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Evolutionary Relationships of the Deep-Sea Pearleyes (Aulopiformes: Scopelarchidae) and a New Genus of Pearleye from Antarctic Waters

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This study investigates the evolutionary relationships among species in the family Scopelarchidae with molecular (eight genes) and morphological data. A new genus of pearleye is diagnosed, *Lagiacrusichthys,* new genus, from a previously described species (*Benthalbella macropinna*) distributed in Antarctic waters. The diagnosis of *Lagiacrusichthys* is based on molecular and anatomical information, including a highly reduced dorsal fin (5–6 rays) and a long anal fin (35–39 rays). The results represent the most taxonomically comprehensive molecular and total evidence hypotheses of the evolutionary relationships of the pearleyes to date (13 of 18 species), and these frameworks are used to comment on the historical biogeography of this widespread group. It is inferred that the pearleyes likely first evolved in central-tropical waters, with two independent invasions into Antarctic waters.

THE pearleyes (Aulopiformes: Scopelarchidae) have a worldwide distribution in deep-sea environments, where they are commonly collected at depths between 500 and 1,000 meters, and are active as pelagic predators. There are currently four recognized genera (*Benthalbella*, *Rosenblattichthys*, *Scopelarchus*, and *Scopelarchoides*) and 18 species (Eschmeyer, 2014). In general, pearleyes are known for their dorsally directed tubular and semi-tubular eyes, which allow them to hunt prey above them in the water column. Recent studies on the functional morphology of the tubular eyes of pearleye fishes (Collin et al., 1998; Wagner et al., 1998) have indicated that they possess an array of visual specializations associated with living in the deep sea, including that their tubular eyes are highly capable of observing bioluminescent light, with the ability to pinpoint bioluminescent emissions from a distance of at least six meters. The common name pearleye is derived from a patch of white tissue found on the eye of scopelarchids that is oval shaped, the ''pearl organ,'' although its function remains obscure (Johnson, 1974). Like most deep-sea aulopiform fishes, pearleyes are simultaneous hermaphrodites (e.g., Johnson, 1974; Davis, 2010) with functional ovotestes. Only a single species of pearleye (*Benthalbella infans*) has been observed to be bioluminescent, and the three ventrally oriented bioluminescent organs of *B. infans* are hypothesized to be derived from muscle tissue (Merrett et al., 1971), as opposed to the bioluminescent liver tissue of the naked barracudinas (Lestidiidae, Ghedotti et al., 2015). A single, ventral bioluminescent organ near the anus has also been observed in *Scopelarchoides kreffti*, but all other scopelarchid taxa appear to lack structures associated with bioluminescence (Johnson, 1974).

The evolutionary relationships among all four currently recognized genera of scopelarchids previously have been examined based on morphological characters (Johnson, 1974, 1982; Baldwin and Johnson, 1996), while previous molecular hypotheses of aulopiform evolutionary relationships (Davis, 2010; Davis and Fielitz, 2010) included two of the four recognized genera (*Scopelarchus* and *Benthalbella*). Johnson (1974) examined the relationships of scopelarchid taxa based on 14 morphological characters and identified a monophyletic *Rosenblattichthys* as the sister group to a clade including the remaining scopelarchid taxa, of which the genera *Benthalbella* and *Scopelarchus* were inferred to be monophyletic. While the family Scopelarchidae was inferred to be monophyletic in Baldwin and Johnson's (1996) study on the relationships of aulopiform fishes (based on 118 morphological characters), relationships among the four genera were inconclusive and formed a polytomy.

The aim of this study is to investigate the evolutionary relationships among fishes in the family Scopelarchidae using a molecular and total evidence approach with robust taxonomic sampling (e.g., Davis et al., 2013; McMahan et al., 2013a; Smith and Busby, 2014). While there is significant morphological (Johnson, 1974, 1982; Baldwin and Johnson, 1996; Sato and Nakabo, 2002), molecular (Davis, 2010; Davis and Fielitz, 2010), and total evidence (Davis, 2010) support for the monophyly of the family Scopelarchidae, the relationships among taxa within this family of deep-sea fishes remain obscure. In addition, a new genus of pearleye is diagnosed for a currently recognized species known predominantly from the Southern Hemisphere and Antarctic waters (formerly *Benthalbella macropinna*, Bussing and Bussing, 1966), and the historical biogeography of the family is discussed in relation to the proposed evolutionary relationships of the family.

