investigation. We examined formalin-fixed and ethanol-preserved fishes, cleared-and-stained specimens, and dried skeletal material using multiple stereomicroscopes with varying magnification and lighting regimes. We explored new morphological data along with previously described variation as an initial investigation into acropomatiform relationships with the goal of finding characteristic features for new clades (Tab. 2). The specimens examined for this study are listed in the material examined, and a more complete morphological examination is underway.

RESULTS

The core 54-taxon concatenated maximum-likelihood analysis (ML) resulted in a single optimal tree (Fig. 3) with a likelihood score of -2087266.778. Most of the 51 nodes (41 or 80%) were well supported by a bootstrap value ≥95, 45 nodes (88%) were moderately well supported by a bootstrap value ≥70, and 49 nodes (98%) were supported in the 50% majority-rule tree (Fig. 3). The core 54-taxon species-tree analysis (ST) resulted in a single tree with most of the 51 nodes (34 nodes or 67%) well supported by an LPP value ≥95, 42 nodes (82%) moderately well supported by an LPP value ≥70, and 49 nodes (96%) supported in the 50% majority-rule tree (Fig. 4). The expanded 57-taxon concatenated analysis resulted in a single optimal tree (Fig. 5) with a likelihood score of -2089599.873. Half of the 54 nodes (27 or 50%) were well supported by a bootstrap value ≥95, 44 nodes (81%) were moderately well supported by a bootstrap value ≥70, and 48 nodes (89%) were supported in the 50% majority-rule tree (Fig. 5). Clearly, the addition of three Sanger-only taxa reduced bootstrap support, but it did not alter the recovered relationships among the taxa with both UCE and Sanger data. However, the placement of Sanger-only species (*Acanthaphritis*, *Crystallodytes*, and *Schuettea*) was not generally well supported with <50 to 88% bootstrap support for these Sanger-only taxa and their sister groups (Fig. 5).

The results of all three analyses (54-taxon ML, 54-taxon ST, and 57-taxon ML) agreed on the most important findings of this study. First, all analyses separated *Hemilutjanus* from its frequent historic taxonomic allies in the Acanthistiidae, Anthiadidae, Epinephelidae, and Serranidae. As has been shown in most recent analyses, the traditional "Serranidae" did not form a monophyletic group (*e.g.*, Chen *et al.*, 2003; Smith, Wheeler, 2004; Smith, Craig, 2007; Lautredou *et al.*, 2013; Near *et al.*, 2013; Figs. 3–5), and we show that these taxa are not particularly closely related to *Hemilutjanus.* Instead, all analyses consistently place *Hemilutjanus* sister to *Malakichthys* with moderate to strong support, deeply nested within the Acropomatiformes. Given the moderate to strong support for this close relationship and overall similarity of the included groups, we formally classify *Hemilutjanus macrophthalmos* as a member of the Malakichthyidae rather than a separate monotypic family. As has been shown in previous analyses (Smith, Craig, 2007; Betancur-R *et al.*, 2013a; Near *et al.*, 2013, 2015; Thacker *et al.*, 2015; Davis *et al.*, 2016; Mirande, 2016; Sanciangco *et al.*, 2016; Ghedotti *et al.*, 2018; Rabosky *et al.*, 2018; Fig. 2), the traditional "Acropomatidae" (*e.g.*, Nelson, 2006) is polyphyletic. Instead, we recover three independent "acropomatid" families that are consistent with the classification of Ghedotti *et al.* (2018) and van der Laan *et al.* (2021): Acropomatidae (*Acropoma* and *Doederleinia*), Malakichthyidae (*Hemilutjanus*, *Malakichthys*, and *Verilus* [not included in our analyses]), and Synagropidae (*Caraibops* [not included in our analyses], *Kaperangus* [not included in our analyses], *Parascombrops*, and *Synagrops*).

In the core 54-taxon ML analysis, our family-level phylogeny for the Acropomatiformes resulted in several relationships that had not been previously proposed (Fig. 2; Tab. 1). Malakichthyidae was recovered sister to a clade composed of *Stereolepis,* Bathyclupeidae, Champsodontidae, Creediidae, and Synagropidae. Together, these taxa were resolved sister to a clade that included the Banjosidae and Pentacerotidae. All these taxa were recovered sister to a clade composed of the Dinolestidae. The sister group to the clade composed of *Stereolepis,* Banjosidae, Bathyclupeidae, Champsodontidae, Creediidae, Dinolestidae, Malakichthyidae, Pentacerotidae, and Synagropidae is a clade composed of *Polyprion*, Glaucosomatidae, Lateolabracidae, and Pempheridae. Finally, the acropomatiform clade sister to all other previously discussed acropomatiform groups is composed of the Acropomatidae, Epigonidae, Howellidae, Ostracoberycidae, and Scombropidae.

As with the core concatenated 54-taxon ML analysis, our ST analysis separated *Hemilutjanus* from the included "serranid" taxa, and the "serranids" that were included were recovered as paraphyletic. As with the concatenated 54-taxon ML analysis, the ST analysis recovered *Hemilutjanus* sister to *Malakichthys* (*i.e.*, we recovered a modified Malakichthyidae) inside a monophyletic Acropomatiformes with identical composition (for the included taxa). The ST analysis also separated the Acropomatidae, Malakichthyidae, and Synagropidae into three distinct and independent clades. Therefore, the core findings of our study were consistent across methods and datasets analyzed. Despite identical findings for the core goals of this study, there were differences between the 54-taxon ML and ST results. Most of the disagreements between these trees were due to the differential placement of *Champsodon*+*Crystallodytes* as the sister group to a clade composed of *Stereolepis,* Bathyclupeidae, and Synagropidae (in ML) *versus* a sister group to all other acropomatiforms (in ST). The ML and ST results also differed in the placement of *Stereolepis* sister to Bathyclupeidae+Synagropidae in ML

