



## Redescription of the eel *Ilyophis arx* Robins, 1976 (Anguilliformes: Synphobranchidae: Ilyophinae) with a description of a new species of *Ilyophis*, and a taxonomic synopsis of the Ilyophinae

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### Abstract

*Ilyophis arx* Robins, 1976 is redescribed based on the four type specimens from south of the Galapagos Islands and 21 additional specimens: 12 specimens from the western Clarion Clipperton Zone in the central Pacific Ocean, four specimens from the eastern Pacific Ocean, and five specimens from several localities in the central North Pacific Ocean. A new species, *Ilyophis maclainei* sp. nov., is described from the eastern North Atlantic. A taxonomic synopsis of the subfamily Ilyophinae is presented, and a key to the known species is provided.

**Key words:** Anguilliformes, Synphobranchidae, Ilyophinae, taxonomy

### Introduction

The Ilyophinae is the most speciose and morphologically diverse of the synphobranchid subfamilies consisting of six genera and ca. 39 species. The number of species in the subfamily is certain to increase as there are several undescribed species under study by the authors and others. In addition, there are a large number of leptocephali types that have been collected which cannot be identified with described adult species, indicating that there are many species awaiting discovery. Ilyophines show great variety in body shape, dentition, presence or absence of pectoral fin, eye size, and ornamentation of the snout.

The genus *Ilyophis* and its type species, *Ilyophis brunneus* were described by Gilbert (1891) based on a single specimen collected near Chatham Island, Galapagos. *Ilyophis* remained monotypic until the description of *Ilyophis arx* by Robins in Robins & Robins (1976). Since then, there have been a total of five additional species described: *Ilyophis blachei* Saldanha & Merrett, 1982, *Ilyophis nigeli* Shcherbachev & Sulak, 1997, *Ilyophis robinsae* Sulak & Shcherbachev, 1997, *Ilyophis saldanhai* Karmovskaya & Parin, 1999 and *Ilyophis singularis* Tashiro & Chen, 2022.

The genus *Ilyophis* can be diagnosed by the following combination of characters: dorsal, anal, and caudal fins present and confluent; pectoral fin present; dorsal-fin origin forward, less than snout length behind gill opening; head length less than trunk length; gill slits separate, below base of pectoral fin; tip of snout and lower jaw plicate and papillose; intermaxillary teeth in an irregular patch; vomerine teeth bluntly conical, arranged in one or more

irregular rows; maxillary teeth in irregular rows, usually with inner row enlarged; dentary teeth also in irregular rows with inner row enlarged; all teeth simple (not compound); hyomandibula near vertical or slightly canted anteriorly. The lack of compound teeth differentiates *Ilyophis* from the genera *Atractodenchelys*, *Dysomma*, *Dysommia*, and *Linkenchelys*. When *Meadia* was redescribed by Robins & Robins (1976), one of the primary characters separating the two genera was the position of the anus (less than one head length posterior to gill slit in *Meadia* versus one-and-two-thirds to two head lengths posterior to gill slit in *Ilyophis*). This character still differentiated the two genera with the description of *Meadia roseni* by Mok *et al.* (1991) (anus ca. 60% of head length posterior to gill slit). However, with the recent description of *Meadia minor* by Vo *et al.* (2021), this distinction breaks down. They report that the anus is well posterior, 2.0 (1.9–2.4) head lengths behind pectoral-fin base. Vo *et al.* (2021) discussed the similarities between *Ilyophis* and *Meadia*, and the reasons why they assigned their new species to *Meadia*. The generic limits between *Ilyophis* and *Meadia* are unclear and the taxonomy of species within these two genera require further review. However, it is clear that *Ilyophis arx* and *I. maclainei* **sp. nov.** belong in the genus *Ilyophis* as presently understood.

*Ilyophis arx* was described from four specimens collected south of the Galapagos Islands. Saldanha & Merrett (1982) reported a single specimen of *I. arx* from the Porcupine Sea-Bight, eastern North Atlantic. Merrett & Saldanha (1985) described that specimen and two additional specimens, also from the vicinity of the Porcupine Sea-Bight, compared them with the original description of *Ilyophis arx* Robins, 1976 and concluded that the three specimens represented individual and geographic variation of *I. arx*. Robins & Robins (1989) suggested that the northeastern Atlantic population probably represents an undescribed species. However, Sulak & Shcherbachev (1997) compared the holotype of *I. arx* with one of the specimens from the northeastern Atlantic and concurred with Merrett & Saldanha (1985) on their identification.

Recent collections in the western Clarion Clipperton Zone (CCZ) in the central Pacific Ocean resulted in the capture of 12 specimens of *Ilyophis arx* (Leitner *et al.* 2021a). Search of museum collection databases resulted in nine additional specimens deposited at the Natural History Museum (London), Scripps Institution of Oceanography (La Jolla) and at Senckenberg Research Institute and Museum of Nature (Frankfurt am Main). Comparison of the 21 additional specimens with the description of the three specimens reported by Merrett & Saldanha (1985) resulted in the conclusion that the northeastern Atlantic specimens represented an undescribed species. They are described below as a new species of *Ilyophis*. In addition, a taxonomic synopsis and key to all known species of the Ilyophinae is presented.

## Materials and methods

General methods for morphometric and meristic data as well as all standard definitions for this study are given in Böhlke (1989). Measurements were made with a standard ruler to the nearest 1 mm and a digital caliper to the nearest 0.1 mm, measurements under 10 mm were taken with an ocular micrometer. All measurements are given as a proportion of the total length (TL) except for subunits of the head which are presented as proportions of the head length (HL). Head length was measured from tip of snout to upper edge of the pectoral fin base. Vertebral and fin ray counts were taken from radiographs. Total vertebral counts are of all elements including the hypural plate. Preanal and predorsal vertebral counts were taken using the definitions of Böhlke (1982). Precaudal vertebral counts are approximate since the closure of the haemal arch could not be seen on the radiographs. The precaudal count includes the first vertebra with a clearly longer and posteriorly curved haemal arch. The number of dorsal rays anterior to the anal origin are counted back to a vertical through the first anal ray base. Cyanine blue was used for staining cephalic sensory and lateral line pores (Saruwatari *et al.* 1997). Lateral line pores include all open pores that are connected by the lateral line tubule. Often, there are sensory pits and papillae extending posteriorly from the open lateral line pores, but they are not included in the counts of total lateral line pores.

