Environ Biol Fish (2023) 106:1747–1754
https://doi.org/10.1007/s10641-023-01452-8

Widespread occurrence and repeated evolution of ultra-black camouflage in the pelagic deep-sea anguilloid eels (Anguilliformes)

Michael J. Ghedotti · Kandice C. Agudo · Flor M. Gonzalez · Benjamin W. Frable

Received: 8 April 2023 / Accepted: 11 July 2023 / Published online: 18 July 2023

Abstract The deep-sea environment is associated with a wide range of anatomically specialized morphologies allowing camouflage in this low or no light environment. Specialized ultra-black coloration has been documented in the pelican eel, *Eurypharynx pelecanoides*, but has not been explored in the other largely deep-sea inhabiting pelagic anguilloid eels. Histological examination of the integument revealed a layer of free melanosomes in the superficial dermis consistent with specialized ultra-black camouflage in the swallower eels *Saccopharynx*, the bobtail snipe eel *Cyema*, the sawtooth eels *Serrivomer*, and the snipe eels *Avocettina* and *Nemichthys*. The anatomy in these taxa is consistent with the previously described ultra-black morphology, except that *Nemichthys*, *Avocettina*, and *Serrivomer* have both large amounts of free melanosomes and melanophores. Consideration of this morphology in the context of anguilloid eel evolution in the deep-sea environment suggests repeated independent evolution of ultra-black coloration within the anguilloids, and greater development in the taxa more specifically associated with the bathypelagic habitats and the production of bioluminescence.

Keywords Coloration · Histology · Integument · Melanocyte · Melanosome · Bioluminescence

M. J. Ghedotti (✉) · K. C. Agudo · F. M. Gonzalez
Department of Biology, Regis University, Denver, CO 80221, USA
e-mail: mghedott@regis.edu

M. J. Ghedotti
Bell Museum of Natural History, University of Minnesota, St. Paul, MN 55108, USA

B. W. Frable
Marine Vertebrate Collection, Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA 92093, USA

Introduction

The deep-sea environment is associated with a wide range of anatomically specialized morphologies that, in some cases, evolved repeatedly in response to the specialized conditions in deep sea environments (Priede 2017). Black coloration is very common in deep-sea fishes and likely provides camouflage by absorbing more of the bioluminescence and limited sunlight in these environments (Herring 2002; Johnsen 2005; Priede 2017). In the more typical form of black pigmentation in fishes, melanin-containing melanosomes within melanophores can be localized in the cell soma, reducing coloration intensity, or be distributed into dendritic processes, increasing the intensity of overall dark coloration (Fujii 2000; Sugimoto 2002; D'Alba and Shawkey 2019). Ultra-black coloration in fishes is produced by a dense layer of free melanosomes in the superficial dermis that are not contained in melanophores (Davis et al. 2020). This layer of melanosomes results in greater light absorption

than in fishes with melanosomes contained within melanophores (Davis et al. 2020). Ultra-black camouflage is currently known to be present in a wide range of distantly related species of fishes, including the pelican gulper eel *Eurypharynx pelecanoides* Vaillant 1882, and it likely evolved many times in the context of the deep-sea environment (Davis et al. 2020). The environment of the deep sea where solar light is dim or absent and bioluminescence is common may provide a context where a highly light-absorbing camouflage is more beneficial than the pigmentation plasticity that melanophore-contained melanosomes can provide. Although ultra-black camouflage is present in diverse taxa, it has not been explored within a monophyletic group of species containing a wide range of particularly black-pigmented, deep-sea taxa.

After transformation from the leptocephalus larval stage, the majority of anguilliform families inhabit the deep sea, below 200 m, and many groups have received limited study due to these difficult-to-access habitats (Böhlke et al. 1989; Fishelson 1994). The suborder Anguilloidei is a mostly deep-sea clade that includes the shallow-water spaghetti eels (Moringuidae) and the catadromous freshwater eels that spawn pelagically in the deep sea (Anguillidae), as well as the primarily deep-sea sawtooth eels (Serrivomeridae), snipe eels (Nemichthyidae), one-jaw eels (Monognathidae), bob-tail snipe eel (Cyematidae), red bob-tail snipe eel (Neocyematidae), pelican eel (Eurypharyngidae), and swallower eels (Saccophayngidae) (Santini et al. 2013; Tang and Fielitz 2013; Poulsen et al. 2018). The deep-sea anguilloids are especially notable for their pelagic habitat, the wide range of jaw structure, and specialized coloration including black, red (in *Neocyema*), and transparent (in *Monognathus*) species, all of which likely evolved in response to their deep-sea habitats (Nielsen and Smith 1978; Nielsen and Bertelsen 1985; Bertelsen and Nielsen 1987; Bertelsen et al. 1989; Nielsen et al. 1989; Poulsen et al. 2018).