MATERIALS AND METHODS

Data collection, alignment, model choice, and morphological characters.—DNA sequence data used in this study (Table 1) includes newly collected (GenBank accession numbers KM983049–KM983094) and previously published sequences (Davis, 2010; Near et al., 2012; Davis et al., 2014). Taxonomic sampling for DNA-only analyses included ten species (of 18) representing all scopelarchid genera, with the total evidence approach incorporating an additional three species. Combinations of mitochondrial and nuclear genes have been demonstrated to provide significant phylogenetic resolution in fishes (e.g., Chakrabarty et al., 2011a, 2011b; Li et al., 2011; McMahan et al., 2013b; Sparks et al., 2014). Mitochondrial and nuclear genes were aligned using the program MAFFT v6.0 with default parameters (Katoh et al., 2002). The phylogenetic analyses presented herein had a total of 7,137 base pairs, including one mitochondrial gene (cytochrome oxidase I, 812 bp) and seven protein-coding genes (ectodermal-neural cortex 1-like gene, 845 bp;

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Table 1. GenBank accession numbers for DNA data. Gene abbreviations: COI = cytochrome oxidase I; ENC1 = ectodermal-neural cortex 1-like gene; glyt = glycosyltransferase gene; myh6 = myosin heavy chain 6 alpha gene; plagl2 = pleiomorphic adenoma protein-like 2-like gene; Ptr = ptr hypothetical protein; rag1 = recombination activating gene 1; zic1 = zic family member protein 1.

Species	COI	ENC1	glyt	myh6	plagl2	Ptr	rag1	zic1
Chlorophthalmus agassizi (KU T3759)	EU366553	EU366600	KM983058	KM983067	KM983077	KM983082	EU366695	EU366740
Benthalbella dentata (KU T3239)	EU366552	EU366598	KM983066	KM983076	EU366647	KM983088	EU366693	EU366738
Benthalbella infans (YFTC 14525)	NA	NA	JX190308	JX190454	JX190580	NA	JX190843	JX191301
Lagiacrusichthys macropinnis (KU T926)	EU366552	EU366599	KM983065	KM983075	EU366648	KM983087	EU366694	EU366739
Rosenblattichthys volucris (SIO 06-293)	KM983049	KM983053	KM983059	KM983068	KM983078	KM983083	KM983089	KM983092
Scopelarchoides danae (CBM-ZF T99-142)	KJ190054	KM983057	KM983063	KM983073	NA	KM983085	KJ190088	NA
Scopelarchoides nicholsi (SIO 06-285)	KM983052	NA	KM983064	KM983074	NA	KM983086	NA	NA
Scopelarchus analis (KU T3783)	EU366574	EU366621	KM983062	KM983071	EU366668	NA	EU366715	EU366758
Scopelarchus guentheri (SIO 10-166)	NA	KM983056	NA	KM983072	KM983081	KM983084	NA	KM983094
Scopelarchus michaelsarsi (SIO 10-167)	KM983051	KM983055	KM983061	KM983070	KM983080	NA	KM983091	KM983093
Scopelarchus stephensi (SIO 10-174)	KM983050	KM983054	KM983060	KM983069	KM983079	NA	KM983090	NA

glycosyltransferase gene, 839 bp; myosin heavy chain 6 alpha gene, 759 bp; pleiomorphic adenoma protein-like 2-like gene, 819 bp; ptr hypothetical protein, 767 bp; recombination activating gene 1, 1449 bp; zic family member protein, 847 bp). For each maximum likelihood analysis, the dataset was partitioned by individual gene codons, for a total of 24 partitions. Models of molecular evolution were chosen by the program jMODELTEST v.2.1 (Posada, 2008), with the best fitting model under the Akaike information criteria (AIC) for each individual gene and codon partition assigned, including: cytochrome oxidase I (TIM1+Γ, HKY, GTR+I+Γ), ectodermal-neural cortex 1-like gene (Trn, TVM, TPM1uf), glycosyltransferase (HKY+Γ, TPM1uf+I+Γ, GTR+I), myosin heavy chain 6 alpha (TIM1+I, F81+G, TVM), pleiomorphic adenoma protein-like 2-like gene (HKY, TrN, TPM1uf+Γ), ptr hypothetical protein (TIM1+Γ, GTR+I, TPM1uf+Γ), recombination activating gene 1 (TPM1uf+I, HKY+G, TVM+G), and zic family member protein (F81, HKY, HKY+Γ).

Total evidence analyses included an additional partition (MK model, Lewis, 2001) incorporating data from 14 morphological and early-life-history characters used to infer the evolutionary relationships among scopelarchid taxa in Johnson (1974) and two additional characters presented herein for a total of 16 morphological characters. Abbreviated character descriptions from Johnson (1974) are found in Appendix 1. For further details regarding these character states, please refer to Johnson (1974). Character state codings for species are listed in Table 2.

