Zootaxa 4226 (4): 509–520
http://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4226.4.4
http://zoobank.org/urn:lsid:zoobank.org:pub:75EDDAA6-7749-4CC3-A340-159A97B9A0A9

Hydrolagus erithacus sp. nov. (Chimaeriformes: Chimaeridae), a new species of chimaerid from the southeastern Atlantic and southwestern Indian oceans

KRISTIN A. WALOVICH[1,5], DAVID A. EBERT[1, 2, 3] & JENNY M. KEMPER[4]

[1]*Pacific Shark Research Center, Moss Landing Marine Laboratories, 8272 Moss Landing Road, Moss Landing, California 95039, USA. E-mail: kwalovich@mlml.calstate.edu*

[2]*Research Associate, South African Institute for Aquatic Biodiversity, Private Bag 1015, Grahamstown, 6140, South Africa*

[3]*Research Associate, Department of Ichthyology, California Academy of Sciences, 55 Music Concourse Drive, San Francisco, California 94118, USA*

[4]*Hollings Marine Laboratory, Medical University of South Carolina, 331 Fort Johnson Road, Charleston, South Carolina 29412, USA*

[5]*Corresponding author*

Abstract

A new species of chimaerid, *Hydrolagus erithacus* sp. nov., is described from nine specimens collected from the southeast Atlantic and southwest Indian oceans from depths of 470–1,000 meters. This species is distinguished from all other *Hydrolagus* species based on the following characteristics: head bulky, relatively large, followed by stocky body; head and body height from about pectoral fin origin to pelvic fin origin similar, then tapering rapidly to filamentous tail; first dorsal fin spine height about equal to, or slightly less than first dorsal fin apex height; second dorsal fin up to 81% of total body length and uniform in height; trifurcate claspers forked for approximately 20% of total length; robust frontal tenaculum nearly uniform in width, prepelvic tenaculae with five to seven medial spines, and a uniform black coloration with robust, non-deciduous skin. Comparison of mitochondrial NADH2 gene sequences with other morphologically similar *Hydrolagus* species suggests that *H. erithacus* is a distinct species.

Key words: Chimaera, ghost shark, taxonomy, NADH2 gene

Introduction

Worldwide the order Chimaeriformes is currently comprised of 49 valid species from three families, Callorhinchidae Garman, 1901, Rhinochimaeridae Garman, 1901 and Chimaeridae Bonaparte, 1831, each group characterized by a distinctive snout morphology (Didier *et al*. 2012; Weigmann 2016). Many of these species are rarely encountered due to the great depths that they inhabit. However, as fisheries move into deeper waters these species are being collected and described at a higher rate than at any previous time. Since 2002, 19 new species (38.8%) have been described, all within the family Chimaeridae. The majority of these new species descriptions (n=10) originated from Australian waters (n = 6) and the eastern Pacific Ocean (n = 4).

The Chimaeridae are comprised of two genera, *Chimaera* Linnaeus, 1758 and *Hydrolagus* Gill, 1862, differentiated based on the presence (*Chimaera*) or absence (*Hydrolagus*) of an anal fin. This diagnostic trait has been subject to much speculation since the two genera are morphologically very similar, but the issue remains unresolved (Didier *et al.* 2012; Ebert 2014). The genus *Hydrolagus*, the most diverse genus in the order and family, has increased by 41% with 9 new species described over the past decade and a half.

The seas around southern Africa, including the southeastern Atlantic and southwestern Indian oceans, are represented by three species of *Hydrolagus*, including *H. africanus* (Gilchrist, 1922), *H. mirabilis* (Collett, 1904), and *H.* cf. *trolli* (Walovich *et al.* 2015). The poorly known *H. africanus,* distributed throughout southern Africa from Kenya to Angola, was recently re-described and a neotype designated (Walovich *et al.* 2015). *Hydrolagus mirabillis* is known throughout the Atlantic, extending south to Angola and may occur into northern Namibia, but this has not been confirmed (Walovich *et al.* 2015). The identification of *H.* cf. *trolli* is tentative pending further

Accepted by M.R. de Carvalho: 14 Nov. 2016; published: 31 Jan. 2017

investigation by the authors (Compagno 1999; Ebert & van Hees 2015; Walovich *et al.* 2015). In addition to the three aforementioned southern African *Hydrolagus* species, a fourth species was recently collected from several seamounts in the southeastern Atlantic and southwestern Indian oceans, and several from locations within the South African Exclusive Economic Zone (EEZ). Upon closer examination of these very large-bodied specimens it was determined through external morphology and molecular data that these specimens represented a new species of *Hydrolagus*. Here we describe this new species.

Materials and methods

External measurements following a modification of Didier & Serét (2002) were taken point-to-point using digital calipers and a measuring tape to the nearest 0.1 millimeter (mm) on fresh and preserved specimens. The following measurements were taken: body length (BDL), dorsal edge of gill opening to origin of dorsal lobe of caudal fin; total length (TL); precaudal length (PCL), snout tip to origin of dorsal lobe of caudal fin; snout-vent length (SVL), snout tip to vent opening; trunk length (TRL), ventral edge of gill opening to vent opening; pre-second dorsal length (PD2), snout tip to origin of second dorsal fin; pre-first dorsal length (PD1), snout tip to origin of first dorsal fin; head length (HDL), snout tip to dorsal opening of gill; pre-orbital length (POB), snout tip to anterior edge of orbit; prenarial length (PRN), snout tip to anterior end of nasal apertures; pre-oral length (POR), snout tip to end of upper labial fold; (D2B), length of second dorsal fin base; (D2AH), maximum height of anterior third of second dorsal fin; (D2PH), maximum height of posterior third of second dorsal fin; (D1B), length of first dorsal fin base; (DSA), dorsal spine height; (D1H), maximum height of first dorsal fin; dorsal caudal margin length (CDM), from origin to insertion of dorsal caudal lobe; (CDH), maximum height of dorsal lobe of caudal fin; total caudal length (CTL), from origin of dorsal caudal lobe to end of caudal filament; ventral caudal margin (CVM), from origin to insertion of ventral caudal lobe; (CVH), maximum height of ventral lobe of caudal fin; caudal peduncle height (CPH), measured at origin of dorsal lobe of caudal fin; pectoral fin anterior margin (P1AM); pelvic fin anterior margin (P2AM); interdorsal space (IDS); dorsal-caudal space (DCS), insertion of second dorsal fin to origin of dorsal caudal lobe; (PPS), posterior base of pectoral fin to anterior base of pelvic fin; pelvic-caudal space (PCS), insertion of pelvic fin to origin of ventral caudal lobe; (D1P1), origin of first dorsal fin to origin of pectoral fin; (D1P2), origin of first dorsal fin to origin of pelvic fin; (D2P1), origin of second dorsal fin to origin of pectoral fin; (D2P2), origin of second dorsal fin to origin of pelvic fin; eye length (EYL); eye height (EYH); total clasper length (CLT), from pelvic fin base to tip; (CLM), length of medial clasper branch from fork to tip; (CLL), length of lateral clasper branch from fork to tip and frontal tenaculum length (FTL), measured from rear end of base to anterior tip.