Absorption of light in the deep sea near or below the limit of sunlight penetration provides better camouflage from bioluminescent sources than light-reflective coloration (Priede 2017). Among the deep-sea anguilloids, only serrivomerids, some of which vertically migrate nearer the surface nightly after post-larval transformation and before reaching adult size, are most common at adult size in the mesopelagic and have some reflective coloration in addition to black pigmentation (Tighe 1989). *Nemichthys scolopaceus* Richardson 1848, the slender snipe eel, and *Avocettina infans* (Günther 1878), the Avocet snipe eel, usually inhabit the mesopelagic above 1000 m (Nielsen and Smith 1978; Smith and Nielsen 1989). Adult-sized individuals of the remaining deep sea anguilloids are most commonly collected in bathypelagic environments (Böhlke et al. 1989; Froese and Pauly 2000). The gulper eels in the genera *Eurypharynx* and *Saccopharynx* are the only known bioluminescent members of Anguilloidea and have a caudal light organ that has been suggested to be a prey lure (Nielsen and Bertelsen 1985; Nielsen et al. 1989; Priede 2017). The gulper eels are most commonly found in the bathypelagic zone and have an intense black coloration in life that has been demonstrated to be ultra-black coloration based on melanin-containing melanosomes in *Eurypharynx* (Nielsen and Bertelsen 1985; Nielsen et al. 1989; Davis et al. 2020). Davis et al. (2020) demonstrated that the very low reflectance of ultra-black camouflage would be particularly advantageous as camouflage from the relatively dim light produced by bioluminescence as compared to solar light and suggested that this was the functional benefit of an ultra-black coloration.

In this study, we explore the presence of ultra-black camouflage in the deep ocean anguilloid eels using gross and histological methods. Ultra-black coloration is known to be present in the putatively bioluminescent *Eurypharynx pelecanoides* and all the black members of this clade inhabit deep-sea environments (Böhlke et al. 1989; Davis et al. 2020). We also expect that this camouflage from bioluminescent illumination once evolved should provide significant adaptive benefits in the deep ocean. Therefore, we predict all the black, deep-sea taxa will exhibit integumentary structures consistent with ultra-black coloration, but that the development of this coloration will be most pronounced in those species that produce their own bioluminescence.

Materials and methods

Specimens

We examined preserved museum specimens and did not work with live animals. We borrowed specimens from the University of Minnesota, Bell Museum of

Natural History (JFBM), the University of California San Diego, Scripps Institute of Oceanography (SIO), and the Natural History Museum, Los Angeles County (LACM). We examined and sampled skin from the following specimens: *Anguilla rostrata* (Lesueur 1817) (JFBM 41279*), *Avocettina infans* (LACM 31172-33*); *Cyema atrum* (Günther 1878) (SIO 14-133*, 21-13); *Eurypharynx pelecanoides* (SIO 60-269*, 72-57, 85-164*); *Monognathus rosenblatti* Bertelsen and Nielsen 1987 (SIO 60-283, 86-43); *Moringua edwardsi* (Jordan and Bollman 1889) (SIO 71-274*), *Nemichthys scolopaceus* (JFBM 49367*), *Saccopharynx lavenbergi* Nielsen and Bertelsen 1985 (SIO 14-167); *Saccopharynx lavenbergi* (SIO 85-163*); *Serrivomer sector* Garman 1899 (LACM 422151-1*; SIO 65-578*) (specimens sampled histologically indicated with an asterisk (*)). We were unable to examine the red-pigmented *Neocyema* because only six specimens are known to science (Poulsen 2015; Poulsen et al. 2018) and we did not histologically sample any of the species of *Monognathus*, all of which are transparent and are notably rare in collections (Bertelsen and Nielsen 1987).

Gross examination

We grossly examined skin surfaces of museum specimens with a Leica MZ 12.5 stereomicroscope for coloration and evidence of discrete melanocytes. We photographed freshly captured whole specimens using an iPhone 8 on a research cruise (SR2007 on the R/V Sally Ride) in August 2020 supported by the National Science Foundation. During whole-specimen image preparation, we removed the background from whole specimen images using image-editing software.

