



Article

# First Records of a *Hydrolagus* Species (*Holocephali*: *Chimaeridae*) from Reunion Island and Mayotte (Southwestern Indian Ocean)

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**Abstract:** Two specimens of large blackish chimaeras of the genus *Hydrolagus* were caught, one off Reunion Island and the other off Mayotte in the southwestern Indian Ocean. The specimens, an adult male of 710 mm BDL and a female of 870 m BDL, are described, compared to similar species (i.e., having a large size, over 110 cm TL, dark blackish colour, and rather long conical snout), and tentatively identified to the small-eyed rabbitfish *Hydrolagus affinis*, pending a taxonomic revision of the large blackish chimaeras is completed.

Keywords: Chondrichthyes; Elasmobranchii; Chimaeridae; Hydrolagus; first records; SW Indian Ocean

**Key Contribution:** Rare deep-sea chimaeras are recorded for the first time from two remote islands in the southwestern Indian Ocean. These records significantly extend the geographic distribution of *Hydrolagus affinis*, native to the Atlantic Ocean.

#### 1. Introduction

Chimaeras or ghost sharks of the family Chimaeridae are cartilaginous fishes (Chondrichthyes) characterised by a very large head (Holocephalii), a soft cone-shaped body, a tapering tail that ends as a caudal filament, a conical snout, short to moderately long, a single external gill opening, conspicuous mucous canals and sensory pores on the head, teeth fused in pairs of dental plates forming a beak, males that have bifurcate or trifurcate claspers, and supplementary clasping organs on the forehead (frontal tenaculum) and a pair in front of pelvic fins (prepelvic tenacula). Sizes of Chimaeras vary from small (38 cm LT) to large (147 cm LT); they live mostly in the deep seas (200–3000 m) of the world ocean. The biology and the ecology of the chimaeras are largely unknown, and their taxonomy is still unclear. A few species are exploited for their meat and liver oil.

Globally, chimaeras (*Chimaeridae*, *Callorhinchidae*, and *Rhinochimaeridae*) have rarely been observed since the description of the first species by Linnaeus [1]. Only 30 species were described for about 250 years (from 1758 to 2000), then 24 new species were described during the last two decades thanks to the development of deep-sea explorations all around the world and the specific works of a number of ichthyologists on this group of fishes [2–12].

Traditionally, two genera were recognized in the family *Chimaeridae*, *Chimaera* and *Hydrolagus*, distinguished by the presence (*Chimaera*) or the absence (*Hydrolagus*) of an anal fin. Today, 42 species are recognized as valid; 21 in the genus *Chimaera* and 21 in the genus *Hydrolagus* (Table 1), plus a doubtful species from Japan ([13]; FishBase and the Eschemeyer's Catalogue of Fishes consulted in 2023). Despite recent studies devoted to these fishes, the taxonomic status of some species is still pending. Furthermore, recent genetic analysis does not support the traditional distinction in two genera and seems in favour of a single genus. However, even if the morphologic criteria "presence/absence of an anal fin" is proved to have no generic significance, it is still useful at the species level.



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**Table 1.** List of *Chimaera* and *Hydrolagus* species, with distribution, depth range, size (TL and BDL), and IUCN Red List status (consulted in 2023). Species presented by genus and chronological order.

Species	Authors	English Name	Distribution	Depth Range	TL	BDL	Red List
Chimaera monstrosa	[1]	Rabbitfish	Eastern North Atlantic: Iceland to Morocco	50–1742 m	119 cm	59 cm	VU
Chimaera ogilbyi (=lemures)	[14]	Ogilbys ghost shark	Indo-Australia: Australia, Indonesia, New Guinea	120–872 m	103 cm	55 cm	NT
Chimaera phantasma	[15]	Silver chimaera	Western Pacific: Japan to Philippines 20–962 m 11		110 cm		VU
Chimaera jordani	[16]	Jordan's chimaera	NW Pacific: Japan	716–780 m	93 cm		DD
Chimaera owstoni	[16]	Owston's chimaera	NW Pacific: Japan	650–900 m	80 cm		DD
Chimaera cubana	[17]	Chimaera	WC Atlantic: Cuba	180–1050 m	80 cm		LC
Chimaera panthera	[18]	Leopard chimaera	SW Pacific: New Zealand	327–1020 m	129 cm		LC
Chimaera lignaria	[2]	Giant chimaera	Southern Pacific: New Zealand + Tasmania	400–1800 m	142 cm		LC
Chimaera argiloba	[19]	Whitefin chimaera	Eastern Indian Ocean: Western Australia	370–520 m	91 cm		LC
Chimaera fulva	[20]	Southern chimaera	Southern Australia	780–1095 m	118 cm		LC
Chimaera macrospina	[20]	Longspine chimaera	Indo-West Pacific: Australia east and west	435–1190 m	103 cm LL		LC
Chimaera obscura	[20]	Shortspine chimaera	SW Pacific: eastern Australia	450–1080 m	95 cm		LC
Chimaera bahamaensis	[8]	Bahamas ghost shark	North Atlantic: Bahamas	732–1506 m	88 cm		LC
Chimaera notafricana	[7]	Cape chimaera	Southern Atlantic: Namibia, South Africa	680–1000 m	93 cm		LC
Chimaera opalescens	[21]	Opal chimaera	NE Atlantic	800–1975 m	110 cm		DD
Chimaera carophila	[22]	Brown chimaera	SW Pacific: New Zealand	846–1350 m	104 cm	60 cm	LC
Chimaera orientalis	[23]	Eastern Pacific black chimaera	Eastern Pacific: Costa Rica, Peru	560–1138 m	86 cm	50 cm	DD
Chimaera buccanigella	[24]	Dark-mouth chimaera	SW Indian Ocean Ridge	495–960 m	86 cm		DD
Chimaera didierae	[24]	Falkor chimaera	SW Indian Ocean: Walters Shoal	1000–1100 m	155 cm		DD
Chimaera willwatchi	[24]	Seafarer's ghost shark	SW Indian Ocean: Madagascar Ridge	89–1375 m	97 cm		DD
Chimaera compacta	[25]	Stubby chimaera	Southern Indian Ocean: Amsterdam	595–655 m	84 cm		
Hydrolagus colliei	[26]	White spotted chimaera	NE Pacific: Alaska to Costa Rica	0–1029 m	60 cm		LC
Hydrolagus affinis	[27]	Small-eyed rabbitfish	NE + NW Atlantic + WIO (South Africa)	300–3000 m	147 cm	96 cm	LC
Hydrolagus mirabilis	[28]	Large-eyed rabbitfish	EN Atlantic to Morocco + WN Atlantic	450–2058 m	80 cm	35 cm	LC
Hydrolagus mitsukurii	[29]	Spookfish / Mitsukuri's chimaera	NW Pacific: Japan, 325–830 m 7		79 cm	37 cm	NT
Hydrolagus purpurescens	[30]	Purple chimaera	Pacific: Japan, Hawaii; 920–1951 m		138 cm +		LC
Hydrolagus barbouri	[31]	Ninepsoy chimaera	NW Pacific: Japan, China	250–1100 m	86 cm	48 cm	DD
Hydrolagus novaezealandiae	[32]	Dark ghost shark	SW Pacific: New Zealand	25–950 m	96 cm		LC
Hydrolagus deani (? = H. misukurii)	[33]	Philippine chimaera	WC Pacific: Philippines	469–770 m	73 cm		