Topology and character state reconstruction.—Maximum likelihood analyses were performed in GARLI v2.01 (Zwickl, 2006). Five analyses were conducted for both the DNA-only and total evidence analyses, and the trees having the best likelihood scores are presented here to evaluate evolutionary relationships. A nonparametric bootstrap analysis (Felsenstein, 1985) was performed for each dataset with 100 random pseudoreplicates using the recommended default settings in the GARLI manual. Ancestral character state reconstruction was performed in Mesquite v.2.75 (Maddison and Maddison, 2010) with maximum parsimony methodology, and distributional data for taxa are based on results presented in Johnson (1974, 1982) and specimen occurrence data in the Global Biodiversity Information Facility (2014, www.gbif.org).

***Lagiacrusichthys*, new genus**

urn:lsid:zoobank.org:act:209AF244-2639-4327-A7CD-16AD95095EBB
Figure 1

Type species.—*Lagiacrusichthys macropinnis*

Benthalbella macropinna. Bussing and Bussing, 1966:53–64, fig. 1.

Diagnosis.—The genus *Lagiacrusichthys* can be distinguished from all other members of Scorpelarchidae based on the unique combination of the following characters modified from Bussing and Bussing (1966) and Johnson (1974): long anal fin with 35–39 anal-fin rays (17–30 in other species of Scopelarchidae); dorsal fin small and approximately same size or smaller than adipose fin, with a low dorsal-fin ray count of 5–6 (6–10 in other species of Scopelarchidae).

Table 2. Morphological data matrix of 16 anatomical and early life history characters from Johnson (1974) and this study. Refer to text for further details regarding characters.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Chlorophthalmus agassizi	0	0	1	0	0	0	0	0	0	0	0	0	0	?	0	0
Benthalbella dentata	0	0	1	1	1	1	1	1	2	1	0	0	0	0	0	0
Benthalbella elongata	0	0	1	1	1	1	1	1	2	1	0	0	0	0	0	0
Benthalbella infans	0	0	1	1	1	1	1	1	2	1	0	0	0	0	0	0
Benthalbella linguidens	?	?	1	?	1	1	1	1	2	1	0	0	?	0	0	0
Lagiacrusichthys macropinnis	0	0	1	1	0	0	1	1	2	0	0	0	0	0	1	1
Rosenblattichthys alatus	?	?	0	?	0	0	0	0	0	0	1	1	0	0	0	0
Rosenblattichthys volucris	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Scopelarchoides danae	1	2	0	1	0	1	3	0	0	0	0	0	0	0	0	0
Scopelarchoides nicholsi	1	1	0	1	0	1	2	0	0	0	0	0	0	0	0	0
Scopelarchus analis	1	3	0	1	1	2	4	1	0	0	0	0	1	1	0	0
Scopelarchus guentheri	1	3	0	1	1	1	4	1	0	0	0	0	1	1	0	0
Scopelarchus michaelsarsi	1	3	0	1	1	2	4	1	1	0	0	0	1	1	0	0
Scopelarchus stephensi	?	?	0	1	1	2	4	1	1	0	0	0	?	1	0	0

Habitat and distribution.—Found predominantly in marine waters in the southern hemisphere with a circumpolar distribution in the Antarctic Circumpolar Current (Bussing and Bussing, 1966; Johnson, 1974; Post, 1990). Collected predominantly from deep-sea open ocean environments (meso-bathypelagic) at depths ranging from 610–2750 meters (Bussing and Bussing, 1966; Johnson, 1974).