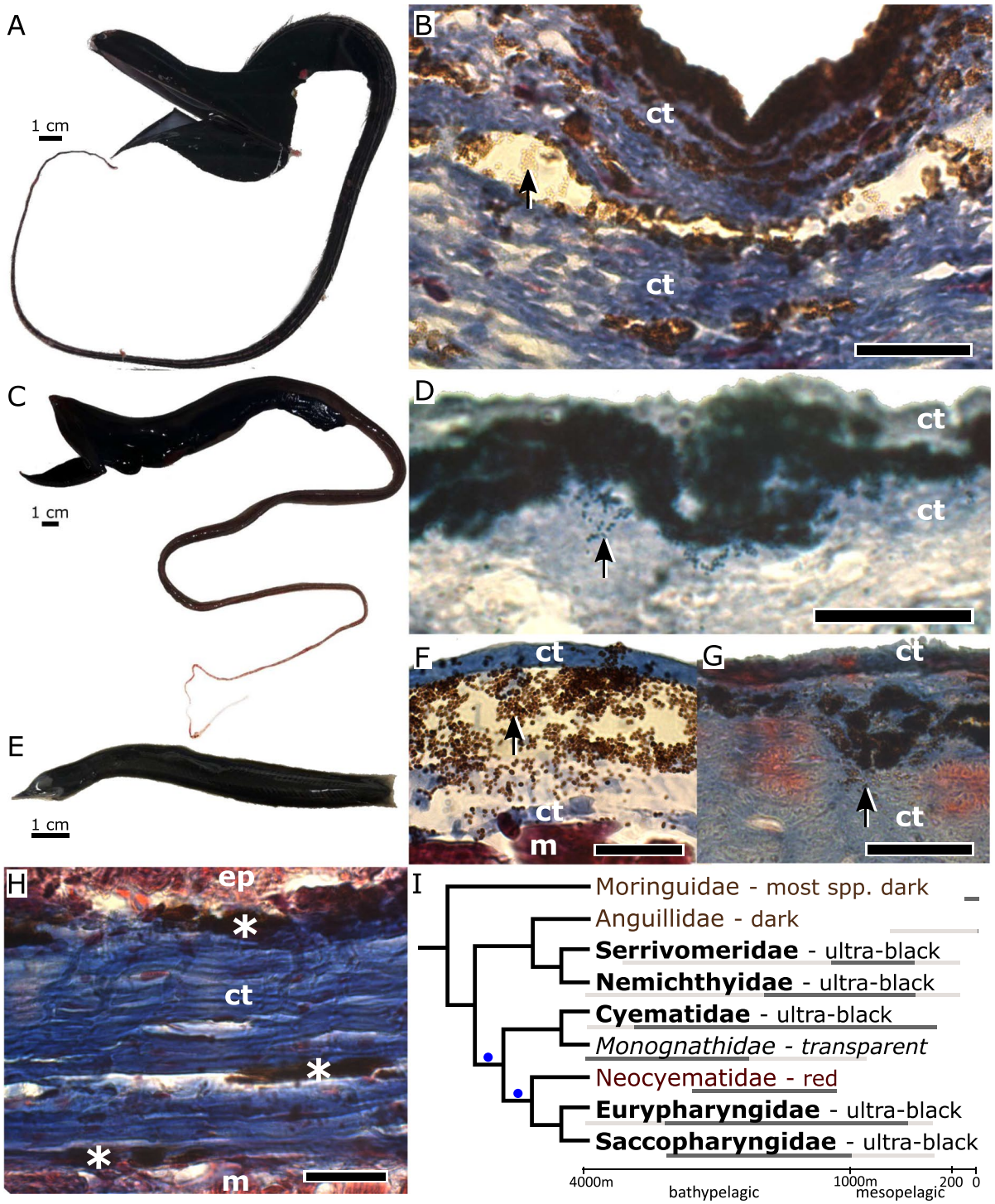
Histology

We took approximately 5 mm × 5 mm histological samples of the right dorsolateral integument, and when possible sampled 2 to 3 mm into the underlying muscle. We dehydrated samples in an ethanol series, followed by clearing in xylene, embedding in paraffin, sectioning every 10 µm on a rotary microtome, and mounting on slides (Humason 1979). We stained every other slide using a Toluidine Blue O pH 4.1-Fast Green procedure (Melrose et al. 2004; Bergholt et al. 2019) and the Masson's trichrome procedure to differentiate muscle and collagen (Sheehan and Hrapchak 1980; Ghedotti et al. 2019, 2021; Suvarna et al. 2019). We examined slides with a Leica DM 2500 compound microscope and took digital images with an attached Retiga R6 Teledyne Qimaging photodocumentation system. During histological image preparation, we adjusted brightness and contrast evenly across the images and eliminated the mounting medium surrounding the tissues using image-editing software. We did not otherwise modify photographic components of images and we did not modify or enhance specific structures.