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Table 1. Cont.

Species	Authors	English Name	Distribution	Depth Range	TL	BDL	Red List
Hydrolagus africanus	[34]	African chimaera	W Indian Ocean 303–1470		98 cm	46 cm	LC
Hydrolagus alberti	[35]	Gulf chimaera	Western Atlantic: Gulf Mexico + Caribbean	348–1470 m	100 cm	45 cm	LC
Hydrolagus macrophthalmus	[36]	Bigeye chimaera	Eastern Pacific: Mexico to Chile	590–1160 m	64 cm	35 cm	LC
Hydrolagus pallidus	[37]	Pale chimaera	North Atlantic: Iceland to Newfoundland	883–2619 m	138 cm	91 cm	LC
Hydrolagus bemisi	[2]	Pale ghost shark	SW Pacific: New Zealand	400–1100 m	112 cm	57 cm	LC
Hydrolagus trolli	[4]	Pointy-nosed blue chimaera	Western Pacific: New Caledonia, New Zealand	612–2000 m	120 cm	79 cm	LC
Hydrolagus matallanasi	[38]	Striped rabbitfish	SW Atlantic: Brazil	416–73 m	70 cm	31 cm	VU
Hydrolagus lusitanicus	[39]	Portuguese rabbitfish / coelho	NE Atlantic: Portugal	1600–2410 m	118 cm PCL		LC
Hydrolagus alphus	[40]	Whitespot ghost shark	EC Pacific: Galapagos	630–907 m	>48 cm	>25 cm	LC
Hydrolagus mccoskeri	[41]	Galápagos ghost shark	EC Pacific: Galapagos	396–606 m	38 cm	37 cm	LC
Hydrolagus homonycteris	[42]	Black ghost shark	Southern Ocean: Australia, Tasmania + New Zealand	400–1450 m	109 cm	66 cm	LC
Hydrolagus marmoratus	[42]	Marbled ghost shark	Western Pacific: eastern Australia	548–995 m	80 cm		LC
Hydrolagus melanophasma	[43]	Eastern Pacific black ghost shark	Eastern Pacific: California to Chile	30–1800 m	128 cm	92 cm	LC
Hydrolagus erithacus	[11]	Robin's ghost shark	SE Atlantic and SW Indian Oceans	470–1000 m	144 cm	91 cm	DD

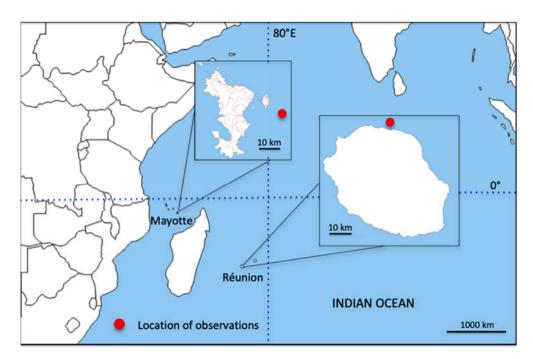
In the course of longline fishing operations, two specimens of large blackish chimaeras were caught off La Reunion (two females were caught, but only one was preserved) and off Mayotte in the southwestern Indian Ocean. They represent the first records of chimaeras for these remote islands in the southwestern Indian Ocean.

Because of their deep-sea habitat offering relatively stable environmental conditions, chimaeras are likely to have a very large distribution in the world ocean; thus, comparisons of the specimens from Reunion and Mayotte have been conducted with all sibling species. These specimens are herein described, compared to the species with the same characteristics (i.e., large size, over 110 cm total length (TL), dark blackish colour, rather long conical snout) and identified as *Hydrolagus affinis*. The discovery of the specimen from Reunion was briefly reported by Séret et al. (2013) [44] without species assignment in the bulletin of a Mauritius conservation association.