Descriptions of the dentition are based upon the following definitions. Maxillary teeth are those borne on the maxillary bone. Dentary teeth are those borne on the dentary bone of the mandible. Vomerine teeth are those borne on the vomerine portion of the fused ethmo-vomerine complex. Intermaxillary teeth are those found on the anterior portion of the ethmo-vomerine complex between the articulation of the maxillary bones with the ethmo-vomerine complex. While these teeth are borne on the ethmo-vomerine complex, the term intermaxillary is used to clearly distinguish them from the vomerine teeth as defined above. Several genera of the Ilyophinae are distinguished by

the presence of compound teeth, usually the vomerine teeth, but sometimes also the intermaxillary teeth and the dentary teeth. Compound teeth were defined as the fusion of 2 teeth by Robins and Robins (1970).

The original types of *Ilyophis arx* Robins 1976 were re-examined by the senior author in order to allow direct comparison with the additional study material. The cleared and stained paratype (ANSP 133810) was previously dissected and could only be used for limited comparisons.

### ***Ilyophis arx* Robins, 1976**

Figures 1–3, Table 1–2

*Ilyophis arx* Robins, 1976 in Robins & Robins 1976:265, Figs. 4, 6, 7b, 8 (original description, Southeastern Pacific, 1° 48' S, 90° 19' W, depth 3225 meters, Holotype: ANSP 133808). Böhlke 1984:158 (listed in type catalog). Merrett & Saldanha 1985: 730–735 (comparison of central Pacific and northeastern Atlantic specimens). Robins & Robins 1989:238 (compiled). Sulak & Shcherbachev 1997: 1163, 1172, 1188 (key, comparison with *Ilyophis nigeli*, distribution). Karmovskaya & Parin 1999: 360 (comparison with *Ilyophis saldanhai*). Smith 1999 (compiled). Causse *et al.* 2005: 414 (comparison with *Ilyophis saldanhai*). Leitner *et al.* 2021a: (occurrence on abyssal seamounts) [Fig. 1].

**Diagnosis.** A species of *Ilyophis* with the following characters. Body without scales. Trunk relatively long (about 21–29% of TL). Dorsal-fin origin (DFO) above posterior third of pectoral fin. Gape of mouth moderate, extending to near rear margin of eye. Teeth not compound. Intermaxillary teeth conical with approximately 16–24 teeth in the tooth patch, inner teeth on the patch nearly twice as large as the outer teeth. Vomerine teeth contiguous with intermaxillary teeth with approximately 25–30 teeth irregularly biserial to triserial anteriorly and uniserial posteriorly. Both intermaxillary and vomerine teeth set in beds of papillose tissue. Maxillary teeth small, set in irregular rows, 3 rows anteriorly to 6 rows posteriorly. Dentary teeth similar to maxillary teeth except they are slightly larger and more uniform in size anteriorly. Lateral line short, confined to anterior half of body (ca. 35–45% of TL). Cephalic lateralis pores: supraorbital (SO) 3, infraorbital (IO) 5 (including adnasal, AD), preoperculomandibular (POM) 6–10. Total vertebrae 129–136.

**Description.** Body moderately elongate, laterally compressed posteriorly (Fig. 2). Body tapers gradually to caudal, deepest body depth anterior to anus. Dorsal-fin origin near posterior half or just behind tip of pectoral fin, predorsal length ca. 14–18 % TL. Trunk length moderate, contained about 4 times in TL. Preanus length approximately 3 times in TL, preanal-fin length about 36% of TL. Head length moderate (ca. 10–14 % TL). Gill slits crescentic and horizontal, located ventrally just anterior to and below pectoral fin base. Anterior nostril tubular, directed anterolaterally. Posterior nostril round, just in front of eye. Eye relatively small (9–14 % HL). Pectoral fin moderate in size (3.2–3.7 % TL, 10–27 % HL) with 15 rays. Gape extends to near posterior half of eye. Snout plicate, two main plicae on each side of mid-line, outermost least developed. Tip of lower jaw also plicate, two main plicae on each side of mid-line and occasionally one smaller plica lateral to the main plicae for a total of six. Teeth conical, arranged in bands along maxillary, dentary and intermaxillary/vomer. Teeth not compound. Maxillary teeth in two to four rows (medially) reducing to one irregular row posteriorly, with anterior teeth somewhat enlarged. Dentary teeth in three to five irregular rows, with anterior ones (in two rows) larger. Intermaxillary teeth with 14–28 strong teeth concentrically arranged around tooth patch with inner teeth slightly larger. Vomerine teeth abutting intermaxillary tooth patch with two irregular rows anteriorly (with ca. 10–16 teeth each) and converging to single row posteriorly (with two to three teeth). Both intermaxillary and vomerine teeth surrounded by papillae. Cephalic lateralis pores: supraorbital pores three, first located between first and second plicae on tip of snout, second on snout at level of the dorsal rim of anterior nostril, third on dorsal of snout above adnasal pore; infraorbital pores five, first (adnasal pore) just posterior to dorsal rim of anterior nostril, second on lip just posteroventral to base of anterior nostril, third on lip halfway between anterior and posterior nostrils, fourth on lip ventral to posterior nostril, fifth just ventral to the posterior margin of the eye; preoperculomandibular pores seven to ten, six to eight pores along mandible with zero to two pores in preopercular position, first very small and located within plicae at the tip of lower jaw, remaining mandibular pores spaced progressively far apart along jaw, last mandibular pore located approximately below rictus, preopercular pores (if present) located posteriorly in the opercular region. Lateral line incomplete, relatively short; pores extend to approximately 35% length of body. Lateral line numbering two to six pores anterior to pectoral-fin base, 8–14 pores anterior to dorsal-fin origin, 31–39 pores anterior to anus, 31–47 total pores. Vertebral numbers: predorsal 9–13, preanal 37–42, total 128–137.