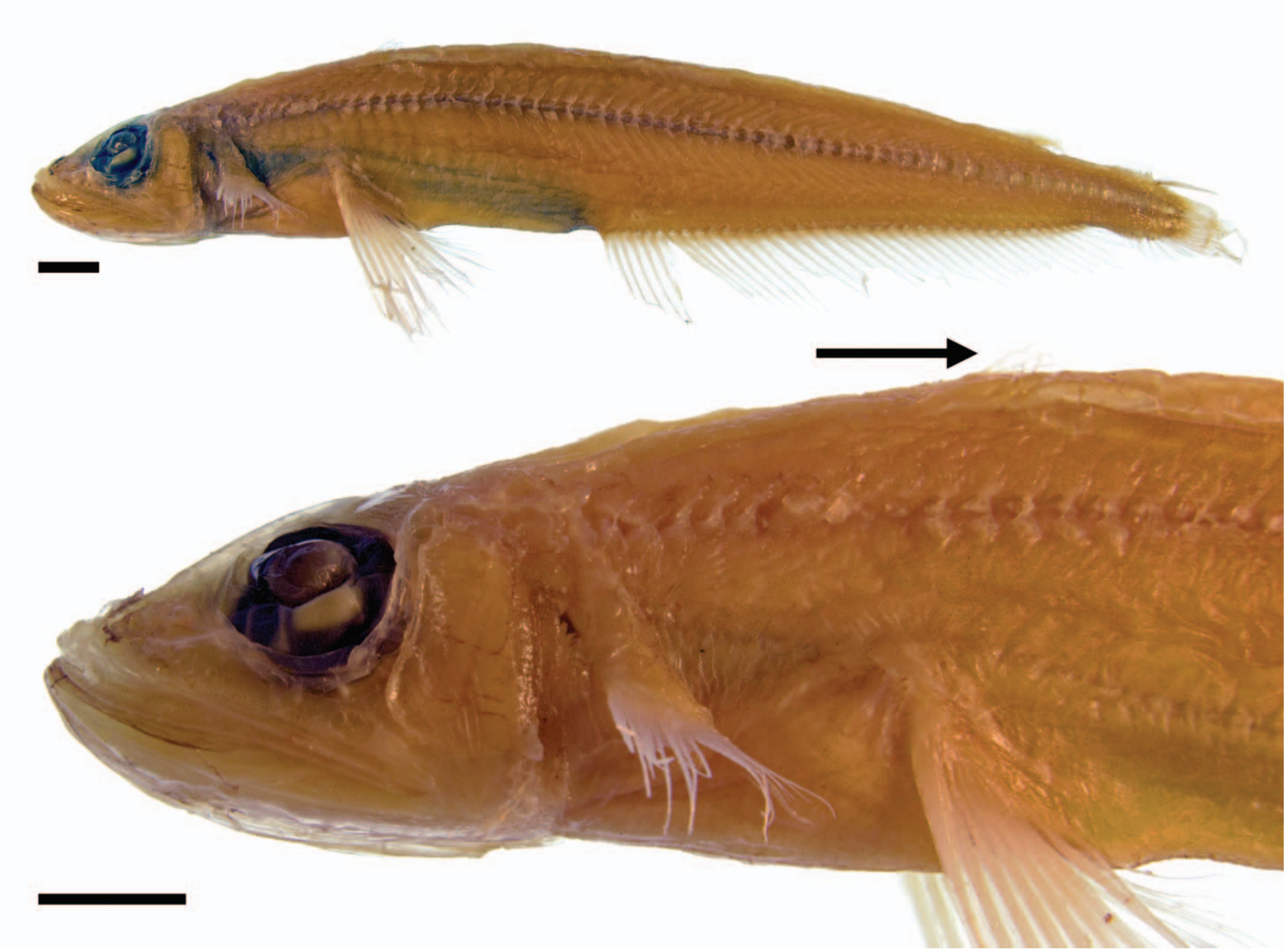

Fig. 1. *Lagiacrusichthys macropinnis*, from meso-bathypelagic Antarctic waters (MCZ 125832). A small dorsal fin (5–6 rays), indicated by the arrow, and a long anal fin (35–39 rays) are differentially diagnostic features of the genus *Lagiacrusichthys*. Scale bars equal 1 cm.