#### 2. Materials and Methods

The two specimens were incidentally caught on swordfish longlines during professional fishing operations off Reunion and Mayotte Islands (Figure 1). They were frozen and sent to the first author, who preserved them in formalin, then in ethanol, and deposited them in the collections of the Museum National d'Histoire Naturelle (MNHN), Paris.

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**Figure 1.** Map showing the localities where the two specimens of *Hydrolagus affinis* were caught off Reunion and Mayotte Islands in the southwestern Indian Ocean.

Morphometric measurements were taken on preserved specimens according to Didier [3] and Didier and Séret [4] and expressed as percentages of the body length (BDL). Measurements of sibling species were extracted from their original descriptions and from subsequent re-descriptions and new records. Terminology and measurements of canals of the lateral line system on the head follow that of Didier [3] and Didier and Séret [4].

Material: MNHN 2015-97, adult male, 1120 mm TL, 710 mm BDL, Mayotte, 20 September 2014, off Bouéni reef, 400–500 m depth, by longliner Bambou of Frederic Cierco fishing company. MNHN 2015-98, adult female (eviscerated), 1300 mm TL, 870 mm BDL, November 2012; caught on a sailfish longline by professional fisherman Charles Delmas, off Sainte-Marie, the longline sunk to about 1000 m depth (Figures 2–5).



**Figure 2.** Lateral view of the two females of *Hydrolagus affinis* freshly caught off Reunion Island. (**top**): preserved specimen, adult female, 870 mm BDL, MNHN 2015-0098; (**bottom**): discarded specimen.

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**Figure 3.** *Hydrolagus affinis* from Reunion Island, dorsal view of adult female, 870 mm BDL, MNHN 2015-0098, freshly caught.



**Figure 4.** *Hydrolagus affinis* from Reunion Island, adult female, 870 mm BDL, MNHN 2015-0098, lateral view.



**Figure 5.** *Hydrolagus affinis* from Mayotte Island, adult male, 710 mm BDL, MNHN 2015-0097, lateral view.

# 3. Results

## 3.1. Description of the Specimens

Both specimens are adult: the male has fully developed claspers, and the female has ripe oocytes. Their morphometric measurements are given in Table 2. They have large robust bodies (1120 and 1300 mm TL, 710 and 870 mm BDL), globulous heads with rather long conical (bluntly pointed) snouts (Figures 6 and 7), and prenarial length 7.8–12.1% BDL. The eyes are large, 6.0–6.1% BDL. The trunks are massive. The tails are tapering, ending as short filaments (probably damaged) (Figures 8 and 9). The skin is naked, rather firm, and not deciduous.

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**Table 2.** Morphometric measurements of the two specimens of *Hydrolagus affinis* from La Reunion and Mayotte expressed as percentage of the body length (BDL) and closely related species with data from the literature [43,45,46].