Results

Gross anatomy

Whole fresh specimens of *Eurypharynx pelecanoides* and *Saccopharynx* spp. have an intense black, matte coloration on the whole body except for the caudal tip (Fig. 1A, C). Under microscopic examination of preserved specimens, *E. pelecanoides* and *Saccopharynx* spp. exhibited a continuous dark coloration without melanophores. *Cyema atrum* has a similar matte black coloration in fresh specimens except for around the jaws and behind the eye, although microscopic examination demonstrates a distinctive microreticulate color pattern without any distinctly stellate melanophores (Figs. 1E and 2B). In the preserved specimens examined of *Moringua edwardsi* and *Anguilla rostrata*, stellate melanophores on a lighter background are visible in most of the integument. In *Avocettina infans*, *Nemichthys scolopaceus*, and *Serrivomer sector*, we observed both areas of continuous dark coloration without distinct melanophores and infrequent, scattered stellate melanophores which were most common on the caudal peduncle (Fig. 2A). Pigmentation in the museum specimens we examined often is more discontinuous and faded as a result of damage to the integument during capture and the long-term effects of preservation. However, stellate melanophores and the diffuse, continuous dark coloration associated with ultra-black coloration usually were discernable when present on most specimens.



Histology

Histological sampling revealed a similar anatomy in all sectioned anguilloid samples with black coloration. In the sectioned samples of all deep-sea species, the epidermis is absent except for occasional, small cellular remnants suggesting that the epidermis is relatively thin and easily dislodged from

◂**Fig. 1** Anatomy of the integument in anguilloid eels. **A** *Eurypharynx pelecanoides*, freshly captured specimen, not cataloged. **B** *E. pelecanoides* dorsolateral skin cross-section (SIO 60-269: 458 mm TL). MT. **C** *Saccopharynx lavenbergi* freshly captured specimen, not cataloged. **D** *S. lavenbergi* dorsolateral skin cross section (SIO 85-163: 780 mm TL). MT. **E** *Cyema atrum* freshly captured specimen with jaw tip damage, not cataloged. **F** *C. atrum* dorsolateral skin cross section (SIO 14-133: 133 mm TL). MT. **G** *Nemichthys scolopaceus* dorsolateral skin cross section (JFBM 49367: 789 mm TL). MT. **H** *Anguilla rostrata* dorsolateral skin cross section (JFBM 41279: 153 mm TL). Scale bars = 50 µm unless otherwise indicated. * = melanocyte; ct = collagen-rich connective tissue in dermis; ep = epidermis; m = muscle; arrow = free melanosome. (i) Phylogeny of relationships depicted in Poulsen et al. (2018). Bold black text indicates taxa with members that have ultra-black coloration (Davis et al. 2020) other colors indicate predominant post-metamorphosis color. Blue dots indicate inferred mitochondrial specific gene rearrangements that have a very low likelihood of occurring and provide especially strong support to nodes. Gray lines indicate depth of occurrence, with darkest gray indicating most common capture depths, based on Froese and Pauly (2000) and sources cited in text

the underlying dermis. Damage during deep-water trawl capture combined with a thin and more loosely adhered epidermis likely explains the consistency of this absence.

In *Moringua ewardsi*, a shallow water species collected using ichthyocides, the thin epidermis consisting of only two to five layers of cells was usually present in specimens but often was separated from the underlying dermis in histological sections, indicating that the epidermis is not tightly adhered to the dermis in at least this anguilloid. The epidermis is present as a thick many-layered stratified epithelium superficial to the underlying dermis to which it is well adhered in the freshwater-stage *Anguilla rostrata* examined in this study, consistent with the morphology observed by Pankhurst and Lythgoe (1982).

In the examined histological samples from *Eurypharynx pelecanoides* and *Saccopharynx lavenbergi*, there is a near continuous layer of free melanosomes in the superficial dermis (Fig. 1B, D) as described in Davis et al. (2020) for ultra-black coloration in *E. pelecanoides*. Samples from *Avocettina infans*, *Cyema atrum* (Fig. 1F), *Nemichthys scolopaceus* (Fig. 1G), and *Serrivomer sector* show a similar morphology with extensive, superficial melanosomes in the superficial dermis; however, the melanosomes are less continuous with occasional small gaps. The melanosomes in *Cyema atrum* are notably larger, approximately twice the size and the melanosomes of other species with free melanosomes (Fig. 1F). The melanosomes in *Serrivomer sector* are more elongate than the melanosomes of other species with free melanosomes and this species also has a distinct layer of muscle tissue present within the dermis. The shallow-water species, *An. rostrata* and *M. ewardsi*, have discrete melanophores. These melanophores are between collagen fibers in the superficial dermis as well as scattered in deeper dermal layers (Fig. 1H). The deep dermis is underlain by the myotomal skeletal musculature in all species examined.