Additional measurements include: pre-pectoral fin length (PP1), snout tip to origin of pelvic fin anterior margin; pre-pelvic fin length (PP2), snout tip to origin of pelvic fin anterior margin; (D2MH), maximum height of middle third of second dorsal fin; pectoral fin width (P1FW), maximum width across pectoral fin perpendicular to anterior margin; pectoral fin base width (P1BW), width of pectoral fin base from origin of anterior margin to insertion of inner margin; pectoral fin base height (P1BH), height of pectoral fin from body to farthest end of fin base; pelvic fin width (P2FW), maximum width across pelvic fin perpendicular to anterior margin; pelvic fin base width (P2BW), width of pelvic fin base from origin of anterior margin to insertion of inner margin; pelvic fin base height (P2BH), height of pelvic fin from body to farthest end of fin base; clasper width at base (CLB); frontal tenaculum bulb height (TBH); frontal tenaculum bulb length (TBL); frontal tenaculum bulb width (TBW) and frontal tenaculum stalk width (TsW).

The following measurements from the lateral-line canals of the head were taken: distance from anterior oronasal fold to center of nasal canal (ONC); length of the rostral canal (LRC); length of the nasal canal measured as a straight line distance from right to left side (LNC); distance between infraorbital and angular canal measured as the straight line distance from junction of the oral and infraorbital canal to the junction of the oral and angular canal (IOA); distance between preopercular canal and main trunk canal measured from their junction with the infraorbital canal (OTM); distance between main trunk canal and supratemporal canal measured from their junctions with the infraorbital and postorbital canals, respectively (OCL); length of supratemporal canal measured across the head from its junctions with the postorbital canal (STL); distance from anterior base of spine to the center of the supratemporal canal (SPS).

Sexual maturity in females was determined by external examination of the oviducal openings; open and

distended oviducal openings indicate maturity compared to closed openings in juveniles. Male maturity was determined by the emergence and development of frontal tenaculum and prepelvic tenaculae, and degree of calcification of pelvic claspers and prepelvic tenaculae spines (Didier & Séret 2002).

Muscle tissue was collected from two specimens, SAIAB 200578 and 200579, and stored in 95% ethanol at 4°C until further processing in the laboratory. Total DNA was extracted using the EZNA® Tissue DNA Kit (Omega Bio-Tek) and stored at -20°C. The complete coding sequence for the NADH dehydrogenase subunit 2 (NADH2) was PCR amplified for each sample; detailed methods follow Kemper *et al.* (2015). The software program Geneious (version 8.1.7) was used to read chromatograms, view base call quality, and align nucleotide and translated sequences using the Geneious algorithm. Representative sequences of three morphologically similar species, one *Hydrolagus* species closest geographically to the new species, and two outgroup species were included in the analysis. The complete dataset included 16 nucleotide sequences from seven species for a total of 1044 base pairs. Maximum likelihood phylogenetic analysis was performed on the aligned nucleotide sequences using the general-time reversible (GTR) + gamma nucleotide substitution model in RAxML v8.1.22 (Stamatakis 2014), with 1,000 bootstrap replicates. NADH2 sequences were deposited in GenBank.

Institutional abbreviations follow Sabaj Pérez (2016) and include American Museum of Natural History, New York (AMNH), Academy of Natural Sciences, Philadelphia Pennsylvania (ANSP), National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM), Izikio South African Museum (iSAM) and South African Institute for Aquatic Biodiversity (SAIAB).

***Hydrolagus erithacus* sp. nov**

Common Name: Robin's Ghostshark
(Figures 1, 2; Table 1)

Hydrolagus sp. nov. (Big black chimaera): Compagno 1999: 120.

Holotype. SAIAB 200578, adult male, 1290 mm TL, 790 mm BDL, Discovery Seamount, Southeastern Atlantic Ocean, 43°46'S, 01°21'W.

Paratypes. (n=8) SAIAB 200579, adult female, 1357 mm TL, 869 mm BDL, Discovery Seamount, southeastern Atlantic Ocean, 43°43S 01°23W; SAM 34432, adult female, 1220 mm TL, 765 mm BDL, R.S.A Seamount, southeastern Atlantic Ocean, 39° 40' S, 6° 40' W, 470-972 m; SAM 34434, adult male, 1185+ mm TL, 863 mm BDL, southwestern Indian Ocean, 44° 46'S, 36° 18'E, 1097 m, 31 Jan 1997; SAM 34723, immature male, 1169 mm TL, 775 mm BDL, Marion Island, southwestern Indian Ocean, 46° 49' 0.11"S, 37° 43' 59.87" E, 1000 m; SAM 35442, adult male, 1324 mm TL, 842 mm BDL, Marion Island, southwestern Indian Ocean, 46° 49' 0.11"S, 37° 45'E, 20 Feb 2000; SAM 34724, adult female, 1442 mm TL, 915 mm BDL, Marion Island, southwestern Indian Ocean, 44° 46' 0.12"S, 36° 17' 59.99"E, 600 m; SAM 35446, adult female, 1399+ mm TL, 945 mm BDL, Schmidt-Ott Seamount, southeastern Atlantic Ocean; SAM 35447, adult female, 1405 mm TL, 915 mm BDL, Schmidt-Ott Seamount, southeastern Atlantic Ocean