TL         total length         157.7         149.4         117.2-293.8         151-163         138.9-160.5           PCL         precaudal length         125.4         124.1         116.1-130.0         121-132         121.8-130.6           BDL         body length         100%         100%         100%         100%         100%           SVL         snout-went length         60.6         72.4         51.9-77.9         62-70         561-73.1           TRL         trunk length         35.9         48.3         30.9-46.8         35-44         31.9-39.7           PD2         pre-D2 length         47.2         50.0         41.1-57.7         53-57         41.7-53.4           PD1         pre-D1 length         27.3         34.5         20.3-33.9         28-35         25.9-29.1           POB         preorbital length         11.1         15.5         8.5-15.0         15-18         8.4-14.2           POR         preoral length         8.0         14.6         5-15         8.3-11.5           PRN         prenarial length         7.8         12.1         4-12         64-12.1           D2B         D2 base length         84.5         74.7         69.6-86.7         71-81         77.3-	H. homonycteris 12 Types 235–630 mm BDL [42]	H. melanophasma 2 Types + 6 Specimens 577–918 mm BDL Data from the Literature (cf Legend)	H. erithacus 9 Types 765–945 mm BDL [11]	H. africanus 65 Specimens 221–465 mm BDL [47]	MNHN 2015-0098 La Reunion Female ad. 870 mm BDL	MNHN 2015-0097 Mayotte Male ad. 710 mm BDL		
BDL         body length         100%         100%         100%         100%           SVL         snout-vent length         60.6         72.4         51.9-77.9         62-70         56.1-73.1           TRL         trunk length         35.9         48.3         30.9-46.8         35-44         31.9-39.7           PD2         pre-D2 length         47.2         50.0         41.1-57.7         53-57         41.7-53.4           PD1         pre-D1 length         27.3         34.5         20.3-33.9         28-35         25.9-29.1           POB         preorbital length         11.1         15.5         8.5-15.0         15-18         8.4-14.2           POR         preoral length         8.0         14.6         5-15         8.3-11.5           PRN         prenarial length         7.8         12.1         4-12         64-12.1           D2B         D2 base length         84.5         74.7         69.6-86.7         71-81         77.3-82.2           D2AH         maxi height at ant. 1/3 D2         3.9         4.4         4.3-7.5         3-5         4.0-5.2           D2PH         maxi height at post. 1/3 D2         4.6         4.6         3.4-6.5         3-5         3-5	140–202	138.9–160.5	151–163	117.2–293.8	149.4	157.7	total length	TL
SVL         snout-vent length         60.6         72.4         51.9-77.9         62-70         56.1-73.1           TRL         trunk length         35.9         48.3         30.9-46.8         35-44         31.9-39.7           PD2         pre-D2 length         47.2         50.0         41.1-57.7         53-57         41.7-53.4           PD1         pre-D1 length         27.3         34.5         20.3-33.9         28-35         259-29.1           POB         preorbital length         11.1         15.5         8.5-15.0         15-18         8.4-14.2           POR         preoral length         8.0         14.6         5-15         8.3-11.5           PRN         prenarial length         7.8         12.1         4-12         6.4-12.1           D2B         D2 base length         84.5         74.7         69.6-86.7         71-81         77.3-82.2           D2AH         maxi height at ant. 1/3 D2         3.9         4.4         4.3-7.5         3-5         4.0-5.2           D2PH         maxi height at post. 1/3 D2         4.6         4.6         3.4-6.5         3-5           D1B         D1 base length         21.5         19.9         9.0-18.9         12-16         13.9-20.0     <	120–136	121.8–130.6	121–132	116.1–130.0	124.1	125.4	precaudal length	PCL
TRL         trunk length         35.9         48.3         30.9-46.8         35-44         31.9-39.7           PD2         pre-D2 length         47.2         50.0         41.1-57.7         53-57         41.7-53.4           PD1         pre-D1 length         27.3         34.5         20.3-33.9         28-35         25.9-29.1           POB         preorbital length         11.1         15.5         8.5-15.0         15-18         8.4-14.2           POR         preoral length         8.0         14.6         5-15         8.3-11.5           PRN         prenarial length         7.8         12.1         4-12         6.4-12.1           D2B         D2 base length         84.5         74.7         69.6-86.7         71-81         77.3-82.2           D2AH         maxi height at ant. 1/3 D2         3.9         4.4         4.3-7.5         3-5         4.0-5.2           D2PH         maxi height at post. 1/3 D2         4.6         4.6         3.4-6.5         3-5           D1B         D1 base length         21.5         19.9         9.0-18.9         12-16         13.9-20.0           DSA         ant. spine to D1         18.6-28.3         21-25         17.6-29.9           D1H         <	100%	100%	100%	100%	100%	100%	body length	BDL
PD2         pre-D2 length         47.2         50.0         41.1-57.7         53-57         41.7-53.4           PD1         pre-D1 length         27.3         34.5         20.3-33.9         28-35         25.9-29.1           POB         preorbital length         11.1         15.5         8.5-15.0         15-18         8.4-14.2           POR         preoral length         8.0         14.6         5-15         8.3-11.5           PRN         prenarial length         7.8         12.1         4-12         6.4-12.1           D2B         D2 base length         84.5         74.7         69.6-86.7         71-81         77.3-82.2           D2AH         maxi height at ant. 1/3 D2         3.9         4.4         4.3-7.5         3-5         4.0-5.2           D2PH         maxi height at post. 1/3 D2         4.6         4.6         3.4-6.5         3-5         3-5           D1B         D1 base length         21.5         19.9         9.0-18.9         12-16         13.9-20.0           DSA         ant. spine to D1         18.6-28.3         21-25         17.6-29.9           D1H         max. height D1         19.0         17.6         11.8-20.5         11-15         18.1-26.3	53–71	56.1–73.1	62–70	51.9–77.9	72.4	60.6	snout-vent length	SVL
PDI pre-DI length 27.3 34.5 20.3–33.9 28–35 25.9–29.1  POB preorbital length 11.1 15.5 8.5–15.0 15–18 8.4–14.2  POR preoral length 8.0 14.6 5–15 8.3–11.5  PRN prenarial length 7.8 12.1 4–12 6.4–12.1  D2B D2 base length 84.5 74.7 69.6–86.7 71–81 77.3–82.2  D2AH maxi height at ant. 1/3 D2 3.9 4.4 4.3–7.5 3–5 4.0–5.2  D2PH maxi height at post. 1/3 D2 4.6 4.6 3.4–6.5 3–5  D1B D1 base length 21.5 19.9 9.0–18.9 12–16 13.9–20.0  DSA ant. spine to D1 18.6–28.3 21–25 17.6–29.9  D1H max. height D1 19.0 17.6 11.8–20.5 11–15 18.1–26.3  CDM dorsal caudal dorsal caudal dorsal length 20.1 19.5 16.0–25.6 21–25 18.5–23.1  CDH max. height caudal dorsal lobe 3.2 3.5 2.3–5.0 3–5 2.0–3.3  CTL total caudal length 31.7 28.2 33.8–xx 25–32 25.3–34.5	33–42	31.9–39.7	35–44	30.9–46.8	48.3	35.9	trunk length	TRL
POB         preorbital length         11.1         15.5         8.5–15.0         15–18         8.4–14.2           POR         preoral length         8.0         14.6         5–15         8.3–11.5           PRN         prenarial length         7.8         12.1         4–12         64–12.1           D2B         D2 base length         84.5         74.7         69.6–86.7         71–81         77.3–82.2           D2AH         maxi height at ant. 1/3 D2         3.9         4.4         4.3–7.5         3–5         4.0–5.2           D2PH         maxi height at post. 1/3 D2         4.6         4.6         3.4–6.5         3–5           D1B         D1 base length         21.5         19.9         9.0–18.9         12–16         13.9–20.0           DSA         ant. spine to D1         18.6–28.3         21–25         17.6–29.9           D1H         max. height D1         19.0         17.6         11.8–20.5         11–15         18.1–26.3           CDM         dorsal caudal margin length         20.1         19.5         16.0–25.6         21–25         18.5–23.1           CDH         max. height caudal dorsal lobe         3.2         3.5         2.3–5.0         3–5         2.0–3.3	42–60	41.7–53.4	53–57	41.1–57.7	50.0	47.2	pre-D2 length	PD2