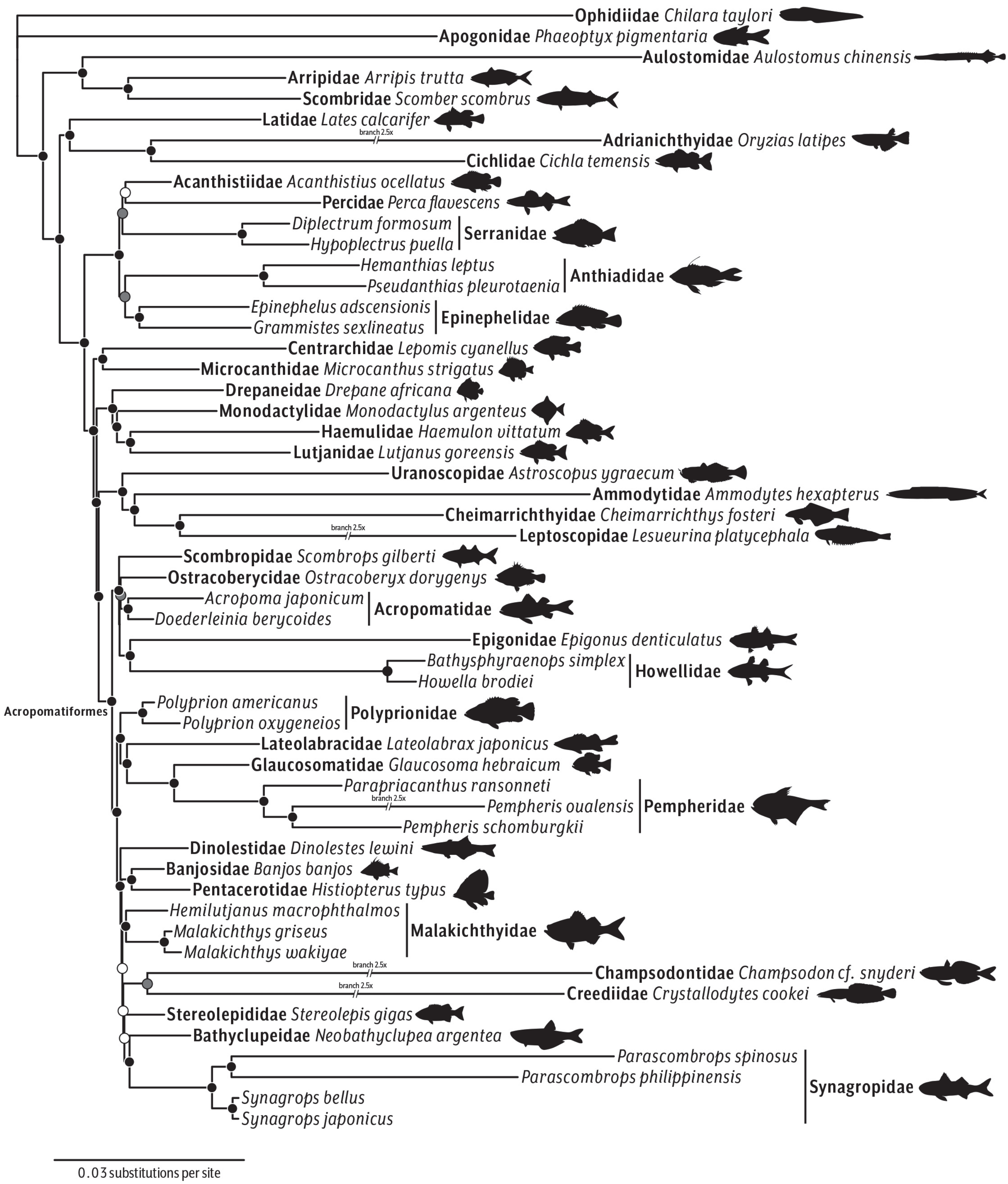

FIGURE 3 | Optimal cladogram resulting from the partitioned-likelihood analysis of the Sanger and UCE dataset of the 54 core taxa and 279.979 nucleotide characters. Clades with ≥95% bootstrap support are identified with a black circle, clades with 70–94% bootstrap support are identified with a gray circle, and clades with ≥50–69% bootstrap support are identified with a white circle.

and sister to Banjosidae+Pentacerotidae in ST, the placement of Dinolestidae sister to Banjosidae+Pentacerotidae in ML and sister to *Stereolepis*+Banjosidae+Pentacerotidae in the ST analysis, the monophyletic (in ML) *versus* paraphyletic (in ST) resolution of *Parascombrops* relative to *Synagrops,* and the placement of gobiiforms at the base of our resulting phylogeny in ML *versus* the sister group to all analyzed taxa except the included Ophidiiformes, Scombriformes, and Syngnathiformes in the ST analysis. In total, 42 of 51 nodes were identical between the core ML and ST analyses with six of the nine (67%) conflicting nodes resulting from the movement of *Champsodon* and *Crystallodytes* (Figs. 3–4).

In all three analyses, the Acropomatiformes was recovered sister to the Uranoscopiformes, and the overall phylogeny was similar to other large-scale studies (Figs. 3–5; Near *et al*., 2013; Davis *et al*., 2016; Sanciangco *et al*., 2016). Together, Acropomatiformes and Uranoscopiformes were recovered sister to the Acanthuriformes. Among the taxa sampled in this study, this clade of three orders had a series of progressively less closely related sister groups: Centrarchiformes, Scorpaeniformes, and Carangiformes+Ovalentaria. The subsequent sister group was Scombriformes+Syngnathiformes in both ML analyses, followed by the Gobiiformes and Ophidiiformes. In contrast, the earliest splits in the ST analysis were composed of Ophidiiformes and Gobiiformes+Scombriformes+Syngnathiformes (Figs. 3–4).

In our expanded 57-taxon concatenated maximum-likelihood analysis that included *Acanthaphritis*, *Schuettea*, and *Symphysanodon* and looked more broadly at the interfamilial relationships among the Acropomatiformes, we recovered identical relationships with the core 54-taxon ML analysis except for the inclusion of the three Sanger-only taxa (Fig. 5). The inclusion of these three species with only 2–9 Sanger sequences resulted in a notable decrease in support for relationships among the Acropomatiformes but the same general relationships (Figs. 3 and 5). The placement of *Acanthaphritis* as the sister group to Creediidae had moderate support, and the placement of *Symphysanodon* as the sister group of Epigonidae+Howellidae was supported with a bootstrap value of 52%. In contrast, the sister-group relationship between *Schuettea* and *Champsodon* was not supported. During the individual IQ-Tree replicates (results not shown), *Schuettea* was always recovered in the clade composed of *Stereolepis*, Banjosidae, Bathyclupeidae, Champsodontidae, Creediidae, Dinolestidae, Hemerocoetidae, Malakichthyidae, Pentacerotidae, and Synagropidae, and it was never allied with its traditional ally, *Monodactylus.* This surprising and well-supported acropomatiform placement for *Schuettea* rather than sister to *Monodactylus* lends support to Tominaga's (1968) suggestion that *Schuettea* may be more closely related to pempherids than monodactylids. While a somewhat close relationship between *Schuettea* and Pempheridae (as members of the Acropomatiformes) was recovered, the analyzed DNA-sequence data do not support the proposed sister-group relationship between *Schuettea* and Pempheridae noted by Tominaga (1968), but clearly much additional work is needed on the placement of *Schuettea* among acropomatiforms given the paucity of data for *Schuettea* in this study.

The family-level limits and relationships of the Acropomatiformes resolved in this study had similarities to, but differed substantially from, all previous acropomatiform phylogenies (Figs. 2–5) and classifications (Tab. 1). The Acropomatiformes resolved in this study includes the Acropomatidae, Banjosidae, Bathyclupeidae, Champsodontidae, Creediidae, Dinolestidae, Epigonidae, Glaucosomatidae, Hemerocoetidae, Howellidae,