Diagnosis. *Hydrolagus erithacus* is a large species at maturity (765–945 mm BDL) distinguished from all other congeners based on the following combination of characters: head bulky, large followed by stocky body, height similar from about pectoral fin origins to pelvic fin origins remaining consistent in height until the insertion of the pelvic fins, tall dorsal spine greater in height than first dorsal fin. Second dorsal fin up to 81% of total body length, uniform in height, and equal to dorsal caudal fin height. Paired claspers trifurcate, forked for approximately 20% of total length with fleshy, bulbous tips. Prepelvic tenaculae with five to seven medial spines and thick frontal tenaculum, nearly uniform in width. Coloration after preservation uniform black with no distinct markings. Comparison of mitochondrial NADH2 gene sequences with other related species suggests a distinct lineage.

Description. Morphometric measurements of the holotype are given followed in parenthesis by a range of eight paratypes and are presented in Table 1. Large bodied species (1169–1442 mm TL, 765–945 mm BDL) with bulky head 28% (27–31%) BDL and pointed snout 15% (15–18% POB) BDL (Figure 2). Body depth uniform from insertion of pectoral fins to insertion of pelvic fins. Pectoral-pelvic space 35% (29–36%) BDL, approximately two-thirds (54–71%) BDL the pelvic-caudal space 51% (46–61%) BDL. Snout-to-vent length 70% (62–69%) BDL, longer than pelvic-caudal space 51% (46–61%) BDL. Eyes oval along horizontal axis, length 6% (5–7%) BDL**,** 17% (18–22%) HDL and height 4% (3–5%) BDL, 15% (12–17%) HDL. Skin firm, not deciduous.

TABLE 1. Measurements in mm and percentage of body length (% BDL) of *Hydrolagus erithacus* **sp. nov.**

	Holotype		Paratypes (n=8)	
	mm	% BDL	mm	% BDL
TL	1290	163	1169–1442	151–159
PCL	1025	130	935–1210	121–132
SVL	550	70	483–635	62–69
BDL	790	-	765–945	-
TRL	320	41	275–383	35–44
HDL	225	28	219.9–282	27–31
PD1	225	28	245–295	28–35
PD2	419	53	431–515	53–57
PP1	245	31	231–380	29–42
PP2	575	73	531–655	69–75
POB	120	15	113.5–163.4	15–18
PRN	85	11	32.5–105	4–12
POR	109	14	46.5–130	5–15
SNL	107	14	97.8–137.8	12–15
EYL	46.4	6	44–58	5–7
EYH	35.1	4	26.5–44.5	3–5
D1P1	150	19	152.3–260	19–28
D1P2	384	49	357–450	43–49
D2P1	270	34	220–285	25–34
D2P2	190	24	157.3–285	20–31
IDS	90	11	65.1–106.9	8–12
DCS	13.6	2	4.5–22.9	1–3
PPS	276	35	233.6–310	29–36
PCS	400	51	361–555	46–61
PRS	250	32	161–235	21–27
P1AM	279	35	263.4–300.2	31–38
P1FW	163	21	155.8–171.2	18–22
P1BW	93	12	80.8–99	9–13
P1BH	75	9	83.1–108.1	9–12
P2AM	164	21	159.1–183.6	18–22
P2FW	62	8	93.1–115.3	10–14
P2BW	44	6	36.8–91.7	4–12
P2BH	127	16	35.5–67.5	4–7
DSA	200	25	174.8	21
D1B	128	16	107.7–128	12–16
D1H	92.8	12	96.7–129.6	11–15
D2B	600	76	557–745	71–81
D2AH	29.7	4	27.1–37.2	3–5
D2PH	36.8	5	28.5–38.7	3–5
D2MH	30.2	4	29.3–40	3–5
CDM	185	23	176.1–196.8	21–25

.....continued on the next page

TABLE 1. (Continued)

	Holotype		Paratypes (n=8)	
	mm	% BDL	mm	% BDL
CDH	32.2	4	25.7–38.1	3–5
CVM	305	39	242.3–299.3	30–36
CVH	29.26	4	21.7–31.2	3–4
CTL	260	33	209.7–267.3	25–32
CLT	151.5	19	151.5–164.2	19–20
CLM	25.3	3	30.43–36	3–4
CLL	37.7	5	28.6–37.7	3–4
CLO	46.8	6	107.7–121.1	14
CLI	113.1	14	113.1–152.1	17–20
CLB	111	14	20.5–25	2–3
FTL	41.8	5	36.6–42.4	4–5
TBH	11.6	1	6.9–12.7	1
TBL	17.5	2	11.2–20.7	1–2
TBW	11.1	1	8.3–12.1	1
TsW	7.5	1	4.6–7.3	1
ONC	25.3	3	19.5–32	3–4
LRC	13	2	11.1–25	1–3
LNC	54.4	7	26.2–64.3	3–7
IOA	26.1	3	5.3–38.6	1–4
OTM	77.2	10	73.1–88.8	8–11
OCL	26	3	31.4–54.5	4–6
STL	50.6	6	39.1–74	5–8
SPS	21.7	3	36.7–57	4–6

Pectoral fins large and triangular; pectoral fin length 35% (31–38% P1AM) BDL, 1.7–1.9 times pectoral fin width 21% (18–22% P1FW) BDL, with a strait anterior margin tapering distally to a rounded apex. Pelvic fin length 21% (18–22% P2AM) BDL, equal to pectoral fin width 21% (18–22% P2FW) BDL and nearly half the pectoral fin length. Pectoral and pelvic anterior margins weakly convex, overall oval in shape. Fins remain intact and do not fray after preservation.