**TABLE 1.** Morphometric, meristic and morphological data of *Ilyophis arx* Robins, 1976 and *Ilyophis maclainei* sp. nov. For bilateral pore counts, the counts are recorded left/right.

	<i>Ilyophis arx</i> (reexamination of type series)		<i>Ilyophis arx</i>	<i>Ilyophis maclainei</i>	
	Holotype	Paratypes	This study	Holotype	Paratype
Total length (mm)	439	353–401 (n=3)	215–610 (n=21)	242	263
Proportions (% TL)		<b>Mean (range)</b>	<b>Mean (range)</b>		
Predorsal length	17.0	17.0 (16.0–17.7)	16.1 (14.1–18.1)	15.6	15.1
Preanal length	36.9	34.8 (32.9–37.2)	36.5 (33.4–43.1)	32.2	30.0
Head length	12.0	12.5 (12.0–13.0)	12.4 (9.9–14.2)	12.6	11.9
Trunk length	24.9	22.3 (20.9–24.2)	24.1 (20.9–28.8)	19.0	18.2
Tail length	63.1	65.2 (62.8–65.7)	63.5 (56.9–66.6)	67.8	70.0
Body depth at anus	6.4	5.2 (4.6–6.1)	6.0 (4.4–7.4)	4.1	4.8
Proportions (% HL)		<b>Mean (range)</b>	<b>Mean (range)</b>		
Snout length	33.9	33.9 (30.7–35.0)	30.9 (25.3–35.7)	38.6	32.8
Eye diameter	11.0	11.7 (10.1–12.8)	11.4 (9.4–13.7)	10.8	13.7
Postorbital distance	57.9	56.8 (52.9–59.8)	57.3 (54.5–62.6)	56.8	54.0
Upper-jaw length	48.4	44.9 (42.8–47.0)	46.9 (39.9–63.2)	46.7	47.8
Interorbital width	24.8	24.8 (14.3–21.0)	22.5 (14.2–31.4)	21.6	21.0
Gill-opening (GO)	12.4	10.3 (9.1–11.6)	11.4 (8.2–16.5)	9.2	11.5
Interbranchial width	20.5	19.8 (17.2–24.9)	19.6 (13.3–27.8)	12.4	12.7
Pectoral-fin length	26.9	22.7 (19.0–22.9)	19.0 (10.3–26.6)	25.5	26.1
Meristics					
SO pores	3/3	3/3	3–4	3/3	3/3
IO (including AD) pores	5/5	5/5	5	6/6	6/6
POM pores	8/8	8/8	7–10	8/8	8/8
PrePectoral LL pores	3/4	3–6	2–6	4/5	5/4
PreDorsal LL pores	9/11	9–11	8–14	7/8	10/9
PreAnus LL pores	32/36	33–38	31–37	28/30	29/31
PreAnalFin LL pores	34/38	31–37	31–39	30/32	31/33
Total LL pores	39/39	38–54	31–47	89/88	94/93
Dorsal rays	322	309–315	281–347	359	339
Anal rays	257	235–261	219–251	288	291
DR-AF origin	75	67–80	70–95	66	67
PreDorsal Vertebrae	10	11–12	10–13	10	8
PreAnus Vertebrae	37	35–38	34–40	31	31
PreAnalFin Vertebrae	39	37–40	37–42	33	34
PreCaudal Vertebrae	58	57–58	54–62	53	54
Total Vertebrae	131	131–135	128–137	132	134
Morphology					
Scales	No	No	No	Yes	Yes
Number of snout plicae	4	4	4	6	6
Lower jaw plicae	4	4–5	4–6	4	4



**FIGURE 1.** *Ilyophis arx*. Swarm of eels attracted to a baited camera near summit of seamount APEI 7 (4° 52' 57.36" N, 141° 46' 45.48" W, 3203 m) (photo grab from <https://oceanexplorer.noaa.gov/explorations/18ccz/logs/photolog/photolog.html#cbpi=../may25/media/DC03.html>)

**Comparative remarks.** *Ilyophis arx* can be distinguished from all members of the genera *Atractodenchelys*, *Dysomma*, *Dysommia*, and *Linkenchelys* by the lack of compound teeth in the dentition (versus at least vomerine teeth compound). Head length differentiates *I. arx* from *Meadia abyssalis* (Kamohara, 1938) and *M. roseni* Mok, Lee & Chan, 1991 (head length less than trunk in *I. arx* versus greater than trunk in *M. abyssalis* and *M. roseni*). Vertebral counts also distinguish these species (128–137 versus 173–178 in *M. abyssalis* and 198–206 in *M. roseni*). The third species of *Meadia*, *M. minor* Vo & Ho, 2021, which has a head length less than trunk, can be differentiated from *I. arx* by its lower vertebral count (128–137 versus 118–122 in *M. minor*).