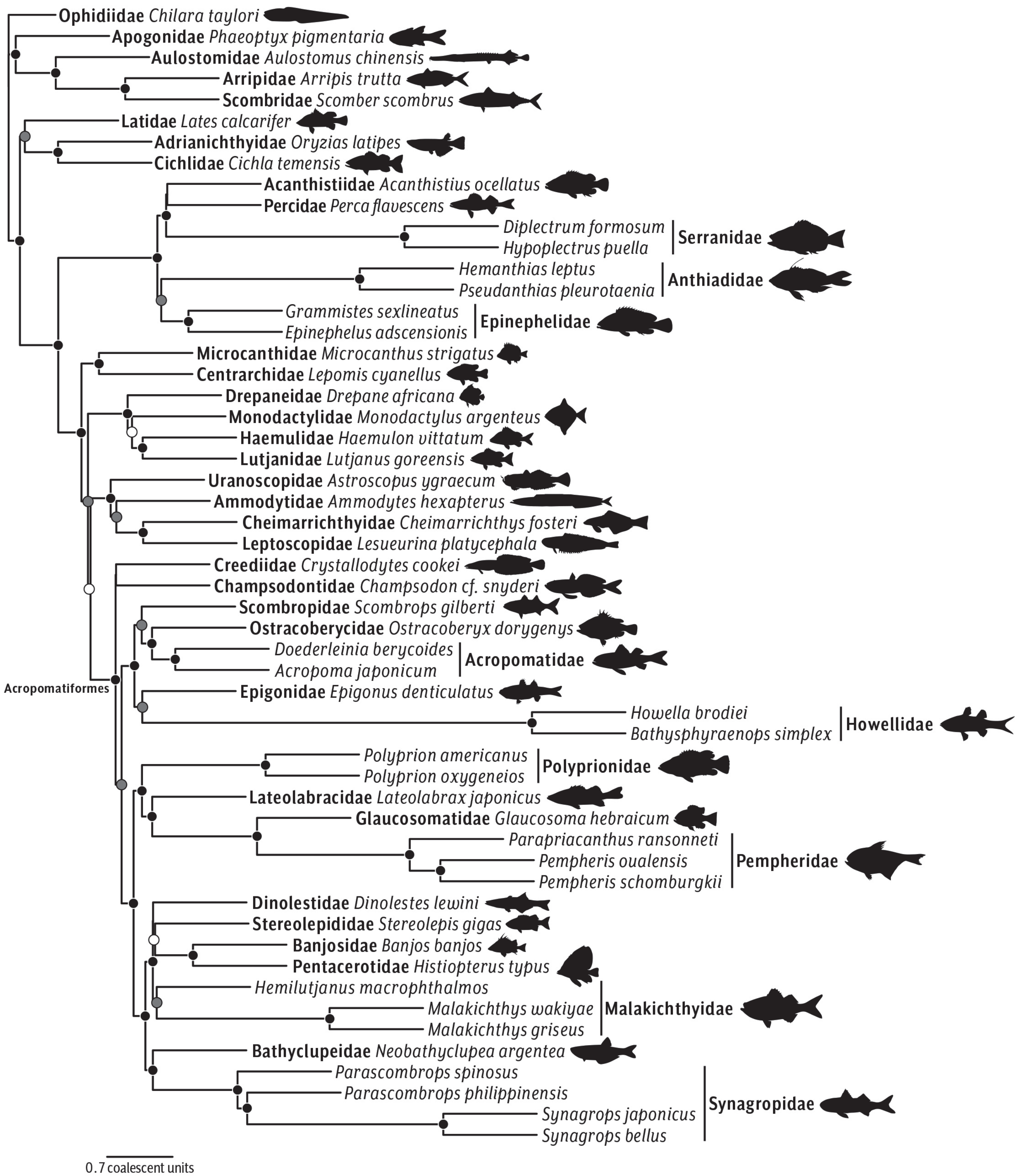

FIGURE 4 | Optimal cladogram resulting from the species-tree analysis of the Sanger and UCE dataset composed of the 54 core taxa and 466 loci. Clades with ≥95% LPP support are identified with a black circle, clades with 70–94% LPP support are identified with a gray circle, and clades with ≥50–69% LPP support are identified with a white circle.

Lateolabracidae, Malakichthyidae, Ostracoberycidae, Pempheridae, Pentacerotidae, Scombropidae, Symphysanodontidae, Synagropidae, and the genera *Polyprion*, *Schuettea*, and *Stereolepis.* The resulting classification differed in composition from all previous formal classifications (*e.g*., Betancur-R *et al*., 2013a, 2017; Rabosky *et al*., 2018; van der Laan *et al*., 2021; Tab. 1) in ways beyond the simple addition of *Hemilutjanus* and *Schuettea*. Unlike the classifications used in Betancur-R *et al.* (2017), Ghedotti *et al.* (2018), Rabosky *et al.* (2018), and van der Laan *et al.* (2021), we excluded Leptoscopidae from the Acropomatiformes. Further, most studies (Tab. 1) excluded one or more of our families from the Acropomatiformes in either their phylogenetic results or their formal classification (Figs. 2–3; Tab. 1). The differences, exclusions, and omissions were substantive with more than half of the families in the clade being excluded in one or more studies (*i.e*., Bathyclupeidae, Champsodontidae, Creediidae, Dinolestidae, Glaucosomatidae, Hemerocoetidae, Ostracoberycidae, Pempheridae, Scombropidae, Symphysanodontidae, Synagropidae, *Hemilutjanus*, and *Schuettea*; Tab. 1). Near *et al.* (2013, 2015), Thacker *et al.* (2015), Davis *et al.* (2016), and Satoh (2018) were the only previous studies with eight or more acropomatiform families that presented phylogenies with a monophyletic Acropomatiformes consistent with the limits presented herein (Tab. 1).

Using the results of the 57-taxon ML analysis, we examined habitat transitions between shallow and deep water at the family level. Using both parsimony and likelihood, we found remarkably large numbers of transitions between shallow and deep-water habitats for a clade of approximately 300 species. Using maximum likelihood, our optimization suggests two independent invasions into the deep sea: the ancestor of the Acropomatiformes and the Champsodontidae. Further, this optimization estimated seven independent returns to shallow water in the Glaucosomatidae+Lateolabracidae+Pempheridae, Champsodontidae+*Schuettea,* Creediidae, Dinolestidae, *Hemilutjanus,* Scombropidae, and *Stereolepis* (Fig. 6). Using parsimony, the Acropomatidae+Epigonidae+Howellidae+Ostracoberycidae+Symphysanodontidae, *Polyprion*, and one or more clades in the Banjosidae+Bathyclupeidae+Champsodontidae+Creediidae+Dinolestidae+Hemerocoetidae+Malakichthyidae+*Stereolepis*+Synagropidae+Pentacerotidae invaded the deep sea. Using maximum likelihood and parsimony, we recover three independent evolutions of bioluminescence at the family level (treating *Schuettea* as a family): Epigonidae+Howellidae, Acropomatidae, and Pempheridae (Fig. 6).

DISCUSSION

This study was first and foremost designed to resolve the placement of *Hemilutjanus*. Given that all our analyses recovered *Hemilutjanus* sister to *Malakichthys* within a monophyletic Acropomatiformes, this discussion begins with this sister-group relationship and its taxonomic implications. Next, this study describes a new family of fishes for *Stereolepis*, discusses the somewhat surprising placement of *Schuettea* in the acropomatiforms, explores the limits and relationships of the Acropomatiformes (including a discussion on the polyphyly of the traditional "Acropomatidae"), and ends with a look at the implications of this revised phylogeny of the Acropomatiformes on the invasion of the deep sea and the evolution of bioluminescence.

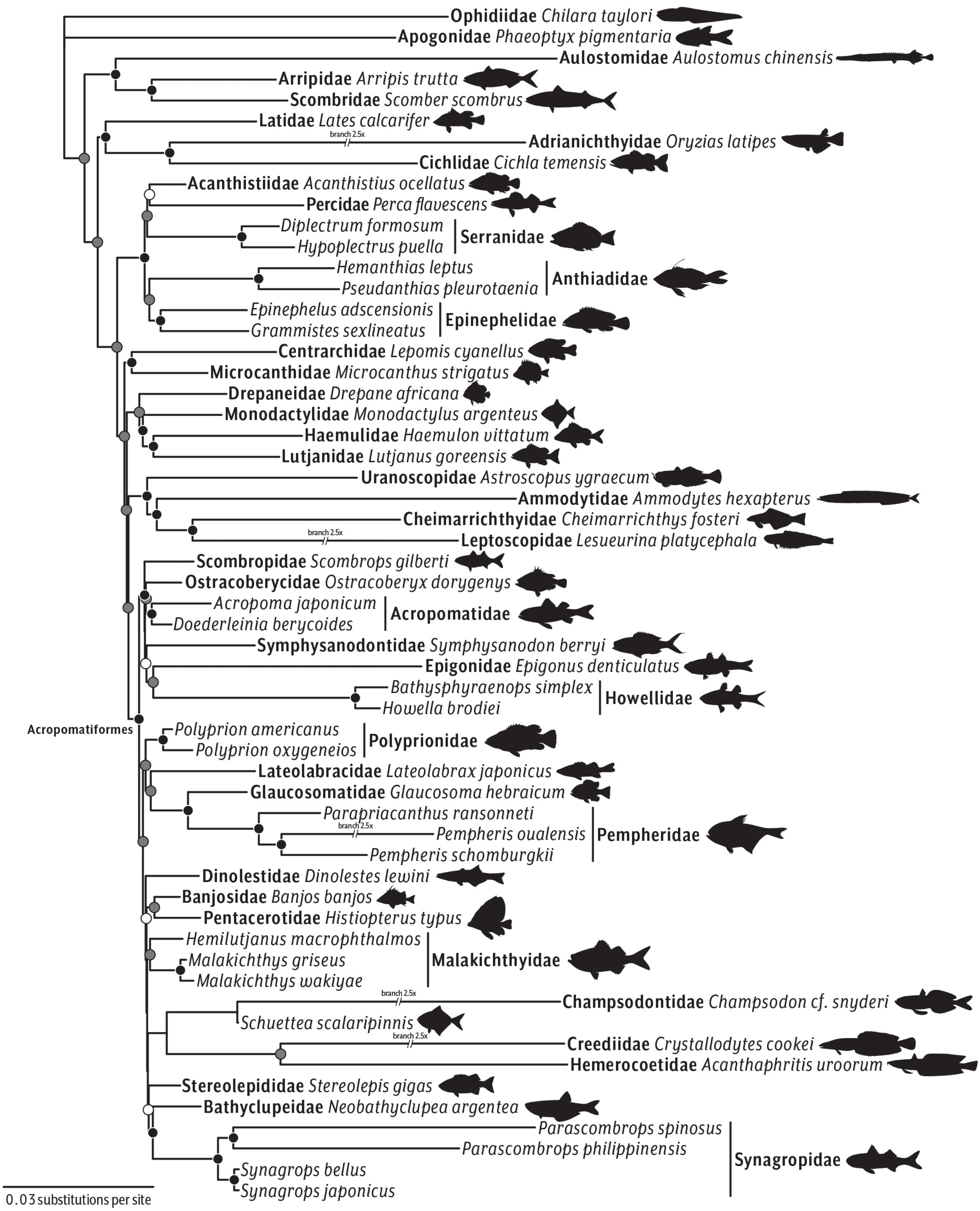

FIGURE 5 | Optimal cladogram resulting from the partitioned-likelihood analysis of the Sanger and UCE dataset of the family-level 57 taxa and 279.979 nucleotide characters. Clades with ≥95% bootstrap support are identified with a black circle, clades with 70–94% bootstrap support are identified with a gray circle, and clades with ≥50–69% bootstrap support are identified with a white circle.