First dorsal fin triangular with straight medial edge, base 16% (12–16%) BDL terminating to a low membrane connecting to second dorsal fin in a gentle slope. Dorsal spine 25% (21%) BDL robust, curving anteriorly and taller than the first dorsal fin height 12% (11–15%) BDL; dorsal spine when depressed is slightly shorter than or just reaches origin of second dorsal fin. Second dorsal fin base long 76% (71–81%) BDL and uniform in height along entire length. Second dorsal fin curves downward toward caudal insertion, but does not meet dorsal body margin before dorsal caudal margin begins.

Caudal ventral margin 39% (30–36%) BDL generally longer than caudal dorsal margin 23% (21–25%) BDL. Caudal dorsal height 4% (3–5%) BDL nearly equal to average second dorsal height 4% (3–5%) BDL, slightly taller than caudal ventral height 4% (3–4%) BDL. No caudal filament observed in available specimens.

Paired claspers trifurcate, forked for ~20% total length of clasper (17–22% BDL). Medial branch slender with small tip, lateral branches with bulbous tips, extending one-third the length of the clasper, covered in small denticles (Figure 2). Frontal tenaculum stalk thick and nearly uniform in width. Bulb round with slender, sporadically arranged spines. Prepelvic tenaculae rectangular in shape with 5 to 7 robust medial spines.

Intraspecific variation of oral (O), preopercular (POP) and infraorbital (IO) canals was observed. In half of the specimens the O and POP canals share a common branch from the IO, in the remaining the O and POP canals connect separately to the IO canal.

FIGURE 1. Photograph of the *Hydrolagus erithacus* holotype, SAIAB 200578, mature male, 1290 mm TL, 790 mm BDL. Scale bar = 5 cm.

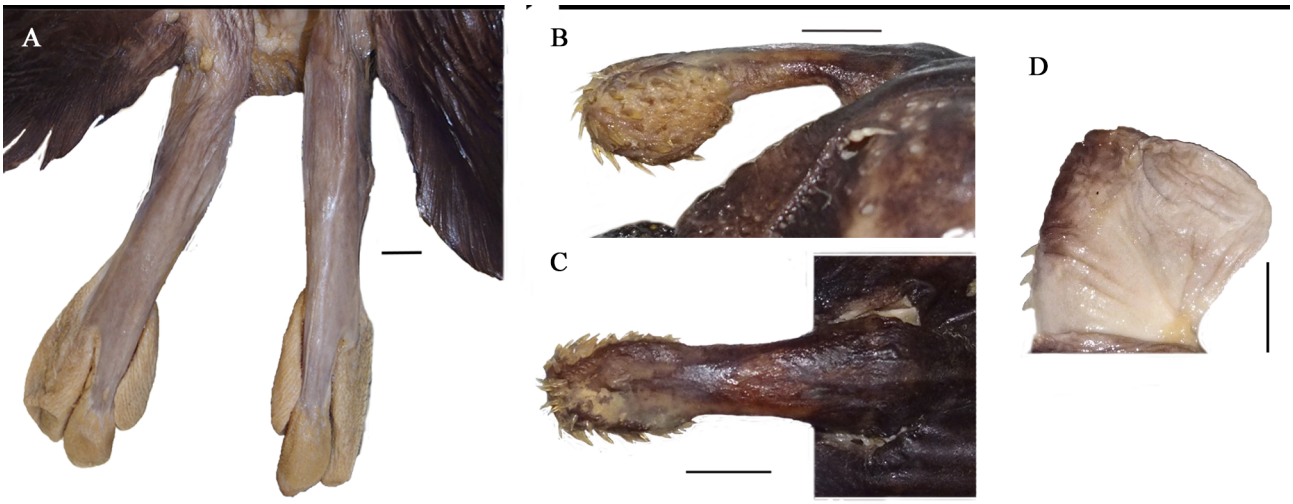

FIGURE 2. Sexual characters of adult *Hydrolagus erithacus* sp. nov. holotype including the (a) claspers (b) frontal tenaculum in lateral view (c) frontal tenaculum in dorsal view and (d) pre-pelvic tenaculum in ventral view. Scale bars = 5mm (a), and 1mm (b)-(d).

Coloration. Body coloration and fins a uniform black with no distinctive patterns or markings based on preserved specimens. Claspers variable in color from black to pale tan, tips light yellow. Frontal tenaculum dark on dorsal surface, light on ventral. Prepelvic tenaculae tan in color along medial edge near spines, darkening to black along on distal and medial edge posterior to spines.

Etymology. The species name *erithacus* derives from the avian genus of the robin (Aves: Passeriformes: Muscicapidae: *Erithacus* Cuvier, 1800). Named after Robin Leslie of South African Department of Agriculture, Forestry and Fisheries (DAFF), a fanatic birder, in recognition of his help and support on this project, and his overall contribution to Chondrichthyan research in southern Africa.

Distribution. *Hydrolagus erithacus* is currently known from the southeastern Atlantic and southwestern Indian oceans, between latitudes 39° to 47° S, from depths of 470–1,000 meters (Figure 3). Based on the depth distribution of similarly sized species and accounts from the Patagonian toothfish *(Dissostichus eleginoides*) fishery operating within its range, this species likely occurs to depths in excess of 2,000 meters (R. Leslie, DAFF unpublished data).

Biological notes. A large bodied species growing to at least 945 mm BDL, 1405 mm TL. Smallest observed mature individuals were 842 mm and 765 mm BDL for males and females, respectively. Largest immature male individual was 775 mm BDL, no immature females were observed. Internal examination of a mature female

specimen (SAM 34724) measuring 915 mm BDL revealed a fully developed uterus and oviducal glands with several oocytes measuring approximately 30 mm in diameter. Fragments of possible crab appendages were recovered from the digestive tract of the holotype specimen, indicating a diet of crustaceans and other benthic fauna.