Morphometric, meristic, and morphological data for all described species of the genus *Ilyophis* are presented in Table 2. The lack of scales distinguishes *Ilyophis arx* from *I. brunneus*, *I. blachei*, *I. nigeli* and *I. maclainei* **sp. nov.** *Ilyophis arx* can also be differentiated from three of these species by its lower vertebrae number (128–137 versus 145–151 in *I. brunneus*, 177–188 in *I. blachei* and 140–152 in *I. nigeli*). It can be distinguished from *I. maclainei* **sp. nov.** (which has a similar range of vertebral number) by its lower lateral-line pore count (31–47 versus 88–94 in *I. maclainei* **sp. nov.**). Among the species without scales, *I. arx* can be differentiated from *I. singularis* and *I. robinsae* by vertebral count (128–137 versus 116–118 in *I. singularis* and 141 in the unique holotype of *I. robinsae*).

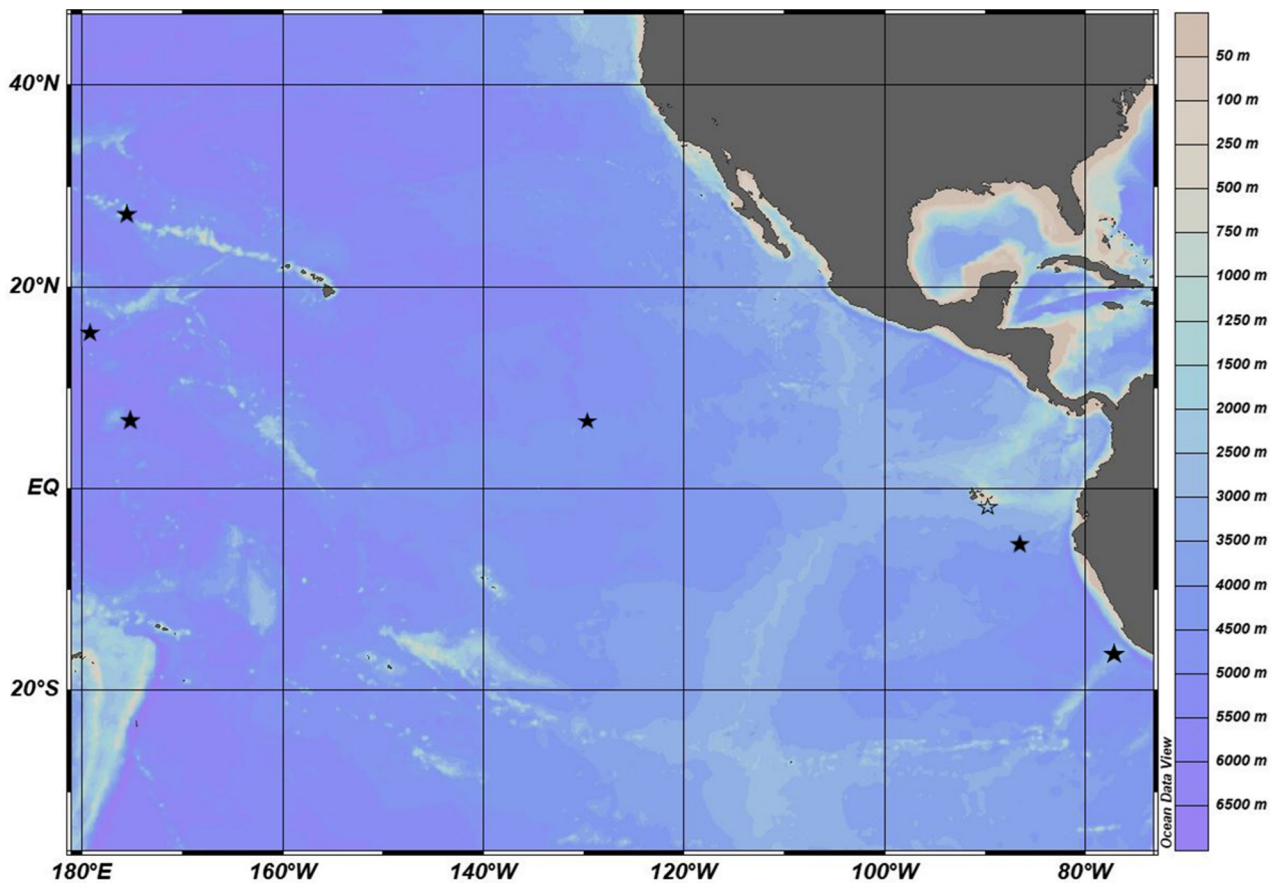
The last species of *Ilyophis* without scales, *I. saldanhai*, is the most difficult to distinguish from *I. arx*. There is almost a total overlap in meristics and morphometrics between the two species. Karmovskaya & Parin (1999) compared their specimens to two specimens from the northeastern Atlantic (described as a new species below) and the data for the type series presented in Robins & Robins (1976). Length of the lateral line differentiates *I. saldanhai* (ca. 35–46% TL in *I. arx* versus 57–62% in *I. saldanhai*). The total number of lateral-line pores also separates the 2 species (31–47 in *I. arx* versus 66–75 in *I. saldanhai*). Karmovskaya & Parin (1999) also distinguished *I. arx* from *I. saldanhai* based on the post-orbital distance (52.9–62.6% HL in *I. arx* versus 43.6–52.3% HL in *I. saldanhai*), but this character shows more variation and does not differentiate the species. Another character used by Karmovskaya & Parin (1999) to distinguish *I. saldanhai* was the number of pores in the preoperculo-mandibular series (POM). They indicated that *I. saldanhai* had 8 to 9 pores, 7–8 mandibular pores and 1 preopercular pore while *I. arx* had only 7 mandibular pores. However, reexamination of three of the types of *I. arx* using carmine blue to highlight

the pores showed that all three specimens had 7 mandibular pores and 1 preopercular pore. Examination of all 21 additional specimens showed variation in the number of POM pores (6–9 mandibular and 0–2 preopercular) and therefore this character should not be used as diagnostic between the two species. Karmovskaya & Parin (1999) also reported an osteological difference between *I. arx* and *I. saldanhai*. *Ilyophis arx* has 0–1 branchiostegals attached to the ceratohyal, 2 branchiostegals attached to the intercalary cartilage, and the remainder articulating with the epihyal. *Ilyophis saldanhai* has 3 branchiostegals attached with the ceratohyal, 2 branchiostegals attached with the intercalary cartilage, and the remainder articulating with the epihyal. The combination of longer lateral line and higher lateral line pore counts do differentiate *I. saldanhai* from *I. arx*. However, the difference in branchiostegal attachment should be investigated further when additional specimens of *I. saldanhai* become available for osteological examination.