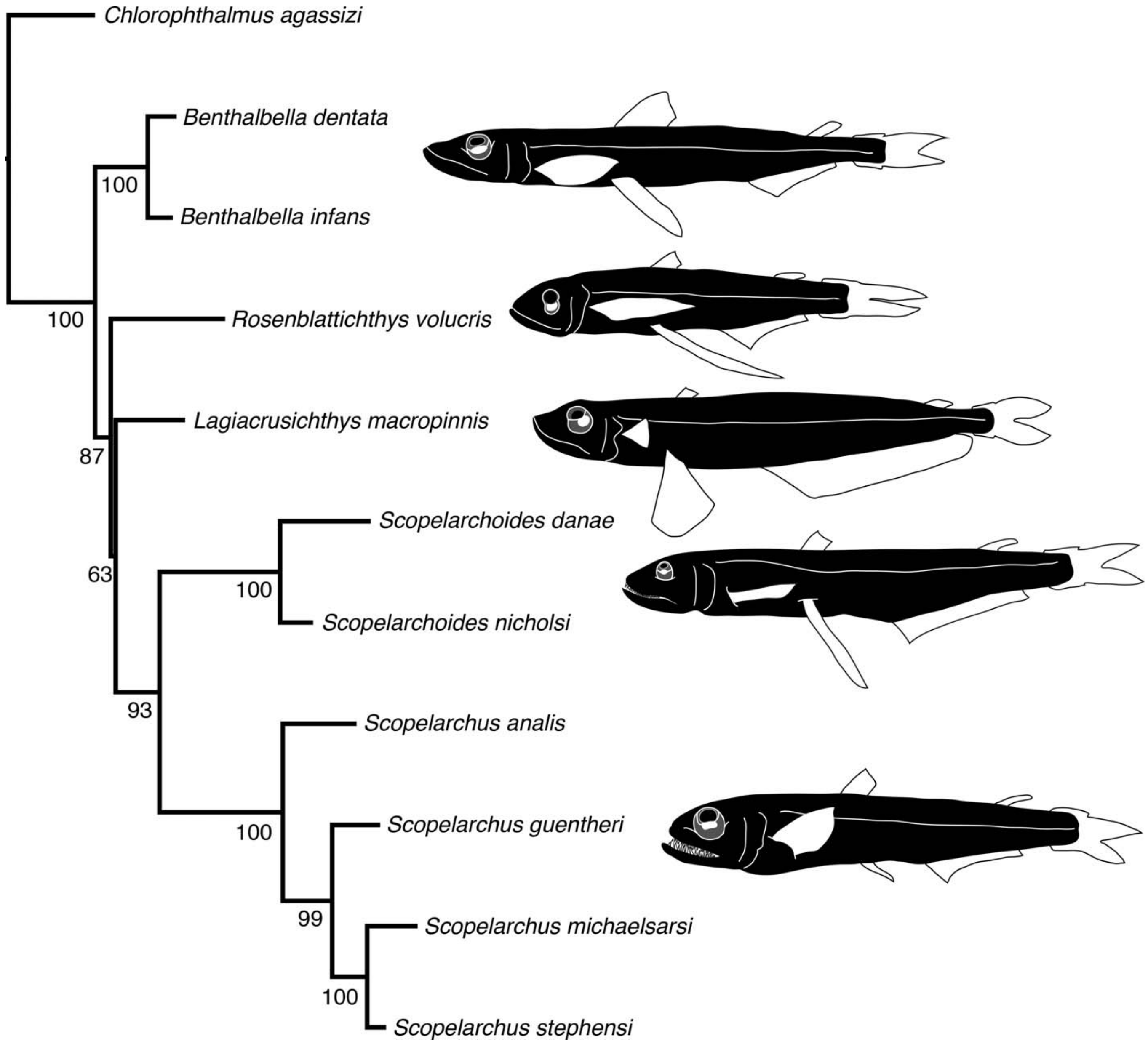

Fig. 2. Evolutionary relationships of the pearleyes (Scopelarchidae) based on eight gene fragments and maximum likelihood topology estimation. Numbers by nodes indicate bootstrap values. Representative line drawings of genera are based on specimens examined and modifications from prior illustrations (Johnson, 1974; Bussing and Bussing, 1966).

Etymology.—Named for a wyvern, a dragon-like creature from mythology, specifically the sea-wyvern Lagiacrus, known for his fierceness and for inhabiting the deep. Treated as masculine.

Phylogenetic placement of* Lagiacrusichthys *and relationships within Scopelarchidae.—The inferred evolutionary relationships among scopelarchid genera were the same for both DNA-only (Fig. 2) and total evidence analyses (Fig. 3). Bootstrap values and unambiguous synapomorphies supporting clades are indicated in Figure 3, following the recommendation of Wiley et al. (2011). The genus *Benthalbella* was identified as the stem pearleye lineage. Four unambiguous synapomorphies support the monophyly of *Benthalbella* (Fig. 3), including the absence of antorbital bones (5:1), a reduced supramaxilla (6:1), an abrupt timing of larval metamorphosis (9:2), and the appearance of pelvic-fin buds anterior to the dorsal fin in larvae (10:1). *Benthalbella* is the sister group to a clade that includes *Rosenblattichthys* as the sister group to a clade that includes *Lagiacrusichthys*, *Scopelarchoides*, and *Scopelarchus* (Figs. 2, 3). The monophyly of *Rosenblattichthys* is supported by two unambiguous synapomorphies (Fig. 3) concerning the early life history of fishes in this lineage, including pectoral fin development precocious in larvae (11:1) and noticeably enlarged heads in larvae (12:1). *Lagiacrusichthys* is the sister group to a *Scopelarchus* and *Scopelarchoides* clade. *Lagiacrusichthys* has two unreversed and unambiguous autapomorphies that differentiate it from all other scopelarchid taxa (Fig. 3), including a significantly long anal fin (15:1) and a significantly reduced dorsal fin (16:1).