POR         preoral length         8.0         14.6         5-15         8.3-11.5           PRN         prenarial length         7.8         12.1         4-12         6.4-12.1           D2B         D2 base length         84.5         74.7         69.6-86.7         71-81         77.3-82.2           D2AH         maxi height at ant. 1/3 D2         3.9         4.4         4.3-7.5         3-5         4.0-5.2           D2PH         maxi height at post. 1/3 D2         4.6         4.6         3.4-6.5         3-5           D1B         D1 base length         21.5         19.9         9.0-18.9         12-16         13.9-20.0           DSA         ant. spine to D1         18.6-28.3         21-25         17.6-29.9           D1H         max. height D1         19.0         17.6         11.8-20.5         11-15         18.1-26.3           CDM         dorsal caudal margin length         20.1         19.5         16.0-25.6         21-25         18.5-23.1           CDH         max. height caudal dorsal lobe         3.2         3.5         2.3-5.0         3-5         2.0-3.3           CTL         total caudal length         31.7         28.2         33.8-xx         25-32         25.3-34.5	24–40	25.9–29.1	28–35	20.3–33.9	34.5	27.3	pre-D1 length	PD1
PRN         prenarial length         7.8         12.1         4-12         6.4-12.1           D2B         D2 base length         84.5         74.7         69.6-86.7         71-81         77.3-82.2           D2AH         maxi height at ant. 1/3 D2         3.9         4.4         4.3-7.5         3-5         4.0-5.2           D2PH         maxi height at post. 1/3 D2         4.6         4.6         3.4-6.5         3-5         3-5           D1B         D1 base length         21.5         19.9         9.0-18.9         12-16         13.9-20.0           DSA         ant. spine to D1         18.6-28.3         21-25         17.6-29.9           D1H         max. height D1         19.0         17.6         11.8-20.5         11-15         18.1-26.3           CDM         dorsal caudal margin length         20.1         19.5         16.0-25.6         21-25         18.5-23.1           CDH         max. height caudal dorsal lobe         3.2         3.5         2.3-5.0         3-5         2.0-3.3           CTL         total caudal length         31.7         28.2         33.8-xx         25-32         25.3-34.5	11–20	8.4–14.2	15–18	8.5–15.0	15.5	11.1	preorbital length	POB
D2B         D2 base length         84.5         74.7         69.6–86.7         71–81         77.3–82.2           D2AH         maxi height at ant. 1/3 D2         3.9         4.4         4.3–7.5         3–5         4.0–5.2           D2PH         maxi height at post. 1/3 D2         4.6         4.6         3.4–6.5         3–5           D1B         D1 base length         21.5         19.9         9.0–18.9         12–16         13.9–20.0           DSA         ant. spine to D1         18.6–28.3         21–25         17.6–29.9           D1H         max. height D1         19.0         17.6         11.8–20.5         11–15         18.1–26.3           CDM         dorsal caudal margin length         20.1         19.5         16.0–25.6         21–25         18.5–23.1           CDH         max. height caudal dorsal lobe         3.2         3.5         2.3–5.0         3–5         2.0–3.3           CTL         total caudal length         31.7         28.2         33.8-xx         25–32         25.3–34.5		8.3–11.5	5–15		14.6	8.0	preoral length	POR
D2AH         maxi height at ant. 1/3 D2         3.9         4.4         4.3-7.5         3-5         4.0-5.2           D2PH         maxi height at post. 1/3 D2         4.6         4.6         3.4-6.5         3-5           D1B         D1 base length         21.5         19.9         9.0-18.9         12-16         13.9-20.0           DSA         ant. spine to D1         18.6-28.3         21-25         17.6-29.9           D1H         max. height D1         19.0         17.6         11.8-20.5         11-15         18.1-26.3           CDM         dorsal caudal margin length         20.1         19.5         16.0-25.6         21-25         18.5-23.1           CDH         max. height caudal dorsal lobe         3.2         3.5         2.3-5.0         3-5         2.0-3.3           CTL         total caudal length         31.7         28.2         33.8-xx         25-32         25.3-34.5		6.4–12.1	4–12		12.1	7.8	prenarial length	PRN
D2PH         maxi height at post. 1/3 D2         4.6         4.6         3.4-6.5         3-5           D1B         D1 base length         21.5         19.9         9.0-18.9         12-16         13.9-20.0           DSA         ant. spine to D1         18.6-28.3         21-25         17.6-29.9           D1H         max. height D1         19.0         17.6         11.8-20.5         11-15         18.1-26.3           CDM         dorsal caudal margin length         20.1         19.5         16.0-25.6         21-25         18.5-23.1           CDH         max. height caudal dorsal lobe         3.2         3.5         2.3-5.0         3-5         2.0-3.3           CTL         total caudal length         31.7         28.2         33.8-xx         25-32         25.3-34.5	74–82	77.3–82.2	71–81	69.6–86.7	74.7	84.5	D2 base length	D2B
D2FH   1/3 D2   4.0   4.6   3.4-6.5   3-5   3-5     D1B	4–8	4.0-5.2	3–5	4.3–7.5	4.4	3.9	maxi height at ant. 1/3 D2	D2AH
DSA         ant. spine to D1         18.6–28.3         21–25         17.6–29.9           D1H         max. height D1         19.0         17.6         11.8–20.5         11–15         18.1–26.3           CDM         dorsal caudal margin length         20.1         19.5         16.0–25.6         21–25         18.5–23.1           CDH         max. height caudal dorsal lobe         3.2         3.5         2.3–5.0         3–5         2.0–3.3           CTL         total caudal length         31.7         28.2         33.8-xx         25–32         25.3–34.5	4.2–7		3–5	3.4–6.5	4.6	4.6		D2PH
D1H         max. height D1         19.0         17.6         11.8-20.5         11-15         18.1-26.3           CDM         dorsal caudal margin length         20.1         19.5         16.0-25.6         21-25         18.5-23.1           CDH         max. height caudal dorsal lobe         3.2         3.5         2.3-5.0         3-5         2.0-3.3           CTL         total caudal length         31.7         28.2         33.8-xx         25-32         25.3-34.5	9–18	13.9–20.0	12–16	9.0-18.9	19.9	21.5	D1 base length	D1B
CDM         dorsal caudal margin length         20.1         19.5         16.0-25.6         21-25         18.5-23.1           CDH         max. height caudal dorsal lobe         3.2         3.5         2.3-5.0         3-5         2.0-3.3           CTL         total caudal length         31.7         28.2         33.8-xx         25-32         25.3-34.5	9–25	17.6–29.9	21–25	18.6–28.3			ant. spine to D1	DSA
CDM         margin length         20.1         19.5         16.0-25.6         21-25         18.5-23.1           CDH         max. height caudal dorsal lobe         3.2         3.5         2.3-5.0         3-5         2.0-3.3           CTL         total caudal length         31.7         28.2         33.8-xx         25-32         25.3-34.5	14–17	18.1–26.3	11–15	11.8–20.5	17.6	19.0	max. height D1	D1H
CDH         dorsal lobe         3.2         3.5         2.5-3.0         3-5         2.0-3.3           CTL         total caudal length         31.7         28.2         33.8-xx         25-32         25.3-34.5	16–24	18.5–23.1	21–25	16.0–25.6	19.5	20.1		CDM
	3–4	2.0–3.3	3–5	2.3–5.0	3.5	3.2	max. height caudal dorsal lobe	CDH
	34–79	25.3–34.5	25–32	33.8-xx	28.2	31.7	total caudal length	CTL
CVM         ventral caudal margin length         23.1         33.3         22.8–44.1         30–36         24.4–43.6	26–34	24.4–43.6	30–36	22.8–44.1	33.3	23.1	ventral caudal margin length	CVM
CVH max. height caudal ventral lobe 2.9 3.0 2.0–5.0 3–4 2.0–2.9	3–4	2.0–2.9	3–4	2.0–5.0	3.0	2.9		CVH
HDL head length 24.5 28.4 17.9–31.3 27–31 21.8–30.6	21–34	21.8–30.6	27–31	17.9–31.3	28.4	24.5	head length	HDL