Discussion

As predicted, all deep-sea anguilloid species examined histologically have extensive free melanosomes in the superficial dermis consistent with an ultra-black morphology associated with camouflage (Davis et al. 2020). An ultra-black dermal morphology is consistent with the freshly caught deeply black coloration observed in *Cyema atrum*, *Eurypharynx pelecanoides*, and *Saccopharynx lavenbergi* (Fig. 1A, C, E), whereas the specimens from shallow-water habitats exhibit the more typical melanophore-based structure and a more brownish coloration (Pankhurst and Lythgoe 1982; Sorensen and Pankhurst 1988; Caruso et al. 2010).

The association of ultra-black coloration with camouflage from bioluminescent sources of light (Davis et al. 2020) is consistent with ultra-black anatomy seen in the examined species. The species observed with this anatomy all have estimated depth ranges between 100 and 7625 m with most occurrences below the depth of sunlight penetration where bioluminescence would be the only source of light (Smith 1989; Froese and Pauly 2000; Coad and Reist 2004; Love et al. 2021). The two examined species that possess caudal bioluminescent lures, *Eurypharynx pelecanoides* and *Saccopharynx lavenbergi*, exhibit the highest observed densities of melanosomes within the superficial dermis of the sampled angulloids (Fig. 1B, D), supporting the suggestion of Davis et al. (2020) that bioluminescence may be associated with a need for greater light absorbance. The effect of the larger size and elongate shape of the melanosomes in *Cyema atrum* and *Serrivomer sector*, respectively, likely can still produce ultra-black coloration as they fall within the range of melanosome size variation documented

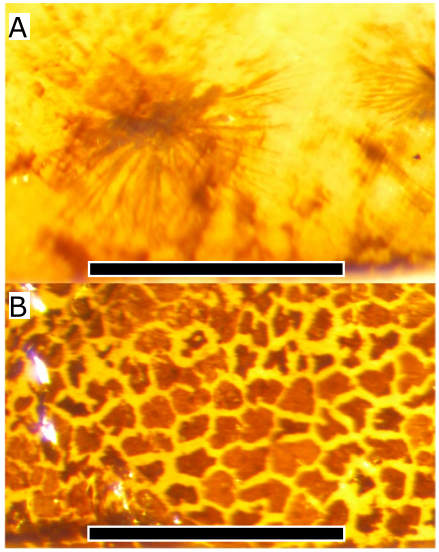


Fig. 2 Gross anatomy of the integument on the caudal peduncle of **A** *Nemichthys scolopaceus* (JFBM 49367) and **B** *Cyema atrum* (SIO 14-133). Scale bars = 0.5 mm

by Davis et al. (2020). Additionally, *E. pelecanoides* exhibited the smallest melanosome size documented in ultra-black fishes (Davis et al. 2020).

Because melanophores likely produce free melanosomes by either extrusion or release from a dying melanocyte, at some point during the ontogeny of all fishes with ultra-black coloration, both melanophore-contained and free melanosomes exist within the same individual (Fujii 2000; D'Alba and Shawkey 2019; Parichy 2021). Therefore, the new observation of melanophores existing in the skin alongside free melanosomes in adult-sized specimens of the examined nemichthyids, *Avocettina infans* and *Nemichthys scolopaceus*, and the serrivomerid, *Serrivomer sector*, is not surprising. *Nemichthys scolopaceus* and *Avocettina infans* are most commonly encountered in the mesopelagic zone where dim solar light is present (Smith and Nielsen 1989; Love et al. 2005) and *Serrivomer sector* occasionally has been collected near the surface at night (Fitch and Lavenberg 1968; Charter 1996). Having both melanophore-based pigmentation that allows rapid change in degree of pigmentation and static but especially light-absorbing ultra-black coloration may allow these fishes some of the benefits of each method of pigmentation on different body regions and in different light environments.

The pattern of ultra-black morphology in the context of the most recent phylogeny (Poulsen et al. 2018) is contrary to our initial assumption and indicates that three separate origins of ultra-black coloration is more likely than a single origin of this anatomy in a common ancestor followed by three losses. Although repeated homoplasy of pigmentation characteristics in fishes is well documented (Davis et al. 2020; Parichy and Liang 2021), these results suggest a high evolutionary lability associated with repeated origin of this characteristic within deep-sea anguilloids.