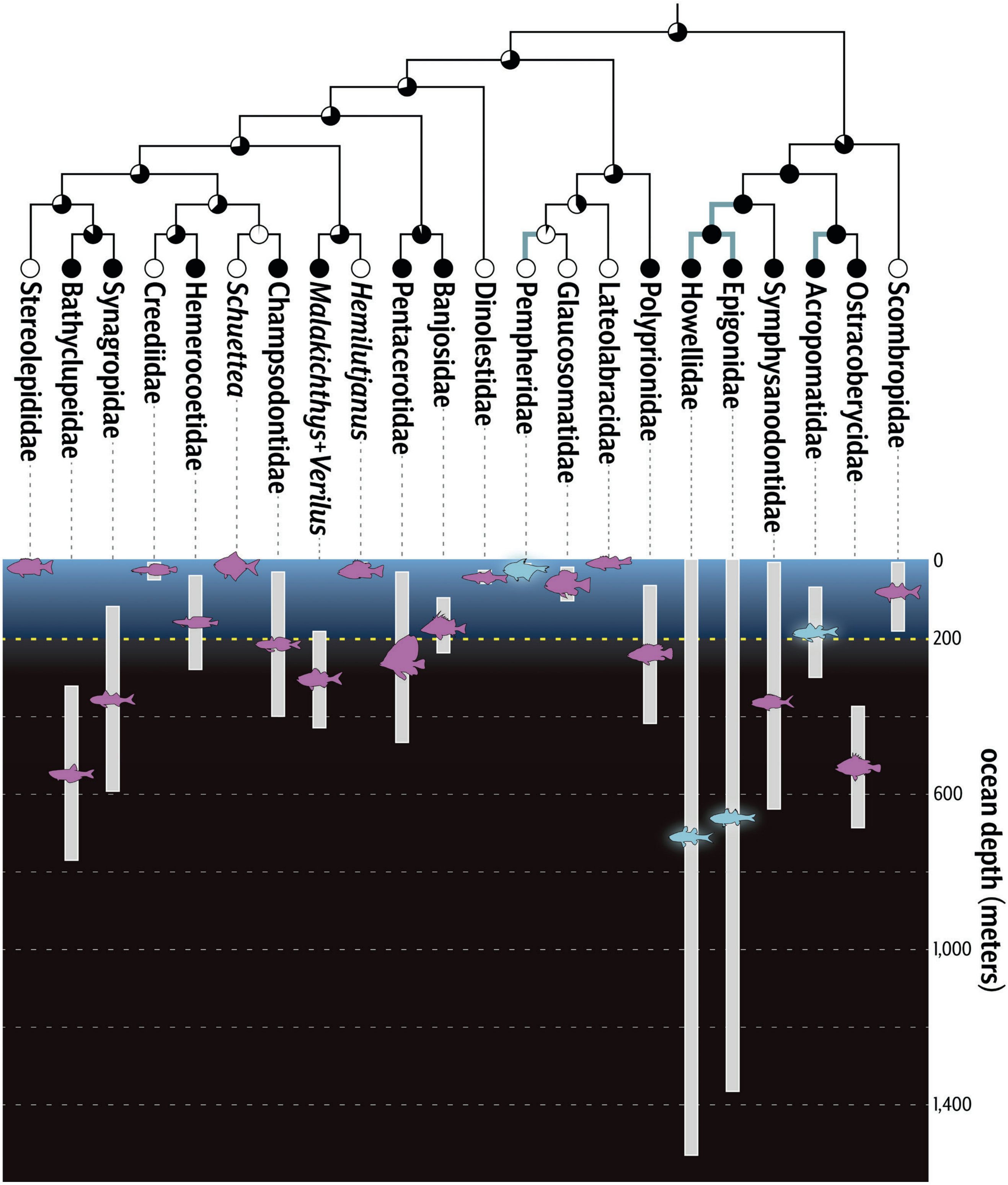

FIGURE 6 | Simplified 57-taxon maximum-likelihood phylogeny of major acropomatiform clades with the maximum-likelihood optimization of depth illustrated as pie charts on the nodes (black: fishes that live in the deep sea; white: fishes that exclusively live in shallow water) and of bioluminescence on the branches (blue: clade includes bioluminescent fishes; black: clade does not include bioluminescent fishes). The depth ranges of the different acropomatiform clades (standard deviation from the mean) are plotted in gray and the depth mean values are represented by the colored silhouettes (blue: families with bioluminescent fishes; pink non-bioluminescent families).

The phylogenetic and taxonomic placement of *Hemilutjanus*. *Hemilutjanus macrophthalmos* has not been included in any previous explicit phylogenetic analyses, but previous studies based on external anatomy or radiographs have suggested possible placements for this species as a "serranid", a close relative of "serranids", among the Arripidae, Banjosidae, Haemulidae, and Lutjanidae, or as *incertae sedis* in the traditional Percoidei (von Tschudi, 1846; Bleeker, 1876; Jordan, Eigenmann, 1890; Boulenger, 1895; Johnson, 1984; Mooi, Gill, 1995; Nelson *et al*., 2016; Parenti, Randall, 2020). No molecular phylogenetic studies have included *Hemilutjanus macrophthalmos*, and the detailed anatomy of this species has not been documented using either cleared-and-stained specimens, dried skeletal material, or micro-computed-tomography scans, so it is not surprising that its placement has remained obscure.

The results of this molecular study clearly place *Hemilutjanus* in the Acropomatiformes and sister to *Malakichthys.* There are no published molecular phylogenetic studies looking broadly at relationships among malakichthyids. There have been species-level external morphological studies across the malakichthyids (Yamanoue, Matsuura, 2004; Yamanoue, 2016) that have documented substantive variation among the species in the family, but there have been limited comparative osteological studies across the "Acropomatidae" or Malakichthyidae (best detailed in Katayama, 1959, and Schwarzhans, Prokofiev, 2017). Katayama (1959) described variation across a diversity of systems for all the known "acropomatids" and allies in Japan, and his primary characters used to separate *Malakichthys* (his Malakichthyinae) from other examined fishes were the absence of a metapterygoid lamina and the lack of canine teeth. Schwarzhans, Prokofiev (2017) provided some osteological differences between malakichthyids and other "acropomatids", but their focus was on the Synagropidae, and they did not discuss the limits and relationships of malakichthyids. Subsequent work by Yamanoue, Matsuura (2004) and Yamanoue (2016) showed that canine teeth were found in some malakichthyids, primarily in *Verilus*, but neither they nor other authors have noted whether species of *Verilus* or species of *Malakichthys* outside of Japan have a metapterygoid lamina. Based on our examination, *Hemilutjanus* has a well-developed metapterygoid lamina and canine teeth, which were absent in our examined material of *Malakichthys*. Thus, previously identified morphological characters are of little use for placing *Hemilutjanus* with *Malakichthys*.