**FIGURE 2.** *Ilyophis arx*. Pictures of fresh specimens after capture and before preservation. Upper specimen: USNM 443829. Lower specimen: BPBM 42217. (photos supplied by Dr. Jeffrey C. Drazen)

In addition to the morphological differences above, there is apparently a habitat difference between *Ilyophis arx* and *I. saldanhai*. *Ilyophis saldanhai* was described from 12 specimens collected at the Broken Spur hydrothermal vent field on the Mid-Atlantic Ridge. All subsequent specimens or sightings including Biscoito *et al.* (2002), Biscoito *et al.* (2006) and Causse *et al.* (2005) are also associated with hydrothermal vent environments. However, none of the specimens of *I. arx* cited here are associated with hydrothermal vents.



**FIGURE 3.** Distribution of *Ilyophis arx* in the eastern and central Pacific Ocean. Open star is the type locality. Closed stars are other study material.

**Distribution.** *Ilyophis arx* is widely distributed in the eastern and central Pacific Ocean from the Nazca Ridge off central Peru to seamounts northwest off Hawaii, between 30° N and 15° S (Fig. 3). However, it is not uniformly distributed within this area. The species seems to be associated with underwater topography such as ridges and seamounts and is not found far away from these features on the abyssal plain. Leitner *et al.* (2021a) reported large numbers of *I. arx* attracted to baited cameras placed near the summits of three seamounts within Areas of Particular Environmental Interest (APEI) within the western CCZ in the central Pacific Ocean, but none attracted to cameras placed on the nearby abyssal plain. Leitner *et al.* (2021a) also reported on 12 specimens collected in a baited trap on the summit of the seamount in APEI (7). In addition, Leitner *et al.* (2021b), in analysis of deep-sea videos and time-lapse still photography from these cameras, found that *I. arx* was only seen in samples on the seamounts, and not in the associated samples from the near-by abyssal plain, concluding that *I. arx* may be a specialist of seamounts, ridges and island slopes and suggesting that the species may only be found associated with rough topographies.

**Material Examined.** ANSP 133808 (holotype, 439 mm TL), ANSP 133809 (paratypes, 2, 344 and 366 mm TL), ANSP 133810 (paratype, cleared and stained, 401 mm TL); Eastern Pacific Ocean, south of Galapagos Islands, 01° 48' S, 90° 19' W, 3225 m. BMNH 1998.11.12.1 (1, 455 mm TL); Eastern Pacific Ocean, ca. 750 km SSE of Galapagos Islands, 7° 3.74' S, 88° 26.33' W, 4157 m. SIO 68-462 (2, 430 and 541 mm TL), North Pacific Ocean, Hamilton Seamount, 15° 33' 30" N, 179° 13' 42" W, 3017 m. SIO 68-494 (1, 610 mm TL); North Pacific Ocean, seamount S of Palmer Seamount, 28° 43' N, 177° 52.5'W, 2375 m. SIO 72-189 (1, 516 mm TL); South Pacific Ocean, Nazca Ridge, off Punta San Juan, 15° 39' 12" S, 76° 13' 36" W, 3475 m. SIO 88-149 (1, 383 mm TL); Pacific Ocean, Magellan Rise, at summit, 7° 16' N, 176° 7' W, ca 3150 m. SMF 28622 (1, 430 mm TL), SMF 28623 (1, 470 mm TL), SMF 28624 (1, 481 mm TL); Eastern Pacific Ocean, ca. 750 km SSE of Galapagos Islands, 7° 3.74' S, 88° 26.33' W, 4157 m. USNM 443827–443846 (10, 215–536 mm TL), BPBM 42216 (KM 1808 TR 03 # 11, 268 mm TL), BPBM 42217 (KM 1808 TR 03 # 16, 511 mm TL); Central Pacific Ocean, western Clarion Clipperton Zone, 4° 52' 57.36" N, 141° 46' 45.48" W, 3203 m.

**TABLE 2.** Comparison of morphometric, meristic, and morphological data for all species of *Ilyophis*. For unique specimens (holotypes and paratypes), the bilateral pore counts are recorded left/right (if recorded in original description).