Although we confirmed melanophore-based dark coloration in the freshwater stages of *Anguilla rostrata*, reproductively transformed freshwater eels develop a pronounced black coloration as they reach their deep-ocean spawning grounds (Sorensen and Pankhurst 1988; Kurogi et al. 2011), and it is unknown if this coloration is associated with changes in melanophores or the production of the free melanosomes associated with ultra-black coloration. Likewise, the condition of chromatosomes and/or chromatophores in the transparent *Monognathus* and the red-colored *Neocyema* is unknown. Transparency is the common condition of the leptocephalus larvae of all eels (Böhlke et al. 1989) and its presence in the small and putatively neotenic *Monognathus* is not surprising (Bertelsen and Nielsen 1987). If specimens of *Neocyema* can be histologically studied, the presence or absence of erythrosomes and/or erythrophores would further contribute to our understanding of evolution of this specialized coloration and its environmental associations in anguilloids.

Acknowledgements Regis University and the Scripps Institution of Oceanography provided facilities and equipment in support of this work. Phillip Hastings of SIO, Tomas Clardy and William Ludt of LACM, and Andrew Simons of JFBM loaned specimens and allowed histological sampling for this study. Comments from two reviewers and the editor significantly improved this manuscript.

Author contribution Michael Ghedotti, Kandice Agudo, and Flor Gonzalez conducted the histological work and tissue photography. Benjamin Frable obtained the whole-fish photographs and assisted Michael Ghedotti with manuscript conceptualization. Michael Ghedotti wrote the first draft and all authors read, provided revisionary comments, and approved the final submitted manuscript.

Funding The research leading to these results received funding from URSC and FDC research grants from Regis University to Michael Ghedotti under award numbers URSC-MJG2018

and FDC-MJG2020, 21, and 22. Secondary funding was provided by NSF Award OCE-1829812 to C. Anela Choy.

Data availability All specimens are cataloged in preserved-specimen collections and are available to researchers for loan from these collections. Histological slides likewise are part of the cataloged material and will be housed by the institutions holding the specimens. Author-used images also available upon reasonable request to the authors.

Declarations

Ethics approval We examined preserved museum specimens and did not work with live animals. The care and use of animals complied with United States Animal Welfare Act as well as University guidelines and policies. Research based on museum specimens that does not involve collection of new live specimens was deemed exempt by the Regis University Institutional Animal Care and Use Committee (2018 letter).

Consent for publication The four authors agree that the paper is original and should be published.

Conflict of interest The authors declare no competing interests.

References

Bergholt NL, Lysdahl H, Lind M, Foldager CB (2019) A standardized method of applying toluidine blue metachromatic staining for assessment of chondrogenesis. Cartilage 10:370–374. https://doi.org/10.1177/1947603518764262

Bertelsen E, Nielsen JG (1987) The deep sea eel family Monognathidae (Pisces, Anguilliformes). Steenstrupia 13:141–198

Bertelsen E, Nielsen JG, Smith DG (1989) Saccophayngidae, Eurypharyngidae, and Monognathidae. In: Böhlke EB, Böhlke JE, Leiby MM, JE MC, Bertelsen E, Robins CH, Robins CR, Smith DG, Tighe KA, Nielsen JG, Hulet WH (eds) Fishes of the Western North Atlantic, Orders Anguilliformes and Saccopharyngiformes: Part 9 Vol. 1. Yale University Press, New Haven, pp 636–655

Böhlke EB, Böhlke JE, Leiby MM, McCosker JE, Bertelsen E, Robins CH, Robins CR, Smith DG, Tighe KA, Nielsen JG, Hulet WH (1989) Fishes of the Western North Atlantic, Orders Anguilliformes and Saccopharyngiformes: Part 9 Vol. 1. Yale University Press, New Haven

Caruso G, Maricchiolo G, Micale V, Genovese L, Caruso R, Denaro MG (2010) Physiological responses to starvation in the European eel (*Anguilla anguilla*): Effects on haematological, biochemical, non-specific immune parameters and skin structures. Fish Physiol Biochem 36:71–83. https://doi.org/10.1007/s10695-008-9290-6

Charter SR (1996) Serrivomeridae: sawtooth eels. In: Moser HG (ed) The early stages of fishes in the California Current Region, California Cooperative Oceanic Fisheries Investigations (CalCOFI) Atlas No. 33. Allen Press, Lawrence, KS, pp 131–133

Coad BW, Reist JD (2004) Annotated list of the Arctic marine fishes of Canada. Can J Fish Aquat 2674:1–112

D'Alba L, Shawkey MD (2019) Melanosomes: biogenesis, properties, and evolution of an ancient organelle. Physiol Rev 99:1–19. https://doi.org/10.1152/physrev.00059.2017