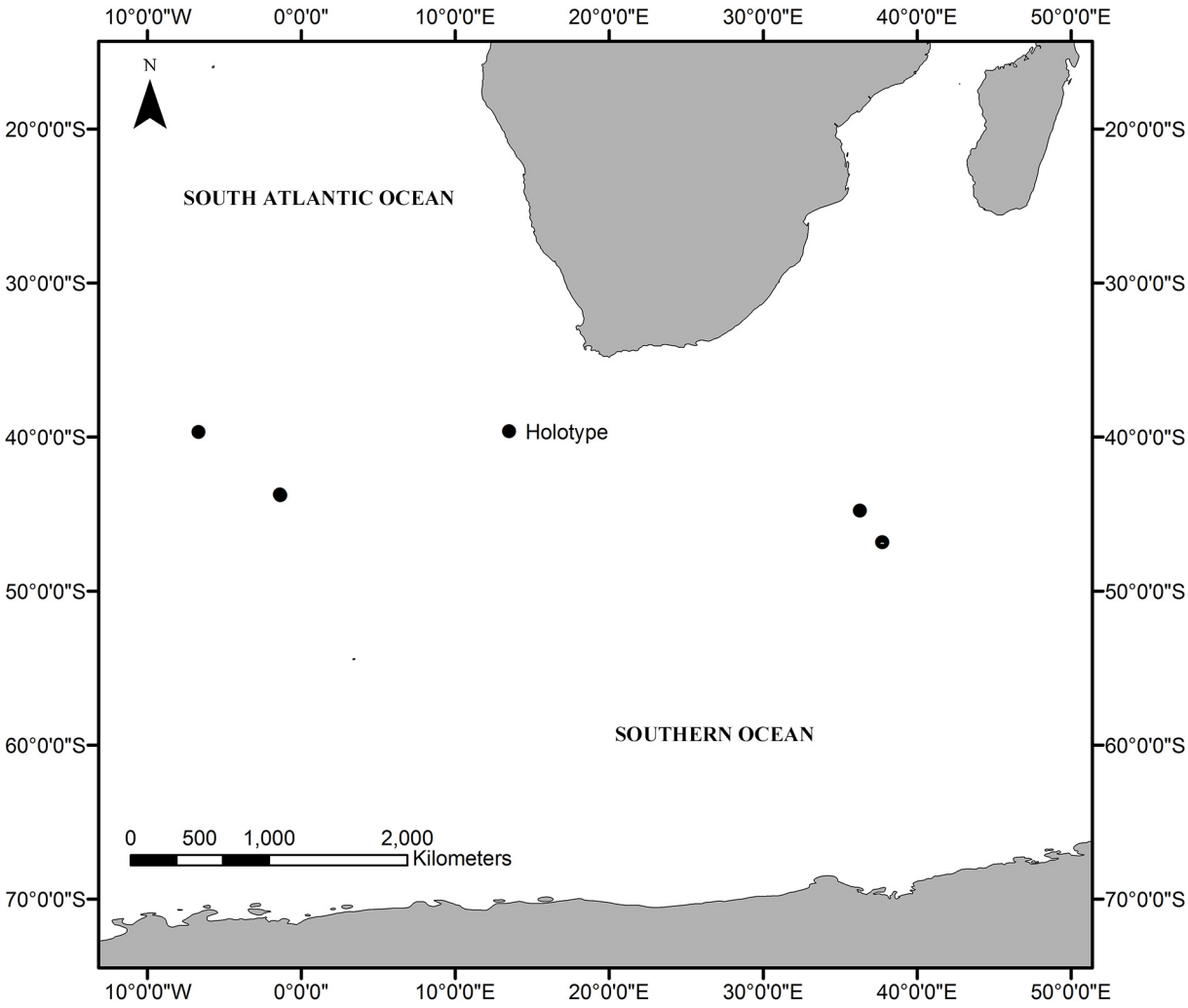

FIGURE 3. Distribution of *Hydrolagus erithacus* sp. nov in the southeastern Atlantic and southwest Indian Oceans

Comparisons. *Hydrolagus erithacus* is the second largest *Hydrolagus* species described to date, and can clearly be differentiated from the small-bodied chimaerids in the genus (e.g. *H. africanus*, *H. alberti, H. alphus, H. barbouri, H. colliei, H. macrophthalmus, H. mirabilis,* and *H. mitsukurii*). *Hydrolagus africanus* occurs nearest in geographic proximity to *H. erithacus*, but does not overlap in distribution, and is a much smaller species (<500 mm BDL, <900 mm TL and size at maturity >300 mm) (Walovich *et al.* 2015). The anterior second dorsal fin height of *H. africanus* is taller (4–8% vs. 3-5% BDL) and the second dorsal height taller across its entire length (2–7% vs. 3–5% BDL D2PH, 1–6% vs. 3–5% BDL D2MH). The coloration of fresh *H. africanus* is silver and brown and when preserved turns a uniform light brown. Additionally, the uniform black color of *H. erithacus* separates it from the patterned species such as *H. alphus*, *H. colliei, H. marmoratus, H. mccoskeri*, and *H. novaezealandiae*.

The seven species most similar to *H. erithacus* in color and body size are compared. Three species of these large bodied *Hydrolagus* are known only to occur in the North Atlantic, *H. affinis, H. pallidus* and *H. lusitanicus* (Ebert & Stehmann 2013). *Hydrolagus affinis* relative to *H. erithacus* differs proportionally by having a smaller snout to second dorsal fin distance (47–55% vs. 53–57% BDL), head length (23–31% vs. 27-32% BDL), pre-