	<i>Ilyophis arx</i> <sup>1</sup>		<i>Ilyophis blachei</i> <sup>2</sup>		<i>Ilyophis brunneus</i> <sup>3</sup>		<i>Ilyophis maclaini</i> <sup>1</sup>		<i>Ilyophis nigeli</i> <sup>4</sup>		<i>Ilyophis robinsae</i> <sup>5</sup>		<i>Ilyophis saldanhai</i> <sup>7</sup>		<i>Ilyophis singularis</i> <sup>6</sup>	
Total length (mm)	215–610 (n=25)	4 1 2 – 7 7 2 (n=12)	15.4–20.4	26.7–31.9	10.5–14.8	242, 263	227–470 (n=45)	348	354–409 (n=3)	270, 248						
Proportions (% TL)	Mean (range)	Range	Range	Range	Range	Holotype, Paratype	Range	Holotype	Mean (range)	Holotype, Paratype						
Predorsal length	16.1 (14.1–18.1)	15.4–20.4	10.5–14.8	26.7–31.9	10.5–14.8	15.6, 15.1	12.8–16.3	15.1	16.4 (15.6–17.5)	14.0, 14.3						
Preal length	36.5 (33.4–43.1)	26.7–31.9	29.0–33.9	26.7–31.9	29.0–33.9	32.2, 30.0	29.4–34.4	31.6	33.4 (33.0–34.2)	37.4, 37.5						
Head length	12.4 (9.9–14.2)	10.7–14.2	7.4–10.6	10.7–14.2	7.4–10.6	12.6, 11.9	10.2–12.5	10.7	13.1 (13.0–13.3)	12.4, 11.7						
Trunk length	24.1 (20.9–28.8)	14.0–17.7	18.3–22.5	14.0–17.7	18.3–22.5	19.0, 18.2	17.8–22.0	--	20.3 (19.7–21.2)	25.9, 26.2						
Tail length	63.5 (56.9–66.6)	68.1–73.3	68.4–72.6	68.1–73.3	68.4–72.6	67.8, 70.0	--	--	66.6 (65.8–67.0)	62.6, 63.3						
Body depth at anus	6.0 (4.4–7.4)	3.6–5.2	--	3.6–5.2	--	4.1, 4.8	3.0–5.5	--	4.1 (3.3–4.5)	4.5, 4.5						
Lateral line length	41.0(35.5–45.7)	ca 87–95	91.0–97.3(n=4) <sup>7</sup>	ca 87–95	91.0–97.3(n=4) <sup>7</sup>	71.7, 75.6	68.2–85.7	ca 75	59.4(57.5–61.9)	80, --						
Proportions (% HL)																
Snout length	30.9 (25.3–35.7)	32.8–38.6	34.2–44.0	32.8–38.6	34.2–44.0	38.6, 32.8	25.7–33.8	37.5	33.5 (30.9–37.5)	37.4, 39.8						
Eye diameter	11.4 (9.4–13.7)	10.2–12.7	7.7–14.3	10.2–12.7	7.7–14.3	10.5, 13.7	8.5–12.1	8.3	11.3 (10.8–11.8)	10.5, 10.0						
Postorbital distance	57.3 (54.5–62.6)	47.7–57.8	42.9–56.7	47.7–57.8	42.9–56.7	56.8, 54.0	--	--	58.8 (57.5–60.0)	52.1, 50.9						
Upper-jaw length	46.9 (39.9–63.2)	43.5–53.1	38.1–63.3	43.5–53.1	38.1–63.3	46.7, 47.8	42.7–49.5	--	51.8 (50.4–53.9)	51.2, 56.4						
Interorbital width	22.5 (14.2–31.4)	11.4–17.3	10.0–24.0	11.4–17.3	10.0–24.0	21.6, 21.0	--	--	18.2(17.7–19.0)	13.5, 13.5						
Gill-opening (GO)	11.4 (8.2–16.5)	--	8.8–20.0	--	8.8–20.0	9.2, 11.5	11.6–17.6	12.8	10.4(9.7–11.2)	10.5, 12.8						
Interbranchial width	19.6 (13.3–27.8)	--	--	--	--	12.4, 12.7	--	--	11.7(10.8–12.8)	--						
Pectoral-fin length	19.0 (10.3–26.6)	10.0–20.5	9.5–24.0	10.0–20.5	9.5–24.0	25.5, 26.1	15.0–24.5	13.6	19.8–21.6	18.0, 16.6						
Meristics																
SO pores	3–4	5–6	3	5–6	3	3/3, 3/3	5–6	3/4	3	3, 3						
IO (including AD) pores	5	7–8	5–6	7–8	5–6	6/6, 6/6	7–9	6/6	5	7/8, 7/7						
Frontal pores	0	1	0	1	0	0	1–2	0	0	0						
Supratemporal pores	0	3	0	3	0	0	0–3	0	0	0						
POM pores	7–10	10–11	9–10	10–11	9–10	8/8, 8/8	9–11	7/7	7	10/8, 8/8						

.....continued on the next page



TABLE 2. (Continued)

	<i>Ilyophis arx</i> <sup>1</sup>	<i>Ilyophis blachei</i> <sup>2</sup>	<i>Ilyophis brunneus</i> <sup>3</sup>	<i>Ilyophis macclainei</i> <sup>1</sup>	<i>Ilyophis nigelti</i> <sup>4</sup>	<i>Ilyophis robinsae</i> <sup>5</sup>	<i>Ilyophis saldanha</i> <sup>7</sup>	<i>Ilyophis singularis</i> <sup>6</sup>
PrePectoral LL pores	2–6	4–7	4–6 (n=5) <sup>7</sup>	4/5, 5/4	6–9	--	4–5	5, --
PreDorsal LL pores	8–14	--	7–9 (n=5) <sup>7</sup>	7/8, 10/9	11–16	--	9–13	6, --
PreAnus LL pores	31–37	41–47	33–36 (n=5) <sup>7</sup>	28/30, 29/31	34–40	31	30–32	33, 34
PreAnalFin LL pores	33–39	--	36–38 (n=5) <sup>7</sup>	30/32, 31/33	36–43	--	32–34	--
Total LL pores	31–47	--	125–135 (n=5) <sup>7</sup>	89/88, 94/93	80–113	87	66–75	--
Dorsal rays	281–347	--	396–432 (n=5) <sup>7</sup>	359, 329	--	--	324	--
Anal rays	219–251	--	290–329 (n=5) <sup>7</sup>	288, 291	--	--	281	--
DR-AF origin	70–95	--	82–98 (n=5) <sup>7</sup>	66, 67	--	--	66–70	--
PreDorsal Vertebrae	10–13	--	6–10	10, 8	10–15	--	12	8, 8
PreAnus Vertebrae	34–40	--	33–40	31, 31	--	--	34–35	36, 37
PreAnal Fin Vertebrae	37–42	--	39–42 (n=5) <sup>7</sup>	33, 34	38–45	--	35–37	--
PreCaudal Vertebrae	54–62	--	56–63 (n=5) <sup>7</sup>	53, 54	--	--	56–61	--
Total Vertebrae	128–137	179–188	139–151	132, 134	140–152	141	132–134	116, 118
Morphology								
Scales	No	Yes	Yes	Yes	Yes	No	No	No
Number of snout plicae	4	7	6	6	Several	Few, simple	4	--
Lower jaw plicae	4–6	ca. 10	4	4	--	--	6	--