Davis AL, Thomas KN, Goetz FE, Robison BH, Johnsen S, Osborn KJ (2020) Ultra-black camouflage in deep-sea fishes. Curr Biol 30:3470–3476.e3. https://doi.org/10.1016/j.cub.2020.06.044

Fishelson L (1994) Comparative internal morphology of the deep-sea eels, with particular emphasis on gonads and gut structure. J Fish Biol 44:75–101

Fitch JE, Lavenberg RJ (1968) Deep-water teleostean Fishes of California. University of California Press, Berkeley, p 155

Froese R, Pauly D (2000) FishBase. World Wide Web Electronic Publication. www.fishbase.org (accessed 2023)

Fujii R (2000) The regulation of motile activity in fish chromatophores. Pigment Cell Res 13:300–319. https://doi.org/10.1034/j.1600-0749.2000.130502.x

Garman S (1899) The fishes. In: Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands ... by the U. S. Fish Commission steamer "Albatross," during 1891, No. XXVI, Mem Mus Comp Zoology Harv Coll 24:1–431.

Ghedotti MJ, DeKay HM, Maile AJ, Smith WL, Davis MP (2021) Anatomy and evolution of bioluminescent organs in the slimeheads (Teleostei: Trachichthyidae). J Morphol 282:820–832. https://doi.org/10.1002/jmor.21349

Ghedotti MJ, Smith WL, Davis MP (2019) The first evidence of intrinsic epidermal bioluminescence within ray-finned fishes in the linebelly swallower *Pseudoscopelus sagamianus* (Chiasmodontidae). J Fish Biol 95:1540–1543. https://doi.org/10.1111/jfb.14179

Günther A (1878) Preliminary notices of deep-sea fishes collected during the voyage of H. M. S. 'Challenger.' Ann Mag Nat Hist, Series 5 2:17–28, 179–187, 248–251.

Herring PJ (2002) The biology of the deep ocean. Oxford University Press, Oxford

Humason GL (1979) Animal tissue techniques (4th Edition). W.H. Freeman, San Francisco

Johnsen S (2005) The red and the black: bioluminescence and the color of animals in the deep sea. Integr Comp Biol 45:234–246. https://doi.org/10.1093/icb/45.2.234

Jordan DS, Bollman CH (1889) List of fishes collected at Green Turtle Cay, in the Bahamas, by Charles L. Edwards, with descriptions of three new species. Proc US Natl Mus 11:549–553

Kurogi H, Okazaki M, Mochioka N, Jinbo T, Hashimoto H, Takahashi M, Tawa A, Aoyama J, Shinoda A, Tsukamoto K, Tanaka H, Gen K, Kazeto Y, Chow S (2011) First capture of post-spawning female of the Japanese eel *Anguilla japonica* at the southern West Mariana Ridge. Fish Sci 77:199–205. https://doi.org/10.1007/s12562-010-0318-3

Lesueur CA (1817) A short description of five (supposed) new species of the genus *Muraena*, discovered by Mr. Le Sueur, in the year 1816. J Acad Nat Sci, Philadelphia 1:81–83

Love MS, Bizzarro JJ, Cornthwaite AM, Frable BW, Maslenikov KP (2021) Checklist of marine and estuarine fishes from the Alaska–Yukon Border, Beaufort Sea, to Cabo San Lucas, Mexico. Zootaxa 5053:1–285. https://doi.org/10.11646/ZOOTAXA.5053.1.1

Love MS, Mecklenburg CW, Mecklenburg TA, Thorsteinson LK (2005) Resource inventory of marine and estuarine fishes of the West Coast and Alaska: a checklist of North Pacific and Arctic Ocean species from Baja California to the Alaska-Yukon border. U.S. Department of the Interior, U.S. Geological Survey, Biological Resources Division, Seattle, Washington

Melrose J, Smith S, Ghosh P (2004) Histological and immunohistological studies on cartilage. In: de Ceuninck F, Sabatini M, Pastoureau P (eds) Cartilage and osteoarthritis, methods in molecular medicine, Vol. 101. Humana Press, pp 039–064. https://doi.org/10.1385/1-59259-821-8:039

Nielsen JG, Bertelsen E (1985) The gulper-eel family Saccopharyngidae (Pisces, Anguilliformes). Steenstrupia 11:157–206

Nielsen JG, Bertelsen E, Jespersen Å (1989) The biology of *Eurypharynx pelecanoides* (Pisces, Eurypharyngidae). Acta Zool 70:187–197. https://doi.org/10.1111/j.1463-6395.1989.tb01069.x

Nielsen JG, Smith DG (1978) The eel family Nemichthyidae (Pisces: Anguilliformes). Dana Rept 88:1–71