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 Table 2. Cont.

		MNHN 2015-0097 Mayotte Male ad. 710 mm BDL	MNHN 2015-0098 La Reunion Female ad. 870 mm BDL	H. africanus 65 Specimens 221–465 mm BDL [47]	H. erithacus 9 Types 765–945 mm BDL [11]	H. melanophasma 2 Types + 6 Specimens 577–918 mm BDL Data from the Literature (cf Legend)	H. homonycteris 12 Types 235–630 mm BDL [42]
P1A	pectoral ant. margin length	35.2	34.5	29.3–41.4	29–42	32.0–41.5	32–40
P2A	pelvic ant. margin length	19.0	19.8	16.3–23.5	18–22	17.8–21.0	13–18
IDS	interdorsal space	2.3	0.0	2.1–12.6	8–12	2.6–10.6	3–14
DCS	dorsal-caudal space	0.0	0.0	0.0-1.3	1–3		2–3
D1P1	ant. D1 to ant. pectoral base	24.2	20.0	14.4–21.9	19–28	16.4–22.4	16–20
D1P2	ant. D1 to ant. pelvic base	45.1	39.1	25.6-44.0	43–49	27.2–43.9	37–43
EYL	eye length	6.1	6.0	5.1-9.7	5–7	5.0-7.1	5–7
EYH	eye height	4.1	4.0	2.9–5.9	3–5	3.7–4.8	4–6
CLT	clasper length from pelvic base	13.4	0.0	3.8–14.2	19–20	13.7–15.0	11
CLM	clasper medial branch from fork to tip	5.1	0.0	4.5–7.7	3–4	3.8-4.0	3
CLL	clasper lateral branch from fork to tip	4.0	0.0	4.3–7.2	3–4	3.9–4.2	3
		% HDL	% HDL		% HDL calcul.	% HDL	
ONC	oronasal fold to centre of nasal canal	8.4	8.9		10.0–13.3	8.2–12.5	
LRC	rostral canal length	3.7	3.9		3.3–10.0	3.8-6.5	
LNC	straight nasal canal length	24.1	21.5		10.0-23.3	23.6–31.5	
IOA	infraorbital to oro-angular junction	15.1	15.1		3.3–13.3	12.9–16.1	
OTM	preopercular to infraorbital distance	29.2	32.4		26.7–36.7	28.1–32.9	
OCL	infraorbital to postorbital distance	15.2	13.8		13.3–20.0	11.1–14.0	
STL	supratemporal to postorbital distance	15.7	15.3		16.7–26.7	14.5–27.0	
SPS	spine to supratemporal distance	19.9	21.0		13.3–30.0	14.9–18.2	

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Figure 6. Hydrolagus affinis from Reunion Island, MNHN 2015-0098, lateral view of head.