Source of data: <sup>1</sup>This study; <sup>2</sup>Saldanha & Merrett, 1982 and Sulak & Sheherbachev, 1997; <sup>3</sup>Merrett & Saldanha, 1985; <sup>4</sup>Tashiro *et al.*, 2010; <sup>5</sup>Sulak & Sheherbachev, 1997; <sup>6</sup>Tashiro & Chen, 2022; <sup>7</sup>Based on examination of Comparative Specimens listed

***Ilyophis maclainei* Tighe, Smith & Merrett, sp. nov.**

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Figures 4–9, Table 1–2

*Ilyophis arx* (not of Robins, 1976). Saldanha & Merrett 1982: 633 (listing of one specimen from Porcupine Sea-Bight, eastern North Atlantic). Merrett & Saldanha 1985: 730–735 (description of northeastern Atlantic specimens). Robins & Robins 1989:238 (suggestion that northeastern Atlantic population was not *Ilyophis arx*). Sulak & Shcherbachev 1997: 1163, 1172, 1188 (key, identification as *Ilyophis arx*, distribution).



**FIGURE 4.** *Ilyophis maclainei* sp. nov. Holotype, BMNH 1995.4.19.31 (male, 242 mm TL)

**Holotype:** BMNH 1995.4.19.31 (male, 242 mm TL), Discovery Collection Station 50710, Goban Spur, off SW Ireland, northeastern Atlantic Ocean, 49° 30' 06" N, 13° 19' 54" E; 1800–2000 m; date: 17 October 1979.

**Paratype:** BMNH 1995.3.29.1 (male, 263 mm TL), Discovery Collection Station 50711, Porcupine Sea-Bight, off SW Ireland, northeastern Atlantic Ocean; 49° 53' N, 15° 36' E; 4788 m; date: 18 October 1979.

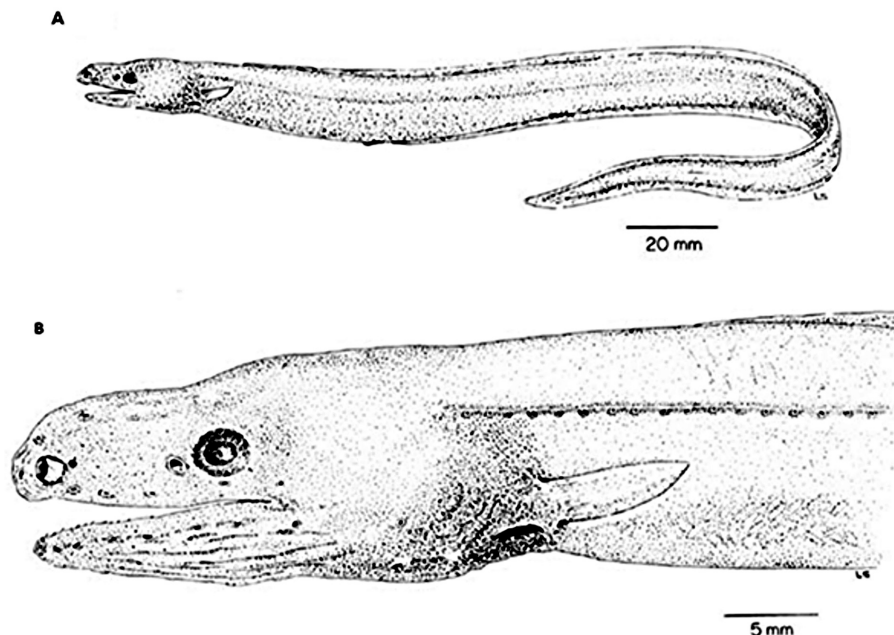
**Referred Specimen:** Discovery Collection Station 50517 (female, 237 mm TL, portion of specimen cataloged as BMNH 1996.3.8.2, see remarks below), Goban Spur, off SW Ireland, northeastern Atlantic Ocean, 49° 33' 30" N, 13° 28' 00" E; 1785–1794 m; date: 7 June 1979.

**Diagnosis.** A species of *Ilyophis* with the following characters. Body covered with scales in an irregular basket-weave pattern. Trunk moderate (about 20% of TL). Dorsal-fin origin above posterior half of pectoral fin. Gape moderate, extending at most to posterior half of eye. Teeth not compound. Intermaxillary teeth conical and acute with approximately 16–18 teeth in the tooth patch. Vomerine teeth abutting the rear of intermaxillary patch with approximately 25 teeth irregularly biserial anteriorly becoming uniserial posteriorly. Both intermaxillary and vomerine teeth set in beds of papillose tissue. Maxillary teeth arranged in bands of one to four (medially) to one irregular row, with anterior teeth somewhat enlarged. Dentary teeth arranged in bands with roughly three to five series of teeth, with anterior ones (in two rows) the largest. Lateral line extends to approximately 70–75% the length of body. Cephalic lateralis pores: supraorbital pores (SO) 3, infraorbital pores (IO) 6 (including adnasal pore just posterior to anterior nostril), preoperculo-mandibular pores (POM) 8–9, 7–8 pores in mandibular region and the eighth or ninth pore in a preopercular position. Total vertebrae 131–134.