pectoral fin length (28–34% vs. 29–42% BDL), pre-orbital length (12–14% vs. 15–18% BDL), dorsal caudal margin (16–21% vs. 21–25% BDL) and dorsal caudal height (2–4% vs. 3–5% BDL). *Hydrolagus affinis* has been described as having 4–6 medial spines on the prepelvic tenaculae (Hardy & Stehmann 1990), however investigation of additional specimens reveals a slightly wider spine count range (4–8 spines, average 6). *Hydrolagus pallidus* is distinct from *H. erithacus* based on a shorter head length (23–30% vs. 27–31% BDL), pre-pectoral fin length (26–34% vs. 29–42% BDL) and pectoral fin length-to-width ratio (1.3–1.7 vs. 1.7–1.9). Previously reported pectoral fin length-to-width ratios are less than 1.5 for *H. pallidus* (Hardy & Stehmann 1990; Ebert & Stehmann 2013), however an additional specimen measured by the authors was outside this range (1.7). *Hydrolagus pallidus* turns white to creamy grey colored in fixative, whereas *H. erithacus* turns a uniform black. *Hydrolagus lusitanicus* appears to reach similar body lengths as *H. erithacus*, however the species was poorly described, did not use standard measurement methods for comparison to other *Hydrolagus* species, and did not provide any maximum size or size at maturity information (Moura *et al.* 2005). However, *H. lusitanicus* has a larger pectoral fin length-to-width ratio (1.9–2.3 vs. 1.7–1.9), longer first dorsal fin base length (19–20% vs. 13–16% BDL), and a distinct coloration from *H. erithacus*, being a uniform rose to light brown with irregular spots and violet-blue fins.

Hydrolagus purpurescens from the central and western North Pacific is poorly known, but can be separated from *H. erithacus* by a longer snout-to-vent length (68–72% vs. 62–69% BDL), shorter distance from first dorsal fin origin to pectoral fin origin (20–21% vs. 19–28% BDL), and greater eye length (6–8% vs. 5–7% BDL) and eye height (4–6% vs. 3–5% BDL). Second dorsal fin height is taller and with a slight dip at the center (4–5% BDL), while remaining a consistent height in *H. erithacus*.

The eastern Pacific *H. melanophasma* has a shorter snout-to-vent length (57–60% vs. 62–70% BDL), larger eyes (22–26% vs. 17–22% HDL), longer pectoral fin anterior margin (39–41% vs. 31–38% BDL), and fewer prepelvic tenaculae spines (3–4 vs. 5–7 spines) (James *et al.* 2009).

Hydrolagus trolli, found in the waters off New Zealand and New Caledonia, is a slightly smaller species, reaching sexual maturity at 550–650 mm BDL (Didier & Séret 2002). *Hydrolagus trolli* has a greater range of snout-to-vent lengths (63–75% vs. 62–69% BDL), longer pre-orbital length (14–19% vs. 15–18% BDL), smaller head (22–26% vs. 23–39% BDL), shorter caudal dorsal height (3–4% vs. 3–5% BDL), shorter caudal ventral margin (30–36% vs. 28–40% BDL) and fewer medial spines on the prepelvic tenaculae (4–5 vs. 5–7 spines). *Hydrolagus trolli* is a uniform pale, blue-grey when fresh, becoming brown to purple when fixed, compared to the uniform black coloration of *H. erithacus.*

Hydrolagus homoncyteris is a medium bodied (667 mm maximum BDL) species from southeast Australia and New Zealand, whose diagnostic short, round pelvic fins (13–18% BDL) make it distinguishable from the larger, oval shaped pectoral fins of *H. erithacus* (18–22% BDL) despite its similar uniform, black coloration (Didier 2008).

The tree topology of the maximum likelihood analysis of sequence data at the NADH2 gene locus suggests five distinct clades, corresponding to *H. africanus*, *H. affinis*. *H. pallidus*, *H. trolli* and *H. erithacus* (Figure 4). *Rhinochimaera atlantica* and *Harriotta raleighana* were used to root the tree. *Hydrolagus africanus* is clearly distinguishable from the other four species based on sequence data. However, the remaining four species show limited sequence divergence at this locus, indicating two potential scenarios: (1) these are valid species, or (2) that they represent populations of a single species. The inference suggests separate species, since they fall out into their respective species lineages and show geographic structure. However, this topological pattern is also typical of little movement between populations of the same species, limiting gene flow due to isolation by distance. Interestingly, *H. affinis* and *H. pallidus* are known to overlap in distribution, and here, are recovered as their respective species, indicating two unique species. While we suggest *Hydrolagus erithacus* as a new species distinct from similar *Hydrolagus* species based on the molecular data, we caution that this inference is the tree topology for only a single mitochondrial gene and may not correspond to the species tree based on multiple markers. It may be necessary to analyze a suite of independent molecular markers to infer a robust species tree. The NADH2 gene it should be noted is a fast-evolving protein-coding mitochondrial gene, and thus, is regarded as a useful marker for assessing species differentiation.

Comparative material. Material examined of *H. alphus*, *H. macrophthalmus*, *H. mccoskeri*, *H. melanophasma*, *H. mitsukurii*, and *H. novaezealandiae* is listed in Barnett *et al*. (2006), Quaranta *et al*. (2006), James *et al*. (2009), and Ebert *et al*. (2013).

Hydrolagus affinis (13 specimens): AMNH 78355, adult female, 1080 mm TL, 740 mm BDL, Tenerife Island, Eastern Central Atlantic, 28° 6’16. 15”N, 16° 8’39. 77W, 01 Oct 1986; AMNH 78358, adult male, 1035 mm TL, 690 mm BDL, Tenerife Island, Eastern Central Atlantic, 28° 6’16’5”N, 16 °8’39.77 W, 01 Oct 1986; AMNH 78365, adult male, 980 mm TL, 655 mm BDL, Tenerife Island, Eastern Central Atlantic, 28° 6’16.15”N, 16° 8’39.77”W, 01 Oct 1986; AMNH 78367, adult male, 1122 mm TL, 760 mm BDL, Tenerife Island, Eastern Central Atlantic, 28° 6’16. 15”N, 16° 8’39’77”W, 01 Oct 1986; AMNH 78368, adult male, 1045 mm TL, 721 mm BDL, Tenerife Island, Eastern Central Atlantic, 28° 6’16.15”N, 16° 8’39.77W, 01 Oct 1986; AMNH 78378, adult female, 1185 mm TL, 760 mm BDL, North Atlantic Ridge, 46°49'18.0"N 27°36'18.0"W; AMNH 78379, immature male, 920 mm TL, 568 mm BDL, North Atlantic Ridge, 46°49'18.0"N 27°36'18.0"W; AMNH 78380, adult female, 1215+ mm TL, 840 mm BDL, North Atlantic Ridge, 46°49'18.0"N 27°36'18.0"W; ANSP 174645 (1 of 3), adult male, 1080 mm TL, 700 mm BDL, Northwestern Atlantic Ocean; ANSP 178569, adult male, 1002 mm TL, 657 mm BDL, Davis Strait, North Atlantic Ocean, 63° 37' N, 56° 37' W, 1415 m, 7 Nov 2001; USNM 38021, adult male, 945 mm TL, 624 mm BDL, Nova Scotia, Canada, 44° 30' 00"N, 58° 30' 00"W, 366 m; USNM 94399, adult female, 1121+mm TL, 853 mm BDL, Browns Bank, Massachusetts, USA; USNM 387795, immature male, 996 mm TL, 653 mm BDL, Bear Seamount, Atlantic Ocean, 39 °55’21.36”N, 67° 25’55.91”W, 1197 m, 19 Apr 2005