The conclusive placement of *Hemilutjanus* sister to *Malakichthys* with molecular data, however, raises the question whether Hemilutjanidae should be retained as a monotypic family or whether *Hemilutjanus* should be classified as a member of the Malakichthyidae as either choice would be a classification that recognizes only monophyletic groups and both family-level names have already been described and are valid and available. We have chosen to place Hemilutjanidae in the synonymy of Malakichthyidae for several reasons. First, there is virtually no tradition of recognizing Hemilutjanidae. The family was only recently described in 2020 by Parenti and Randall, and that description was in the context of a checklist of the "Serranidae". The authors emphasized the "serranids", and they appear to have described Caesioscorpididae and Hemilutjanidae, so that they could properly exclude them from their "Serranidae". There was no material of *Hemilutjanus* listed as examined in that study, and the family-level diagnosis obviously drew heavily from Hildebrand (1946). The lack of comparative material appears to have resulted in some inaccuracies or misinterpretations of the original study. For example, Parenti, Randall (2020) listed the number of lateral-line scales in *Hemilutjanus* as 108–115, but the lateral-line scale count in *Hemilutjanus* is 64–66, which overlaps with the 37–69 lateral-line scales found in other malakichthyids (Jordan, Eigenmann, 1890; Tab. 2; current study). Given their focus elsewhere, the limited time since the publication of their work, and the limited discussion of *Hemilutjanus* over the last 175 years, we believe that it is preferable to refer *Hemilutjanus* to Malakichthyidae to emphasize the close relationship between *Hemilutjanus*, *Malakichthys*, and *Verilus* and to avoid the recognition of a monotypic family that is substantially like its sister group in physiognomy and meristics. Additionally, the placement of *Hemilutjanus* in the Malakichthyidae represents the addition of an Eastern Pacific representative in the family such that the family is now distributed (generally in deep water) in the eastern and western tropical and temperate regions of the Atlantic, Indian, and Pacific Oceans. A preliminary morphological examination across the Acropomatiformes suggests that *Hemilutjanus, Malakichthys*, and *Verilus* can be united as a clade and separated from all other acropomatiforms by a suite of four characters: 25 vertebrae (10 precaudal and 15 caudal), 10 dorsal-fin spines, the presence of a supramaxilla, and 37–69 lateral-line scales. Comparative meristic and character data that are useful for recognizing an expanded Malakichthyidae among all acropomatiform families can be found in Tab. 2.

Given the revised classification of *Hemilutjanus* among the malakichthyids, the implications for these findings relative to the historic allies in Bleeker's Lutjanini and the "Serranidae" need clarification. The lutjanins, although only a handful of families, have been consistently recovered across multiple orders (Near *et al*., 2013; Davis *et al*., 2016; Sanciangco *et al*., 2016; current study) including the Acanthuriformes (Haemulidae and Lutjanidae), Acropomatiformes (Banjosidae), and Scombriformes (Arripidae). The "Serranidae" used by Katayama (1959) is demonstrably polyphyletic with representatives spread across the Acanthuriformes, Acropomatiformes, Centrarchiformes, and Scorpaeniformes (*e.g*., Davis *et al*., 2016; Sanciangco *et al*., 2016). Unlike Bleeker's Lutjanini, the "Serranidae" has received a lot of attention. Initially, Gosline (1966) and later Johnson (1983) progressively restricted Katayama's (1959) "Serranidae" to a subset of its former taxa with four characters, most notably the presence of an opercle with three spines. Beginning with Imamura, Yabe (2002), ichthyologists began recognizing that the "serranids" may be more closely related to mail-cheeked fishes than most other so-called percoid fishes. Shortly thereafter, numerous molecular studies using 3–10 loci corroborated this close relationship with mail-cheeked fishes, notothenioids, and percids; these studies demonstrated that the "Serranidae" was not monophyletic, and that many of the historic "serranids" excluded by Gosline (1966) and Johnson (1983) belong among the Acropomatiformes (*e.g*., Chen *et al*., 2003; Dettaï, Lecointre, 2004, 2005; Smith, Wheeler, 2004, 2006; Craig, Hastings, 2007; Smith, Craig, 2007; Li *et al*., 2009; Smith *et al*., 2009; Lautredou *et al*., 2013; Near *et al*., 2013). Our analysis included seven "serranids" and one percid in our genome-scale analysis, and we recovered a paraphyletic "Serranidae" relative to the one included percid. Our results provide further evidence for the non-monophyly of the "Serranidae" and the recognition that several former "percoid" and mail-cheeked fish groups are nested among a non-monophyletic "Serranidae" as was first studied in detail by Smith, Craig (2007).

Stereolepis. Our results separated *Stereolepis* from its frequent ally, *Polyprion*. While these two genera have been frequently classified in the Polyprionidae (*e.g*., Nelson, 2006; Nelson *et al*., 2016), there are no synapomorphies that unite these two genera, and several studies have also treated them as independent clades (*e.g*., Gosline, 1966; Johnson, 1983, 1984). There are no morphological phylogenetic analyses that have included both genera, and half of the eight prior molecular studies that included both *Polyprion* and *Stereolepis* have recovered the two genera independently in their resulting phylogenies (Smith, Wheeler, 2006; Smith, Craig, 2007; Betancur-R *et al*., 2013a; Rabosky *et al*., 2018; Fig. 2).

Given the separation of *Polyprion* and *Stereolepis* in most molecular phylogenetic analyses (Figs. 2–5), the lack of morphological evidence placing them together in the Polyprionidae, and the strong support for their separation in this and previous studies, we herein describe a new family for the two charismatic species in *Stereolepis.* Correspondingly, Polyprionidae is hereby restricted to species in the genus *Polyprion.* The recognition of new and revised families for separate clades is critical as we move toward a well-supported monophyletic classification of the Acropomatiformes and Percomorpha.

Stereolepididae new family Smith, Ghedotti & Davis

urn:lsid:zoobank.org:act:420088FA-8845-4090-8616-646A766F05CE

Type genus. *Stereolepis* Ayres, 1859.

Species included. *Stereolepis doederleini* Lindberg & Krasyukova, 1969 and *S. gigas* Ayres, 1859.

Diagnosis. Species in Stereolepididae can be distinguished from all other acropomatiforms by a unique combination of 26 vertebrae (12 precaudal and 14 caudal), 9–12 dorsal-fin spines, and the presence of a supramaxilla (Tab. 2). Species in Acropomatidae, Banjosidae, Epigonidae, Glaucosomatidae, Malakichthyidae, Pempheridae, Synagropidae, and *Schuettea* have 24–25 vertebrae, and species in Champsodontidae, Creediidae, Dinolestidae, and Lateolabracidae have 27 or more vertebrae. The remaining acropomatiform families have overlapping total vertebral counts, but there is also diagnostic variation in the number of precaudal vertebrae. Among acropomatiforms with 26 vertebrae, Howellidae, Ostracoberycidae, Scombropidae, and Symphysanodontidae have 10–11 precaudal vertebrae and species in *Polyprion* have 13 precaudal vertebrae. These counts differ from the 12 precaudal vertebrae found in *Stereolepis*. Among acropomatiforms with 26 vertebrae (and 12 precaudal vertebrae), species in the Bathyclupeidae and Hemerocoetidae have eight or fewer dorsal-fin spines compared with the 9–12 dorsal-fin spines found in *Stereolepis*. Finally, the Pentacerotidae can be separated by its lack of a supramaxilla; whereas, this element is present in the jaws of stereolepidids. These features and a variety of other meristic counts and character states for acropomatiforms are summarized in Tab. 2.

Schuettea. The two species in *Schuettea* are Australian shallow water marine fishes that have been traditionally classified as monodactylids (*e.g*., Regan, 1913; Nelson *et* *al*., 2016). In contrast, Tominaga (1968) suggested that *Schuettea* belonged in its own family that is closely allied with the Pempheridae (a family Regan [1913] allied with Monodactylidae). We included *Monodactylus* and the available sequences for *Schuettea* in our phylogenetic analysis of acropomatiforms following Tominaga's (1968) suggestion.