The genera *Scopelarchoides* and *Scopelarchus* were inferred to be sister groups (Figs. 2, 3), with one unambiguous synapomorphy supporting this clade: the absence of parietal bones (1:1). There are no unambiguous morphological

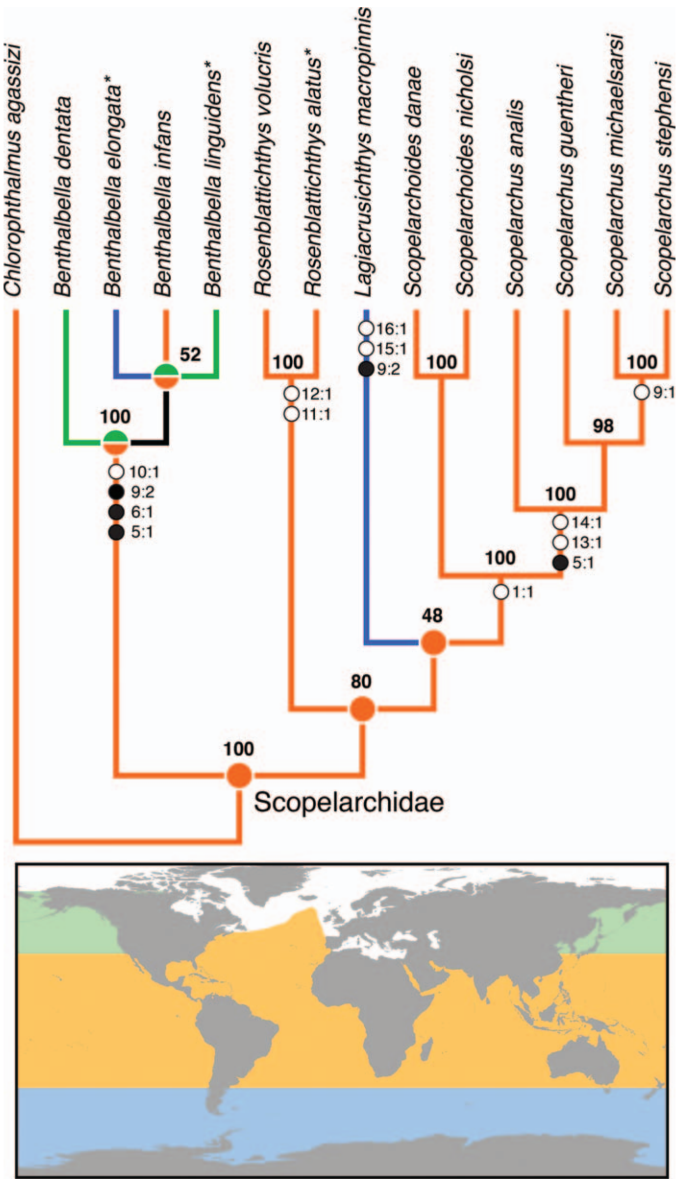

Fig. 3. Evolutionary relationships of the pearleyes (Scopelarchidae) based on total evidence (eight gene fragments and 16 anatomical and early-life-history characters) from maximum likelihood topology estimation. Asterisks indicate taxa that do not have DNA data. Bold numbers by nodes indicate bootstrap values. Numbers near circles on branches indicate unambiguous synapomorphies, with the first number corresponding to one of the 16 anatomical and early-life-history characters (see text for details), with the second number indicating character state. White circles represent unreversed characters, while black circles represent homoplastic characters. Colors on branches and distribution map correspond to the regions of the oceans where each species has been predominantly collected (note that many species have more restricted ranges within these zones). Circles at nodes indicate results from parsimony ancestral character reconstruction of regions (green: boreal and subarctic waters of North Pacific, orange: central-tropical waters, blue: Antarctic waters).

synapomorphies that support the monophyly of *Scopelarchoides*, although this clade is well supported by molecular data (Figs. 2, 3). Three unambiguous synapomorphies support the monophyly of *Scopelarchus* (Fig. 3). These include the absence of antorbital bones (5:1), the absence of a posterior arm on the hyomandibular bone (13:1), and unarranged dermal pigment spots on the body (14:1).