Hydrolagus africanus (42 specimens): CAS 241488, 3 male, 1 female, Western Cape, South Africa, 3459'38.4" S, 01820'04.8" E, 631 m, 10 Feb 2015; CAS 241490, 1 male, 1 female, Western Cape, South Africa, 31°27'33.0"S 15°52'07.2"E, 543 m, 28 Feb 2015; CAS 241491, male, Western Cape, South Africa, 30°56'57.6"S 15°27'53” E, 725 m, 5 Mar 2015; CAS 241492, 2 male, Western Cape, South Africa, 30°19'20.4"S 14°54'38.4"E, 511 m, 6 Mar 2015; CAS 241493, female, Western Cape, South Africa, 30°19'20.4"S 14°54'38.4"E, 511 m, 6 Mar 2015; SAIAB 186459, adult female, 393+ mm TL, 321 mm BDL, Durban, South Africa, 30° 05.244' S, 31° 22.969' E, 25 Aug 2010; SAIAB 14040A, adult female, 620 mm TL, 293 mm BDL, Mombasa, Kenya, 4° 16’ 59.99” S, 40° 6’ 59.99” E, 10 Dec 1908; SAIAB 14040B, adult male, 655 mm TL, 413 mm BDL, Mombasa, Kenya, 4° 16’ 59.99” S, 40° 6’ 59.99” E, 10 Dec 1908; SAIAB 17324A, adult male, 459 mm TL, 285 mm BDL, Durban, South Africa, 29° 51' 0" S, 31° E, Sept 1967; SAIAB 25211, adult male, 790 mm TL, 325 mm BDL, 22 Jan 1984; SAIAB 25712, adult male, 443 mm TL, 304 mm BDL, Western Cape, South Africa, 28° 22' 59.99" S, 14° 25' 18" E, 3 Feb 1986; SAIAB 17325, adult female, 407 mm TL, 285 mm BDL, Durban, South Africa, 29° 51' 0" S, 31° E, Sept 1967; SAIAB 81688, adult male, 646 mm TL, 308 mm BDL, Mozambique, 26° 10.5' S, 34° 7.5' E, 29 Sept 2007; SAM 33058, adult female, 744 mm TL, 364 mm BDL, Port Elizabeth, South Africa, 34° 25' 0.11" S, 25° 56' 59.99" E, 309 m; SAM 33412A, adult male, 773 mm TL, 330 mm BDL, Lüderitz, Namibia, 27° 22' 12" S, 14° 16' 11.99"E, 475 m; SAM 33412B, adult male, 735 mm TL, 295 mm BDL, Lüderitz, Namibia, 27° 22' 12" S, 14° 16' 11.99"E, 475 m; USNM 438927, male, Western Cape, South Africa, 31°34'55.8"S 15°51'41.4"E, 563 m, 28 Feb 2015; USNM 438929, male, Western Cape, South Africa, 31°27'33.0"S 15°52'07.2"E, 543 m, 28 Feb 2015; USNM 438930, female, South Africa, 33°30'31.2"S 17°20'04.2"E, 561 m, 20 Feb 2015; USNM 438931, female, South Africa, 31°34'55.8"S 15°51'41.4"E, 563 m, 28 Feb 2015; USNM 438932, male, Western Cape, South Africa, 30°19'20.4"S 14°54'38.4"E, 511 m, 6 Mar 2015;

Hydrolagus pallidus (1 specimen): ANSP 178019, immature male, 1010 mm TL, 800 mm BDL, Outer Hebrides, Scotland, United Kingdom, 57° 30’ N, 9° 30’ W, R/V Galibier

Hydrolagus purpurescens (2 specimens): AMNH 3, adult female, 1321 mm TL, 826 mm BDL, Honshu Island, Japan, 28 Mar 1903; USNM 051594, Type Specimen, adult female, 868 mm TL, 514 mm BDL, Hawaiian Islands, USA, 26 Sept 1904

Hydrolagus trolli (7 specimens): ANSP 177750, adult female, 1020 mm TL, 610 BDL, Northwest Chatham Rise, New Zealand, 42° 32' 6" S, 176° 30' 48" E, 1481 m, 16 June 1990; ANSP 177751, adult male, 985 mm TL, 626 mm BDL, Veryan Bank, Chatham Rise, New Zealand, 44° 39' 48" S, 176° 41' 0" E, 1153 m, 4 Nov 1986; ANSP 177752 (2 of 2), immature male, 715 mm TL, 418 mm BDL, Bounty Trough, New Zealand, 39°54'06"S, 174°26'06"E, 1356 m, 23 Nov 1989; ANSP 177754 (1 of 2), adult male, 1010 mm TL, 658 mm BDL, Chatham Rise, New Zealand, 42° 31' 12" S, 178° 30' 30" W, 1452 m, 16 June 1992; ANSP 177754 (2 of 2), immature male, 920 mm TL, 562 mm BDL, Chatham Rise, New Zealand, 42° 31' 12" S, 178° 30' 30" W, 1452 m, 16 June 1992; ANSP 177755 (1 of 2), adult female, 1036 mm TL, 685 mm BDL, Chatham Rise, New Zealand, 42° 41' 38" S, 172° 38' 2" E, 1694 m, 21 May 1994; ANSP 177755 (2 of 2), adult female, 930 mm TL, 564 mm BDL, Chatham Rise, New Zealand, 42° 41' 38" S, 172° 38' 2" E, 1694 m, 21 May 1994