In our analysis, *Schuettea* was recovered among the Acropomatiformes with strong support, and it was separated from its traditional ally, *Monodactylus.* The specific placement of *Schuettea* was not well supported in our analysis (Fig. 5); it was resolved sister to *Champsodon* in our most likely hypothesis (Fig. 5). Our analysis did not place *Schuettea* sister to Pempheridae, and there are multiple moderately or strongly supported nodes separating these two clades (Fig. 5). In support of his pempherid-*Schuettea* hypothesis, Tominaga highlighted that these clades share 10+15 vertebrae, a lateral line that reaches to the posterior margin of the caudal fin, and anteriorly extended epaxial muscles that reach the frontals. Additionally, Tominaga highlighted three features that were unique to *Schuettea* in his study: rib-like ossicles on the first and second hemal spines, a posterior extension of the gas bladder, and three anal-fin pterygiophores inserted anteriorly to the first hemal spine. Our preliminary osteological investigation focusing on acropomatiforms found that *Schuettea* (based on a dried skeleton) has cycloid scales (also shared with some or all acropomatids, bathyclupeids, creediids, dinolestids, hemerocoetids, pempherids, scombropids, synagropids, and *Verilus*), has a reduced number of dorsal-fin spines (five) and a larger number of dorsal- and anal-fin rays (28–32), has a spineless first dorsal-fin pterygiophore, and lacks a procurrent spur and supramaxilla (Johnson, 1984; Rosa, 1995; Nelson, 2006; Yamanoue, 2016; current study; Tab. 2). While externally dissimilar, many of these features are shared with the Champsodontidae, Creediidae, and Hemerocoetidae that have been typically recovered as a clade (Near *et al*., 2013, 2015; Thacker *et al*., 2015; Sanciangco *et al*., 2016; Ghedotti *et al*., 2018; Satoh, 2018; Fig. 2) and where we recovered *Schuettea* in our analysis (Fig. 5). Clearly, a more detailed examination using morphological and molecular data is needed to conclusively place *Schuettea.* Because of the nature of the preliminary morphological examination and the poor molecular support, we are not prepared to describe a new family for *Schuettea.* There remains a good chance that it is sister to or within a currently recognized acropomatiform family, and subsequent research will be needed to determine whether it should be classified within that family or in its own family. For now, we classify both species of *Schuettea* as *incertae sedis* in the Acropomatiformes, and this clade can be diagnosed from all other acropomatiforms by having 24 vertebrae (10 precaudal and 14 caudal), five dorsal-fin spines, and 28–32 anal-fin and 28–31 dorsal-fin rays (Tab. 2).

Phylogeny of the Acropomatiformes. The Acropomatiformes is one of the major clades in the recently recognized Eupercaria, and several early large-scale molecular phylogenies circumscribed this clade without recognizing it or focusing on its intrarelationships (Smith, Wheeler, 2006; Smith, Craig, 2007; Betancur-R *et al*., 2013a; Near *et al*., 2013, 2015; Thacker *et al*., 2015; Fig. 2; Tab. 1). Davis *et al.* (2016), Mirande (2016), Sanciangco *et al.* (2016), and Rabosky *et al.* (2018) all provided phylogenies and family-level classifications for the acropomatiforms, but Ghedotti *et al.* (2018) and Satoh (2018) were the first studies to explicitly focus on the intrarelationships of the Acropomatiformes (Fig. 2). Across previous acropomatiform studies (Fig. 2), the lack of consistent clades, the few repeated results, and the limited number of strongly supported nodes is somewhat surprising. In an attempt to resolve relationships within the Acropomatiformes with strong support, we purposefully chose taxa to cover the diversity of acropomatiforms, and we greatly expanded the number of base pairs (Tab. 1). Increasing the number of base pairs in an analysis often results in phylogenies with more support and well-supported hypotheses (*e.g.*, Harrington *et al*., 2016; Longo *et al*., 2017; Martin *et al*., 2018). This increase in data combined with being the first study to include all families of acropomatiforms resulted in phylogenies with considerably more support than previous studies (Figs. 3–4). Despite many new hypothesized relationships in our study, there are several clades of acropomatiforms that we recovered that recent molecular studies have also recovered. There are four clades shared among our analyses and many previous studies that we will focus on beyond the placement of *Hemilutjanus*: 1) Acropomatidae, Epigonidae, Howellidae, Ostracoberycidae, Scombropidae, and Symphysanodontidae; 2) Banjosidae and Pentacerotidae; 3) Champsodontidae, Creediidae, Hemerocoetidae, and potentially *Schuettea*; and 4) Glaucosomatidae and Pempheridae (Figs. 2–5).

The largest repeated clade found within the acropomatiforms is the Acropomatidae, Epigonidae, Howellidae, Ostracoberycidae, Scombropidae, and Symphysanodontidae or what we refer to as the Acropomatoidei. The acropomatoids were first grouped together by Near *et al.* (2013) who included the Acropomatidae, Howellidae, and Ostracoberycidae in their study. Subsequent studies by Near *et al.* (2015), Thacker *et al.* (2015), Davis *et al.* (2016), Sanciangco *et al.* (2016), Ghedotti *et al.* (2018), and Satoh (2018) continued to recover this clade as new families and more data were added to the analyses. Interestingly, the acropomatoids were not recovered in analyses based on fewer than 5.000 base pairs (*i.e.*, Smith, Wheeler, 2006; Smith, Craig, 2007; Tab. 1) or in analyses with substantial (>50%) missing data (*e.g.*, Betancur-R *et al*., 2013a; Mirande, 2016; Rabosky *et al*., 2018; Tab. 1). Given the recurrent discovery of this clade in studies that had sufficient DNA-sequence data (*i.e.*, more than 5.000 bps) and studies that emphasized overlapping data relative to increased taxonomic sampling (*i.e.*, studies with less than 30% missing data), it is possible that many of the conflicting results depicted in Fig. 2 are due to data insufficiency rather than data conflict. The acropomatoids have substantial morphological variation, and our preliminary morphological investigation did not identify any synapomorphies for this group. Species in this clade are predominantly found in the deep sea (although many deep-sea families have species that reside in shallower waters; Fig. 6), and the acropomatoids include many of the acropomatiforms that were formerly included in the "serranids" (*sensu* Katayama, 1959).

In addition to the acropomatoids, one of the most frequently recovered clades in studies that have included many acropomatiforms is the sister-group pairing of Banjosidae and Pentacerotidae. This sister-group pairing has been recovered in every molecular analysis that included both families (Fig. 2) except Satoh (2018). In a detailed morphological study of the Pentacerotidae, Kim (2012) included Banjosidae as one of his outgroup taxa. Although there was no formal outgroup analysis, Kim suggested that Chaetodontidae and Ostracoberycidae were the most likely sister groups to the Pentacerotidae. Subsequent molecular analyses consistently place the Chaetodontidae within the Acanthuriformes and Ostracoberycidae in the Acropomatiformes (Near *et al*., 2013; Davis *et al*., 2016; Sanciangco *et al*., 2016; Smith *et al*., 2016). Most molecular studies have recovered ostracoberycids among the acropomatoids (Fig. 2). Interestingly, Kim (2012) noted that he allied the chaetodontids with the pentacerotids because chaetodontids shared four of the pentacerotid synapomorphies (his SA3, SA4, SA5, and SA7) and because they have strongly compressed bodies. Banjosids share these four formal synapomorphies and this one informal synapomorphy (compressed bodies) with the pentacerotids (Kim, 2012). There is no explanation in Kim (2012) for why chaetodontids were preferred over banjosids, but given the molecular results presented by Near *et al.* (2013, 2015), Thacker *et al.* (2015), Davis *et al.* (2016), Mirande (2016), Sanciangco *et al.* (2016), Ghedotti *et al.* (2018), Rabosky *et al.* (2018), and the current study (Figs. 2–5), it is clear that this banjosid sister-group relationship is supported and should be explored more explicitly with morphological data.

Another clade of acropomatiforms that is consistently recovered is the group that includes Champsodontidae, Creediidae, Hemerocoetidae, and, potentially, *Schuettea.* We refer to this clade informally as the "champsodontoids". While Creediidae and Hemerocoetidae have been consistently recovered together in previous studies (Fig. 2; Tab. 1), the placement of Champsodontidae among, or even in, the acropomatiforms has been the most problematic family-level placement in the order (Tab. 1). Despite some ambiguity, this clade has been consistently recovered in previous studies (Near *et al*., 2013, 2015; Thacker *et al*., 2015; Sanciangco *et al*., 2016; Ghedotti *et al*., 2018; Satoh, 2018; Tab. 2) with a few exceptions that potentially lacked sufficient data (Smith, Craig, 2007) or had extensive missing data (Mirande, 2016; Rabosky *et al*., 2018). Relative to other acropomatiforms, the champsodontoids are characterized generally by larger vertebral counts, the loss of both the procurrent spur and supramaxilla, more median fin-ray elements, and few to no dorsal- and anal-fin spines (Tab. 2). The monophyly and support of this clade will depend on the inclusion, or not, of *Schuettea* and the phylogenetic placement of the clade given its movement in our analyses (Figs. 3–5).