Figure 7. Hydrolagus affinis from Mayotte Island, MNHN 2015-0097, lateral view of head.

The first dorsal fin is triangular, pointed, and preceded by a long spine exceeding the fin tip in the female (spine broken in the male). There is no interdorsal space. The second dorsal fin is long and evenly high in its whole length. The pectoral fins are large, triangular, and with a rather pointer apex, reaching the origin of pelvic fins when depressed on the body. The pelvic fins are well developed, triangular, and with a rather pointer apex. There

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is no dorsal-caudal space, but instead a long pelvic-caudal space. The caudal fin is leaf-like, with almost symmetrical oblong lobes, with the ventral lower lobe being a little larger than the dorsal lobe; the origin of the dorsal lobe is behind the level of that of the ventral lobe. There is no anal fin; no notch is visible at the origin of the lower caudal lobe.



Figure 8. Hydrolagus affinis from Reunion Island, MNHN 2015-0098, tail tip.



Figure 9. Hydrolagus affinis from Mayotte Island, MNHN 2015-0097, tail tip.

The mouth is small, and the jaws have 7–8 vomerine tritors (upper tooth plates) and four incisor-like mandibular tritors (lower tooth plates) that look like a beak (Figures 10 and 11).



Figure 10. Hydrolagus affinis from Reunion Island, MNHN 2015-0098, jaws.

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Figure 11. Hydrolagus affinis from Reunion Island, MNHN 2015-0097, jaws.

Lateral line sensory pores and mucous canals are very conspicuous on the head; their measurements are given in Table 2. The preopercular canal (POP) shares a common branch with the oral canal (O), which is connected to the otic (OT) and infraorbital (IO) canals. There are numerous pores on the head, some more conspicuous along or on cephalic canals or forming groups close to the canals: a group of 11/11 pores in front of the occipital canal (OC) in MNHN 2015-0097/MNHN 2015-0098), a line of 7-8/9 below the posterior branch of the infraorbital canal (IO) and 10-11/10 pores on the anterior branch of IO, 6/10 larger pores on the angular canal (AN), a line of 14/14 pores along the mandibular canal (M), and a group of 12/15 pores in the concavity of the suborbital canal (SO); no conspicuous pores along the otic canal (OT) and the preopercular canal (POP). The lateral line on the body starts at the junction of the otic (OT) and occipital (OC) canals, smoothly sloping on the trunk and then running almost straight on the tail to its tip (Figures 6 and 7).

Claspers of the male are robust, slightly extending over the pelvic rear tip, with a muscular base and fleshy bulbous tips covered with fine denticles; they are bifurcate, divided distally for 1/3 their length, with a third fleshy lobe that lies along the dorsal side of the medial cartilaginous arm (Figure 12). The frontal tenaculum is thumb-shaped and spinulous with about 40 clow-like denticles; its dorsal surface is smooth (Figure 13). There is a pair of prepelvic tenacula retractable in slit-like pouches in front of the pelvic-fin base; they are spatulate, with a row of five strong hooked denticles on the inner edge. The distal edge is indented but covered by an integument so that it appears straight (Figure 14).

Coloration. Freshly caught specimens were plain dark brown to blackish, with some purple reflections; fins darker, almost jet black. The body is chocolate brown in preservation. The tooth plates are yellowish. The eyes are opalescent. The cephalic lateral line sensory pores are whitish. The claspers are brownish with a purple tint; terminal fleshy bulbs are whitish. The prepelvic tenacula are creamy white.

## 3.2. Species Comparisons

#### 3.2.1. Comparison with H. affinis

Few morphometrical measurements of *H. affinis* are available in the scientific literature. The measurements used for comparisons (Table 2) were calculated from data expressed in percentage of PCL in Bigelow and Schroeder [48] for two specimens, a male of 797 mm PCL and a female of 973 mm PCL. These calculated values are mostly in the ranges of the specimens from Reunion and Mayotte, except for the pectoral anterior margin (P1A) 34.5–35.2 (measured) versus 41% BDL (calculated) and eye height (EYH) 4.0–4.1 (measured) versus 5.3% BDL (calculated). Despite these slight differences, the specimens from Reunion

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and Mayotte are tentatively identified as *H. affinis* as they share similar prepelvic tenacula with 4–8 denticles in *H. affinis* and five strong denticles in the male from Mayotte and a distinct indentation on the distal edge covered by integument. This later feature was already observed by Hardy and Stehmann [37] for *H.affinis*, which seems unique.



Figure 12. Hydrolagus affinis from Mayotte Island, MNHN 2015-0097, claspers.

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Figure 13. Hydrolagus affinis from Mayotte Island, MNHN 2015-0097, frontal tenaculum.



Figure 14. Hydrolagus affinis, MNHN 2015-0097, prepelvic tenaculum.

Hydrolagus affinis is mainly a North Atlantic species [37] but extends to Uruguay in the western Atlantic, to Angola in the eastern Atlantic, and possibly in South Africa and Mozambique [49]. Hydrolagus affinis was also tentatively reported from Tanzania [50] based on Baited Remote Underwater Video (BRUV) photos and videos taken during the deep-sea expedition SERPENT off Tanzania (https://serpentproject.com/, Accessed on 17 November 2023). With the dentification on photos and videos being delicate, the same observed specimen is legended Hydrolagus sp. in Gates et al. [51].