Pankhurst NW, Lythgoe JN (1982) Structure and colour of the integument of the European eel *Anguilla anguilla* (L.). J Fish Biol 21:279–296. https://doi.org/10.1111/j.1095-8649.1982.tb02833.x

Parichy DM (2021) Evolution of pigment cells and patterns: recent insights from teleost fishes. Curr Opin Genet Dev 69:88–96

Parichy DM, Liang Y (2021) Evolution of pigment pattern formation in teleosts. In: Hashimoto H, Goda M, Futahashi R, Kelsh R, Akiyama T (eds) Pigments, Pigment Cells and Pigment Patterns. Springer, Singapore, pp 309–342. https://doi.org/10.1007/978-981-16-1490-3_10

Poulsen JY (2015) Fifth confirmed record and North Atlantic range expansion of the rare pelagic bobtail snipe eel genus *Neocyema* (Cyematidae, Elopomorpha). Mar Bidivers Rec 8:e53. https://doi.org/10.1017/S175526721500024X

Poulsen JY, Miller MJ, Sado T, Hanel R, Tsukamoto K, Miya M (2018) Resolving deep-sea pelagic saccopharyngiform eel mysteries: identification of *Neocyema* and Monognathidae leptocephali and establishment of a new fish family "Neocyematidae" based on larvae, adults and mitogenomic gene orders. PLoS One 13:e0199982. https://doi.org/10.1371/journal.pone.0199982

Priede IG (2017) Deep-sea fishes: biology, diversity, ecology and fisheries. Cambridge University Press, Cambridge

Richardson J (1848) Fishes. In: Adams A (ed) The zoology of the voyage of H. M. S. Samarang; under the command of Captain Sir Edward Belcher, during the years 1843-1846. Reeve and Benham, London, pp 1–28 pl. 1–10

Santini F, Kong X, Sorenson L, Carnevale G, Mehta RS, Alfaro ME (2013) A multi-locus molecular timescale for the origin and diversification of eels (Order: Anguilliformes). Mol Phylogenet Evol 69:884–894. https://doi.org/10.1016/j.ympev.2013.06.016

Sheehan DC, Hrapchak BB (1980) Theory and practice of histotechnology (2nd ed.). Mosby, Maryland Heights

Smith DG (1989) Family Cyematidae. In: Böhlke EB, Böhlke JE, Leiby MM, McCosker JE, Bertelsen E, Robins CH, Robins CR, Smith DG, Tighe KA, Nielsen JG, Hulet WH (eds) Fishes of the Western North Atlantic, Orders Anguilliformes and Saccopharyngiformes: Part 9 Vol. 1. Yale University Press, New Haven, pp 630–639

Smith DG, Nielsen JG (1989) Family Nemichthyidae, Snipe eels. In: Böhlke EB, Böhlke JE, Leiby MM, JE MC, Bertelsen E, Robins CH, Robins CR, Smith DG, Tighe KA, Nielsen JG, Hulet WH (eds) Fishes of the Western North Atlantic, Orders Anguilliformes and Saccopharyngiformes: Part 9 Vol. 1. Yale University Press, New Haven, pp 441–459

Sorensen PW, Pankhurst NW (1988) Histological changes in the gonad, skin, intestine and olfactory epithelium of artificially-matured male American eels, *Anguilla rostrata* (LeSueur). J Fish Biol 32:297–307. https://doi.org/10.1111/j.1095-8649.1988.tb05363.x

Sugimoto M (2002) Morphological color changes in fish: regulation of pigment cell density and morphology. Microsc Res Tech 58:469–503. https://doi.org/10.1002/jemt.10168

Suvarna SK, Layton C, Bancroft JD (2019) Bancroft's theory and practice of histological techniques, 8th edn. Elsevier, London

Tang KL, Fielitz C (2013) Phylogeny of moray eels (Anguilliformes: Muraenidae), with a revised classification of true eels (Teleostei: Elopomorpha: Anguilliformes). Mitochondrial DNA 24:55–66. https://doi.org/10.3109/19401736.2012.710226

Tighe KA (1989) Family Serrivomeridae. In: Böhlke EB, Böhlke JE, Leiby MM, JE MC, Bertelsen E, Robins CH, Robins CR, Smith DG, Tighe KA, Nielsen JG, Hulet WH (eds) Fishes of the Western North Atlantic, Orders Anguilliformes and Saccopharyngiformes: Part 9 Vol. 1. Yale University Press, New Haven, pp 613–627

Vaillant LL (1882) Sur un poisson des grandes profondeurs de l'Atlantique, l'*Eurypharynx pelecanoides*. C r hebd séances Acad sci, Sci nat 95:1226–1228