The final acropomatiform clade that is consistently recovered is the grouping of Glaucosomatidae and Pempheridae (Betancur-R *et al*., 2013a; Near *et al*., 2013, 2015; Thacker *et al*., 2015; Davis *et al*., 2016; Mirande, 2016; Sanciangco *et al*., 2016, Ghedotti *et al*., 2018; Rabosky *et al*., 2018 [albeit outside of the Acropomatiformes]; Satoh, 2018; current study; Figs. 2–5). This sister-group pairing is the most consistent result across all acropomatiform studies, and it has been found in all analyses with more than six loci (Fig. 2; Tab. 1). While there are no known morphological synapomorphies to unite this group, the ubiquity of their relationship across molecular studies (Fig. 2) provides striking support for the placement of these two families together. This clade, while frequently recovered with DNA-sequence data, has not been recovered in morphological analyses and would benefit from morphological investigations, particularly considering Tominaga's (1968) hypothesis that pempherids and *Schuettea* are closely related.

While we are beginning to recognize well-supported clades across a diversity of studies examining the Acropomatiformes, the monophyly of the traditional "Acropomatidae" is continually being rejected, and it should not be recognized further. The family Acropomatidae was described (as Acropomidae) by Gill (1893) as one of the families of his Percoidea. Most studies in the late 19th century and early 20th century allied members of the modern Acropomatidae, Malakichthyidae, and Synagropidae with the Apogonidae or "Serranidae" (*sensu* Katayama, 1959) and did not treat them as a single natural group (*e.g*., Jordan, Richardson, 1910; Regan, 1913; Schultz, 1940).

Katayama (1959), in the most extensive comparative morphological investigation of the “Acropomatidae”, split these taxa across three subfamilies (his Acropominae, Döderleininae, and Malakichthyinae), none of which has the same composition as any modern “acropomatid” family. Despite Katayama (1959: fig. 39) classifying these species in three subfamilies, he did illustrate the included genera as what we would refer to as a monophyletic group in his pre-cladistic phylogeny. Further, he placed this assemblage in a trichotomy with (*Stereolepis* + (*Coreoperca*+*Siniperca*)) and *Lateolabrax.* This clade was sister to a clade composed of *Niphon* and *Ostracoberyx,* and these taxa were referred to as the “*Acropoma*-stem group”. Gosline (1966) treated the “acropomatids” as part of his “oceanic percichthyids”. Johnson (1984: 464) recognized the modern “Acropomatidae”, but he noted that he knew “of no synapomorphy that unites the acropomatids, and further work will be necessary to test their monophyly”. Following Johnson’s (1984) study, many studies treated the “Acropomatidae” as a family that included the modern Acropomatidae, Malakichthyidae, and Synagropidae (Nelson *et al*., 2016), but other authors variously included members of the Howellidae, Scombropidae, Symphysanodontidae, and Polyprionidae within the Acropomatidae (*e.g*., Heemstra, 1986; Nelson, 1994, 2006; Heemstra, Yamanoue, 2003). More recent authors conducting morphological analyses (*e.g*., Prokofiev, 2007; Schwarzhans, Prokofiev, 2017) have provided evidence to refute the monophyly of the “Acropomatidae”. Across all these morphological studies, it is clear that a close relationship among a number of acropomatiform clades were being recognized, but the limits and relationships of the families and the order as a whole remained unclear.

Beginning with Smith, Craig (2007), molecular studies began to include multiple genera of “acropomatids” and were consistently finding the family polyphyletic (Betancur-R *et al*., 2013a; Near *et al*., 2013, 2015; Thacker *et al*., 2015; Davis *et al*., 2016; Mirande, 2016; Sanciangco *et al*., 2016; Ghedotti *et al*., 2018; Rabosky *et al*., 2018; Fig. 2; Tab. 1). Across the previous and current molecular studies, the Acropomatidae, Malakichthyidae, and Synagropidae were always found independent of each other (Figs. 2–5). The sister groups of each family varied among studies. Seven of the previous studies and the current study recovered a clade composed of the acropomatoids (Near *et al*., 2013, 2015; Thacker *et al*., 2015; Sanciangco *et al*., 2016; Ghedotti *et al*., 2018; Satoh, 2018; Figs. 2–5). Among these studies and the current study, the most common sister group for the Acropomatidae was the Ostracoberycidae, which was not one of the families that traditional studies had classified within the Acropomatidae. The sister group to Malakichthyidae was less consistent across studies or across methods in our study (Figs. 2–5). Our core ML analysis recovered Malakichthyidae sister to a clade composed of Bathyclupeidae, Champsodontidae, Creediidae, Stereolepididae, and Synagropidae (Fig. 3). In contrast, our results from the ST analysis place a clade composed of Banjosidae, Dinolestidae, Pentacerotidae, and Stereolepididae sister to Malakichthyidae (Fig. 4). The only shared member from the malakichthyid sister-group clades between our two analyses was Stereolepididae, which is, overall, the most consistent sister group in previous studies (Near *et al*., 2013, 2015; Thacker *et al*., 2015; Davis *et al*., 2016; Rabosky *et al*., 2018). The specific sister group to Malakichthyidae remains contentious (Figs. 2–5). The third “acropomatid” family is Synagropidae, which we consistently recovered sister to Bathyclupeidae across methods and datasets with strong support (Figs. 3–5). In contrast, no previous studies recovered a bathyclupeid sister group for Synagropidae, and the only repeated sister group in previous analyses was Howellidae (Mirande, 2016; Rabosky *et al*., 2018; Fig. 2). While these two studies recovered a howellid sister group, most studies (noted above) place Howellidae in a distantly related and well-supported clade with Acropomatidae, Epigonidae, Ostracoberycidae, Scombropidae, and Symphysanodontidae. Therefore, every previous molecular study with multiple "acropomatid" families and the current study show that the "Acropomatidae" is polyphyletic (Figs. 2–5). Most studies have found the Acropomatidae sister to Ostracoberycidae (Near *et al*., 2013, 2015; Thacker *et al*., 2015; Davis *et al*., 2016; current study; Figs. 2–5). The current study shows that Synagropidae is sister to Bathyclupeidae (Figs. 3–5) and the placement of Malakichthyidae among the acropomatiforms has conflicting results (Figs. 2–5).

Our study included considerably more data than all previous studies that included substantive acropomatiform taxa (Tab. 1), and it was the first study to include every acropomatiform family and every genus classified as *incertae sedis*. Our results were recovered with considerable support (>80% of nodes were well or moderately well supported across all three analyses; Figs. 3–5), and outside of the placement of the champsodontoids, most relationships were shared among the acropomatiforms across methods (Figs. 3–4). Relative to studies with limited sequence data (*e.g*., Smith, Craig, 2007) and studies with extensive missing data or goals well outside of the Acropomatiformes (*e.g*., Betancur-R *et al*., 2013a; Sanciangco *et al*., 2016; Rabosky *et al*., 2018), there is more consistency of relationships than not (*e.g*., Near *et al*., 2013, 2015; Thacker *et al*., 2015; Davis *et al*., 2016; Ghedotti *et al*., 2018; Satoh, 2018; current study). Perhaps much of the conflict that researchers are finding among studies of percomorph groups is due more to insufficient data rather than conflicting data. Certainly, including as many species as possible has benefits (Wiens, Tiu, 2012; Borden *et al*., 2013; Tang *et al*., 2021), but the inclusion of taxa with insufficient comparable data has resulted in contradictory phylogenies for the Acropomatiformes (Figs. 2–5; Tab. 1).

Evolution of the Acropomatiformes. Through our work to resolve the placement of *Hemilutjanus*, we have taken this opportunity to examine the limits and relationships of the Acropomatiformes. One of the striking changes in our understanding of percomorph relationships that came following our improved understanding of fish relationships or Smith's (2010:523) impending "renaissance" brought on by molecular systematics is that we have approximately 20 repeatedly recovered clades (orders in Davis *et al*., 2016) of percomorphs of which three-quarters of these clades are completely new to science. These are newly recognized clades, so we have studied little more than their phylogeny since their identification over the last decade (Betancur-R *et al*., 2013a; Near *et al*., 2013; Davis *et al*., 2016; Sanciangco *et al*., 2016; Smith *et al*., 2016; Rabosky *et al*., 2018). This is a dynamic time in fish phylogenetics because the classification of fishes is fluid and changing, and we are now able to explore the morphology, biology, and evolution of these percomorph orders (*e.g*., Thacker, 2014; Davis *et al*., 2016; Harrington *et al*., 2016; Ghedotti *et al*., 2018; Rabosky *et al*., 2018; Girard *et al*., 2020). The dominant biological phenomena that have been recognized among acropomatiforms are that this relatively small order of ~300 species includes a surprisingly large number of bioluminescent and deep-water species (for percomorphs) that previous studies have suggested evolved independently multiple times (Davis *et al*., 2016; Ghedotti *et al*., 2018) and that they are poorly represented in the Eastern Pacific (Schwarzhans, Prokofiev, 2017).