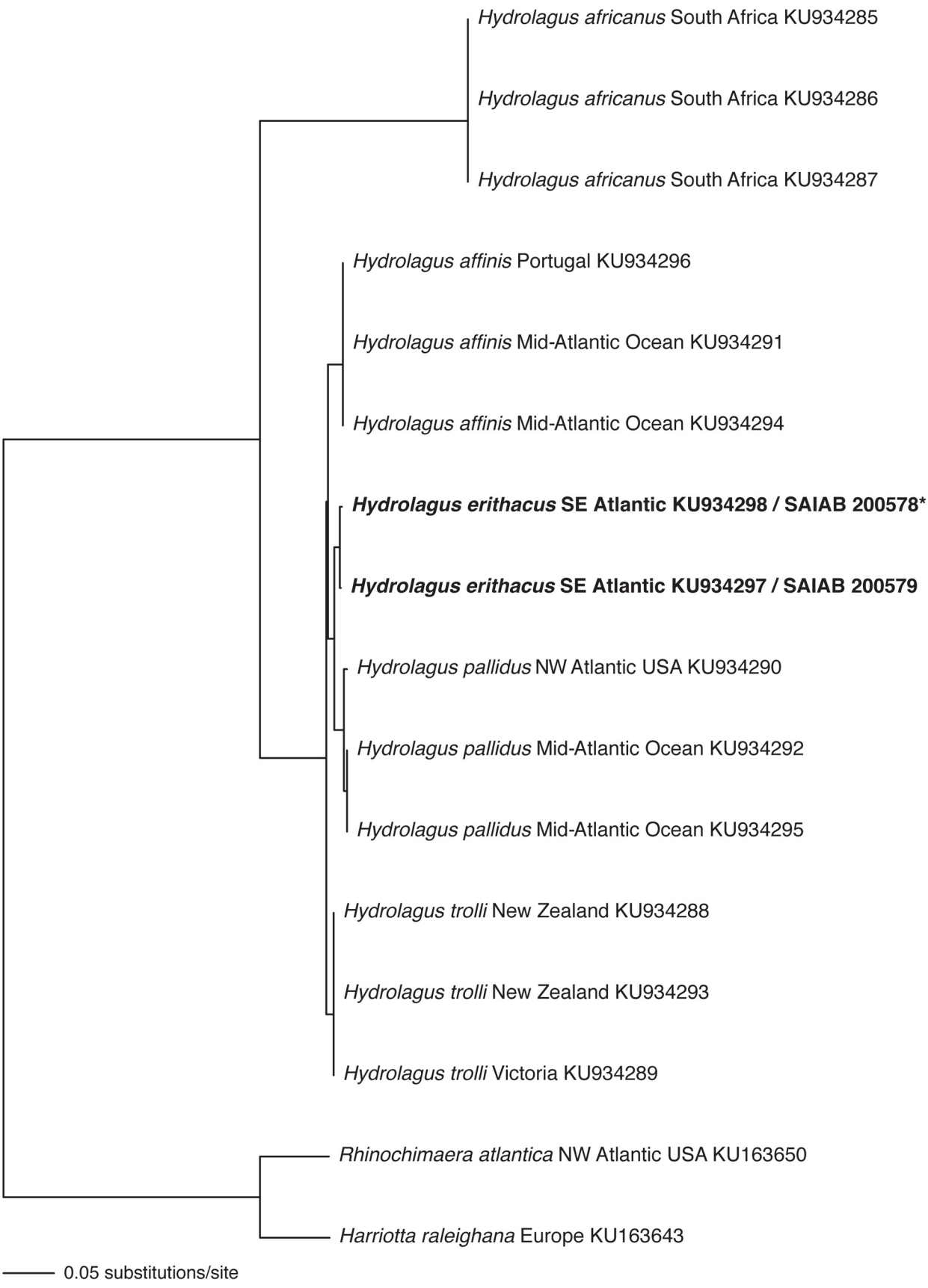

FIGURE 4. Maximum likelihood tree estimate using general-time reversible (GTR) + gamma model based on NADH2 sequence data of *Hydrolagus erithacus* and comparative species. GenBank accession numbers follow species names. *Hydrolagus erithacus* position indicated in bold; collection number follows GenBank accession number. * = holotype.

Acknowledgements

We are grateful to Gavin Naylor (College of Charleston, South Carolina) for the gracious use of his resources and time. For assistance in collections, we thank Mark Sabaj-Pérez (Academy of Natural Sciences Philadelphia, Drexel University), Radford Arrindell (American Museum of Natural History, New York), Kris Murphy and Jeffery Williams (National Museum of Natural History, Smithsonian Institute), Roger Bills, Paul Cowley, and Alan Whitfield (South African Institute of Aquatic Biodiversity), Rob Leslie, Robb Copper, and Larvika Singh (South African Department of Agriculture, Forestry and Fisheries), Mike Bougaardt, Dylan Clarke, Liz Hoenson and Candice Untiedt (Izikio South African Museum), Dave Catania and Jon Fong (California Academy of Sciences), and Paul Clerkin (Pacific Shark Research Center, Moss Landing Marine Laboratories).

This project was supported in part by the National Science Foundation (NSF) Collaborative Research: Jaws and Backbone: Chondrichthyan Phylogeny and a Spine for the Vertebrate Tree of Life (DEB 1132229 and 1036505), the Council on Ocean Affairs, Science and Technology (COAST) Travel Award, the American Society of Ichthyologists and Herpetologists Raney Award, the Systematics Research Fund Grant, the Dr. Earl H. Myers and Ethel M. Myers Oceanographic and Marine Biology Trust Grant, and the South African Institute for Aquatic Biodiversity.

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