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## 3.2.2. Comparison with *H. erithacus*

The morphometrics of the Reunion and Mayotte specimens were compared to those of the original description of *H. erithacus* [13]. The differences are the following (Table 2): preorbital length (POB) 11.1–15.5 versus 15–18% BDL in *H. erithacus*; first dorsal-fin base length (D1B) 19.9–21.5 versus 12–16% BDL; ventral caudal margin length (CVM) 23.1–33.3 versus 30–36% BDL; interdorsal space (IDS) 0–2.3 versus 8–12% BDL; oronasal fold to centre of nasal canal (ONC) 8.4–8.9 versus 19.0–13.3% head length (HDL); infraorbital to oro-angular junction (IOA) 15.1 versus 3.3–13.3 % HDL; supratemporal to postorbital distance (STL) 15.3–15.7 versus 16.7–26.7% HDL.

#### 3.2.3. Comparison with H. melanophasma

The morphometrics of the specimens from Reunion and Mayotte were compared to those of the two types from California [43] and six additional specimens reported in the literature [45,46,52]. Most of the ranges overlap; however, several measurements have only slight overlaps (Table 2): pre-D1 length (PD1) 27.3–34.5 versus 25.9–29.1% BDL in *H. melanophasma*; preorbital length (POB) 11.1–15.5 versus 8.4–14.2% BDL; maximum height of caudal dorsal lobe (CDH) 3.2–3.5 versus 2.0–3.3% BD;, anterior D1 to anterior pelvic base (D1P2) 20.0–24.2 versus 16.4–22.4% BDL; straight nasal canal length (LNC) 21.5–24.1 versus 23.6–31.5% HDL; spine to supratemporal distance (SPS) 19.9–21.0 versus 14.9–18.2% HDL; interdorsal space (IDS) 0–2.3% BDL versus 6.4–9.0% TL.

Furthermore, *H. melanophasma* has prepelvic tenacula with only 3–4 denticles and without indentation on the distal edge; a straight trunk lateral line without regular undulations versus trunk lateral line starting with a strong curve then slightly wavy rearward in the specimens from Reunion and Mayotte.

# 3.2.4. Comparison with *H. homonycteris*

The morphometrics of the specimens from Reunion and Mayotte were compared to those of the 12 types of the original description [42]. The following differences were observed (Table 2): D1 base length (D1B) 19.9–21.5 versus 9–18% BDL in *H. homonycteris*; total caudal length (CTL) 28.2–31.7 versus 34–79 % BDL; pelvic anterior margin length (P2A) 19.0–19.8 versus 13–18% BDL; interdorsal distance (IDS) 0–2.3 versus 3–14% BDL.

Furthermore, *H. homonycteris* has a distinctly rounded, almost fan-like pelvic fin versus pointed distally in specimens from Reunion and Mayotte, with prepelvic tenacula with only 3–4 denticles and without indentation on the distal edge. The frontal tenaculum of *H. homonycteris* has more denticles (50 versus 40) than that of the male from Mayotte.

# 4. Discussion

A specimen preserved in the MNHN collections, MNHN 2004-0820, adult male of 1065 mm TL and 700 mm BDL, is similar to the specimens from Mayotte and La Reunion and is here identified as the same species. It was caught during a fishing cruise of the commercial longliner "Croix du Sud" off Saint-Paul Island by 37°36′7.2″ S, 78°4′12″ E, and 1035–1045 m depth, on 8 June 2001. This specimen is mentioned here because it has a particularity: on the left side of the head, the preopercular canal (POP) shares a common branch with the oral canal (O) that is connected to the otic (OT) and infraorbital (IO), but on the right side of the head, they have no common branches and are connected separately, POP to OT and O to IO canals (Figures 15 and 16). This means that this character (POP and O canals commonly branched or not) has less taxonomic significance than usually thought.

The present assignment of the specimens from Reunion and Mayotte to *H. affinis* is provisional, pending a revision of the group is completed. Comparative anatomy seems insufficient to solve the complex situation of this group of chimaeras, so genetic analysis should be obtained for all nominal species. However, it seems that many sequences in genetic banks are extracted from specimens whose species identification remains uncertain and hardly verifiable, as most are not illustrated or described.

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**Figure 15.** *Hydrolagus affinis* from Saint-Paul Island, MNHN 2004-0820, lateral line canals on the left side of the head showing the common branch shared by POP and O canals.



**Figure 16.** *Hydrolagus affinis* from Saint-Paul Island, MNHN 2004-0820, lateral line canals on the right side of the head showing the direct connections of POP and O canals to OT and IO canals.

Trials of genetic analysis have been performed with tissue samples from the specimens of Reunion and Mayotte, thanks to Dr. G. Naylor (Florida Museum of Natural History). The provisional results are not herein included because of the uncertainty of the identification of the species whose sequences are stored in genetic banks; similarities have been found with *H. affinis* but also with other species (G. Naylor person. com, accessed on 8 June 2017). It would be highly valuable that the sequences are deposited in genetic banks supplemented by illustrations of the sampled specimens. This will greatly help taxonomic revisions.

# 5. Conclusions

Deep-sea chimaeras are globally poorly known. Although several new species have been described in recent years, their inventory is still to be established with accuracy, and the status of some nominal species should be confirmed. The present records contribute to improving our knowledge of this group of ghost fishes that is still somewhat mysterious to scientists. Any piece of information collected on these fishes is useful.

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**Institutional Review Board Statement:** Ethical review and approval were waived for this study since the specimens were caught as by-catches of commercial fisheries, and the species is not listed in any international convention, such as CITES and CMS, and in any UE regulations.

Data Availability Statement: The data presented in this study are available in this published article.

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