The evolution of bioluminescence among acropomatiforms has been explicitly studied by Davis *et al.* (2016) and Ghedotti *et al.* (2018). Both studies highlighted that approximately 10% of acropomatiforms are bioluminescent, and both studies included representatives of all four acropomatiform families that have bioluminescent species (Acropomatidae, Epigonidae, Howellidae, and Pempheridae; Tab. 1). Davis *et al.* (2016) suggested that bioluminescence evolved in the Acropomatidae, Epigonidae+Howellidae, and Pempheridae. Ghedotti *et al.* (2018) hypothesized that representatives of each family with bioluminescent species evolved bioluminescence independently in their analysis. Their study included more acropomatiforms, but it included fewer acropomatiform families and less DNA-sequence data. Further, they noted that bioluminescence may have evolved multiple times independently among epigonids. Our results present a different phylogeny of acropomatiform fishes relative to these two prior studies, and our phylogeny suggests three independent evolutions of bioluminescence: Acropomatidae, Pempheridae, and the ancestor of Epigonidae and Howellidae (Fig. 6). However, and as noted by Ghedotti *et al.* (2018), none of these families is wholly bioluminescent with between 6% and 92% of the species in each family being bioluminescent (Acropomatidae: 12 of 13 species are bioluminescent; Epigonidae: 3 of 47 species; Howellidae: 1 of 9 species; Pempheridae: 5 of 85 species). Further, Ghedotti *et al.* (2018) noted that the epigonids in *Epigonus* and *Rosenblattia* have different anatomies for their bioluminescent organs (Ghedotti *et al*., 2018). Taken together, this not only suggests that each bioluminescent family of acropomatiforms evolved bioluminescence independently, but it also suggests that epigonids may have evolved bioluminescence twice. If our higher-level phylogeny is correct and the species-level phylogeny and anatomical descriptions for the Epigonidae in Ghedotti *et al.* (2018) are correct, bioluminescence would have likely evolved at least five times in the Acropomatiformes, once in shallow water (Pempheridae) and four times in the deep sea (Acropomatidae, Howellidae, and twice in the Epigonidae). To further resolve questions around the evolution of bioluminescence in the Acropomatiformes, we need denser taxon sampling in the Acropomatidae, Epigonidae, Howellidae, and Pempheridae, with a particular emphasis on the Epigonidae and Pempheridae. Given our phylogenetic hypothesis, it is noteworthy that the shallow water bioluminescent pempherids obtain all necessary bioluminescent molecules through their diets, whereas the deep-water bioluminescent acropomatiforms rely on symbiotic bacteria (Ghedotti *et al*., 2018; Bessho-Uehara *et al*., 2020) and are restricted to the acropomatoids that invaded the deep sea prior to the evolution of bioluminescence.

Although not explicitly discussed in previous acropomatiform studies, the acropomatiforms are unusual for percomorphs in that more than half of the species can be found in deep water ≥ 200 m (Froese, Pauly, 2021). Relative to other percomorph ordinal-level clades identified by Davis *et al.* (2016), no other order is dominated by deep-sea fishes (Davis *et al*., 2016; Nelson *et al*., 2016; Froese, Pauly, 2021). Optimizing the invasions of the deep sea among acropomatiforms using parsimony and maximum likelihood demonstrate that acropomatiforms invaded the deep sea and shallow water multiple times (Fig. 6). Using parsimony, there is much ambiguity in the specific acropomatiform clades that have invaded the deep sea. Using maximum likelihood, we found that there was one invasion in the ancestor of the Acropomatiformes and one invasion in the ancestor of the Champsodontidae. The number of returns to shallow water suggested by our parsimony optimization are hampered by many ambiguous or equally parsimonious reconstructions, but in maximum likelihood, we see independent invasions in the Glaucosomatidae+Lateolabracidae+Pempheridae, Champsodontidae+*Schuettea*, Creediidae, Dinolestidae, *Hemilutjanus*, Scombropidae, and Stereolepididae (Fig. 6). Transitions between shallow water and the deep sea and the evolution of bioluminescence are not that common in the Eupercaria (Froese, Pauly, 2021). Repeated transitions between shallow and deep environments within the 300 acropomatiform species is noteworthy. Similarly, the multiple evolutions of bioluminescence among just 300 species of acropomatiforms is also startling. These habitat invasions and luminescent adaptations are uncommon (but not rare) among percomorphs, but the frequency of these specializations and transitions demands further research on this largely unexplored and newly discovered order of fishes.

Finally, this study highlights our natural biases to compare fishes from similar habitats. One of the likely reasons that no one had found the closest relatives to *Hemilutjanus* is that, while a shallow water fish, its closest relatives are in the deep sea. Further, its deep-sea relatives are poorly represented in the Eastern Pacific Ocean. By searching broadly for its potential relatives and benefiting from the molecular phylogenies that have grouped many of the species excluded from the "serranids" (*sensu* Johnson, 1993) into the Acropomatiformes (*e.g*., Smith, Wheeler, 2006; Smith, Craig, 2007; Betancur-R *et al*., 2013a; Near *et al*., 2013, 2015; Thacker *et al*., 2015; Davis *et al*., 2016; Mirande, 2016; Sanciangco *et al*., 2016; Rabosky *et al*., 2018; Tab. 1), we have been able to place *Hemilutjanus* in the Malakichthyidae. This phylogenetic placement also adds to the diversity of acropomatiforms in the Eastern Pacific Ocean, particularly in shallow waters. The addition of another shallow water fish in the Acropomatiformes, particularly one sister to a deep-sea clade, serves as a good reminder that acropomatiforms have many transitions between deep-sea and shallow-water habitats (Fig. 6), particularly for a recent group in the Eupercaria. Most orders dominated by deep-sea fishes have few to no transitions between shallow and deep-water habitats (*e.g*., Alepocephaliformes, Myctophiformes, Stomiiformes; Davis *et al*., 2016; Nelson *et al*., 2016). These transitions and the biases scientists have for making comparisons of fishes from similar locations and habitats may best explain why the Acropomatiformes was not recognized earlier and why its relationships have been so poorly understood.

Material examined. Acropomatiform specimens and skeletal material examined for meristic and anatomical features – abbreviations: ALC (formalin-fixed and alcohol-stored material); C&S (cleared-and-stained material); DS (dried-skeletal material); X (radiographed material). Acropomatidae (*Acropoma hanedai*, KUI 41815, ALC 2, C&S 2; *A. japonicum*, KUI 41855, ALC 2, C&S 2; *Doederleinia berycoides*, KUI 41745, ALC 1, C&S 1); Banjosidae (*Banjos banjos*, KUI 41491, C&S 1); Bathyclupeidae (*Bathyclupea*, SIO uncat., C&S 1); Champsodontidae (*Champsodon snyderi*, FMNH 120679, C&S 1); Dinolestidae (*Dinolestes lewini*, SIO 75-502, C&S 1); Epigonidae (*Epigonus pandionis*, FMNH 67480, C&S 1); Malakichthyidae (*Hemilutjanus macrophthalmos*, LACM 44038, X 1; *H. macrophthalmos*, SIO 12-3086, C&S 1; *H. macrophthalmos*, USNM 77623, ALC 1; *Malakichthys wakiyae*, KUI 41723, ALC 2, C&S 2); Pempheridae (*Pempheris schomburgkii*, FMNH 93774, C&S 1); Polyprionidae (*Polyprion oxygeneios*, KUI 19354, DS 1); Stereolepididae (*Stereolepis gigas*, SIO 15-1314, ALC 1); Symphysanodontidae (*Symphysanodon octoactinus*, FMNH 70766, C&S 1); Synagropidae (*Parascombrops philippinensis*, KUI 41495, C&S 1); *incertae sedis* (*Schuettea scalaripinnis*, ANSP 78163, DS 1).

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