DISCUSSION

Relationships of the pearleyes (Scopelarchidae).—This work represents the most taxonomically comprehensive molecular phylogeny of the family Scopelarchidae to date, including representatives from all four previously recognized genera and the newly recognized *Lagiacrusichthys*. Previous molecular studies on aulopiform fishes (Davis, 2010; Davis and Fielitz, 2010) have included only a single representative for three pearleye genera (*Benthalbella*, *Lagiacrusichthys*, and *Scopelarchus*), and recent morphological studies into the evolutionary relationships of aulopiform fishes (Baldwin and Johnson, 1996) inferred a polytomy among the four scopelarchid genera recognized at that time (*Benthalbella, Rosenblattichthys, Scopelarchus*, and *Scopelarchoides*). Results from the DNA-only and total evidence analyses (Figs. 2, 3) infer the same pattern of evolutionary relationships among the five scopelarchid genera, with *Benthalbella* identified as the stem pearleye lineage. Of the remaining four scopelarchid genera, *Rosenblattichthys* is inferred to be the sister group to a clade that includes *Lagiacrusichthys* sister to a clade including the genera *Scopelarchoides* and *Scopelarchus* (Figs. 2, 3).

The taxon *Lagiacrusichthys macropinnis* was initially placed within *Benthalbella* (e.g., Bussing and Bussing, 1966; Johnson, 1974, 1982) based primarily on its elongated body and the presence of pelvic fins that are anterior to the base of the dorsal fin. Earlier studies on the relationships and taxonomy of scopelarchid taxa (Marshall, 1955; Rofen, 1966) identified a significant distinction between two body types within the pearleyes (of which only three genera were diagnosed at that time): an elongated body form with pelvic fins anterior to the base of the dorsal fin (*Benthalbella*) and a comparatively shorter body form with pelvic fins posterior to the base of the dorsal fin (*Scopelarchus*, *Scopelarchoides*). Newly considered molecular evidence presented here indicates that the Antarctic Pearleye (*Lagiacrusichthys macropinnis*) represents a distinct lineage from the other four described species of *Benthalbella* (Figs. 2, 3). This finding is also supported by a number of anatomical and early-life-history characters (Fig. 3). The Antarctic Pearleye (*Lagiacrusichthys macropinnis*) has two unreversed and unambiguous autapomorphies that differentiate it from all other scopelarchid taxa (Fig. 3), including a long anal fin (15:1) and a reduced dorsal fin (16:1). While *Lagiacrusichthys macropinnis* and species of *Benthalbella* share pelvic fins that are anterior in position to the origin of the dorsal fin, the development of these pelvic fin positions differ significantly between the two genera, with *Benthalbella* having pelvic-fin buds that appear entirely anterior to the dorsal-fin origin in larvae (10:1). In *Lagiacrusichthys*, the pelvic-fin buds appear posteriorly to the dorsal-fin origin in larvae (10:0), as they do in all other scopelarchid taxa (with the exception of *Benthalbella*).

The circumglobal distribution of Scopelarchidae in mesobathypelagic environments.—Johnson (1974) hypothesized that the common ancestor of the family Scopelarchidae most likely evolved in central-tropical marine waters, with various invasions into boreal and subarctic waters of the North Pacific (*Benthalbella*) and Antarctic south of Subtropical Convergence (*Benthalbella* and *Lagiacrusichthys*). Based on the evolutionary relationships presented herein (Fig. 3), it is inferred that the common ancestor of the pearleyes most likely evolved in central-tropical waters, and the majority of pearleye diversity is found in these environments. Two independent invasions into Antarctic waters are identified within the scopelarchids: once in *Benthalbella* (*B. elongata*, Southern Pearleye), and once in *Lagiacrusichthys* (*L. macropinnis*, Antarctic Pearleye). Two species within *Benthalbella* (*B. linguidens* and *B. dentata*) are restricted to boreal and subarctic waters of the North Pacific (Fig. 3), although further molecular and morphological data collection is needed to clearly resolve the relationships among the four species in *Benthalbella*, which would aid in inferring the number of independent invasions into the North Pacific or central-tropical waters. At present, the results from the parsimony ancestral character reconstruction of regions identify that a North Pacific or central-tropical ancestor is an equally parsimonious possibility for the common ancestor of *Benthalbella*.

MATERIAL EXAMINED

Benthalbella dentata: FMNH 79658, SIO 88-53.
Benthalbella infans: SIO 94-79.
Benthalbella linguidens: MCZ 127117.
Chlorophthalmus agassizi: BMNH 1939.5.24.445-456.
Lagiacrusichthys macropinnis: MCZ 125832.
Rosenblattichthys volucris: SIO 68-582-25.
Scopelarchoides danae: MCZ 127125.
Scopelarchoides signifer: SIO 61-32.
Scopelarchus analis: FMNH 79651, FMNH 79720, MCZ 127130, SIO 92-34.
Scopelarchus guentheri: MCZ 70909, SIO 71-386.

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APPENDIX 1. Abbreviated character descriptions from morphological and early-life-history characters used to infer the evolutionary relationships among scopelarchid taxa

1. Presence of parietal bones (character 1, Johnson, 1974).
    (01_0) Parietal bone present.
    (01_1) Parietal bone absent.
2. Support of the first epibranchial dorsally (character 2, Johnson, 1974).
    (02_0) Suspensory pharyngobranchial present; hooklike arms on first epibranchial and second pharyngobranchial connected by a ligament.
    (02_1) Suspensory pharyngobranchial absent, support of first epibranchial near proximal end of second pharyngobranchial; hooklike arms on first epibranchial and second pharyngobranchial connected by a ligament.
    (02_2) Suspensory pharyngobranchial absent, support of first epibranchial at middle of second pharyngobranchial; no hooklike arms.
    (02_3) Suspensory pharyngobranchial absent, support of first epibranchial at point of articulation between second pharyngobranchial and second epibranchial; no hooklike arms.
3. Presence of basibranchial teeth (character 4, Johnson, 1974).
    (03_0) Basibranchial teeth present.
    (03_1) Basibranchial teeth absent.
4. Presence of supraorbital bones (character 8, Johnson, 1974).
    (04_0) Supraorbital present.
    (04_1) Supraorbital absent.
5. Presence of antorbital bones (character 9, Johnson, 1974).
    (05_0) Antorbital present.
    (05_1) Antorbital absent.
6. Presence and size of supramaxillary bones (character 10, Johnson, 1974).
    (06_0) Supramaxilla large, length of supramaxilla one-fourth to one-third the maxillary length.
    (06_1) Supramaxilla reduced to a splint-like element, length of supramaxilla less than one-ninth of maxillary length.
    (06_2) Supramaxilla absent.
7. Number of peritoneal sections in larvae (character 14, Johnson, 1974).
    (07_0) Zero.
    (07_1) One.
    (07_2) Three, with the posterior paired sections appearing later in development than anterior sections and entirely anterior to pelvic-fin base.
    (07_3) Three, with the posterior paired sections appearing later in development than anterior sections and over the pelvic-fin base.
    (07_4) Three, with the posterior paired sections appearing in near synchrony with the anterior sections and entirely posterior to the pelvic-fin base.
8. Presence of accessory pigment spots or areas (character 15, Johnson, 1974).
    (08_0) Pigment spots or areas present.
    (08_1) Pigment spots or areas absent.
9. Timing of metamorphosis (character 16, Johnson, 1974).
    (09_0) Gradual; onset at 12–15 mm SL or smaller; completion at 30–35 mm SL or smaller.
    (09_1) Gradual; onset at 16–20 mm SL or larger; completion at 40–60 mm SL or larger.
    (09_2) Abrupt; onset at 49.6–89.1 mm SL or larger; completion at 68.3–98.6 mm SL or larger.
10. Appearance of pelvic-fin bud in larvae (character 17, Johnson, 1974).
    (10_0) Pelvic-fin buds appear behind dorsal origin.
    (10_1) Pelvic-fin buds appear anterior to dorsal fin.
11. Development of pectoral fin (character 18, Johnson, 1974).
    (11_0) Pectoral fin not precocious, all other fins with completely differentiated rays prior to ossification of the ventralmost rays of the pectoral fin.
    (11_1) Pectoral fin precocious, developing completely differentiated rays prior to the formation of the complete complement of rays of all other fins (except caudal).

12. Head length in larvae (character 19, Johnson, 1974).
    - (12_0) Head length in larvae not exceeding 30 percent of SL.
    - (12_1) Head length in larvae (up to 28 mm SL) exceeding 30 percent of SL.
13. Hyomandibular articulation with opercle (character 20, Johnson, 1974).
    - (13_0) Discrete posterior arm of hyomandibular bone present.
    - (13_1) Discrete posterior arm of hyomandibular bone absent.
14. Dermal pigment stripes (character 21, Johnson, 1974).
    - (14_0) Dermal pigment on body as equal or subequal stripes above and below the lateral line.
    - (14_1) Dermal pigment on body not so arranged.
15. Length of anal fin.
    - (15_0) Anal fin short (15–30 rays).
    - (15_1) Anal fin long (35–40 rays).
16. Size of dorsal fin.
    - (16_0) Dorsal fin not reduced in size.
    - (16_1) Dorsal fin reduced in size, approximately same size or smaller than adipose fin.