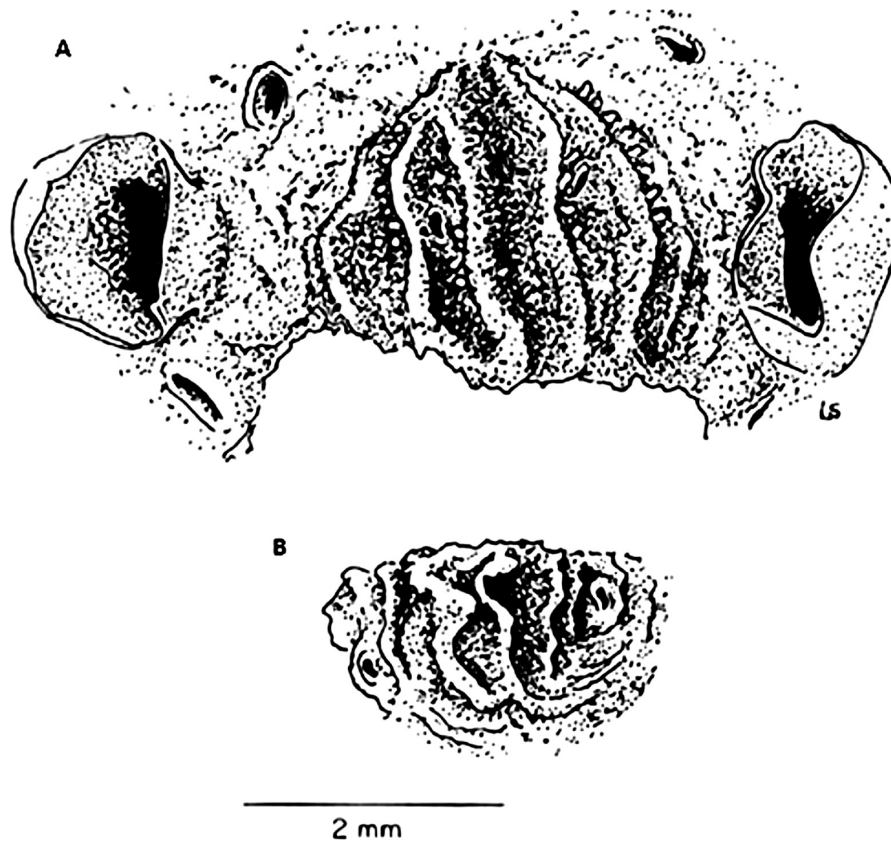
**Description.** Measurements of holotype: total length 240 mm, preanal length 76 mm, predorsal length 36.4 mm, head length 30.0 mm, trunk length 46 mm, snout length 11.8 mm, upper jaw length 14.0 mm, eye diameter 3.3 mm, interorbital width 6.6 mm, gill opening 2.8 mm, intrabronchial distance 5.8, pectoral fin length 7.8 mm, depth at anus 9.9 mm. Meristics and proportional morphometrics of the holotype and paratype are presented in Table 1. Rest of description based on data presented by Merrett & Saldanha (1985). However, it should be noted that the two specimens available for examination have shrunk since originally measured by Merrett and Saldanha (1985).

Body moderately elongate, laterally compressed posteriorly (Fig. 5A). Body tapers gradually to caudal, deepest body depth anteriorly, near anus. Dorsal-fin origin near posterior half or just behind tip of pectoral fin, predorsal length ca. 14–15 % TL. Trunk length moderate (ca. 18–19 % TL), contained about 5 times in TL. Preanal length approximately 3 times in TL, preanal fin length about 31% of TL. Head length moderate (ca. 10–12 % TL) (Fig. 5B). Gill slits crescentic and horizontal, located ventrally just anterior to and below pectoral fin base. Anterior nostril tubular, directed anterolaterally. Posterior nostrils round, just in front of eye. Eye relatively small (10.3–14.3

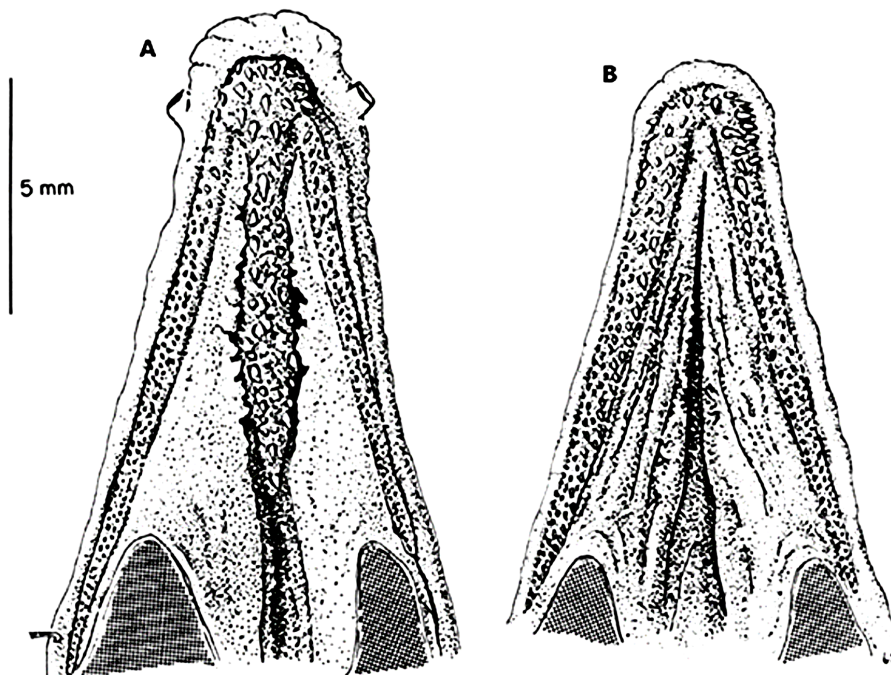
% HL). Pectoral fin moderate in size (3.2–3.7 % TL, 25–36 % HL) with 15 rays. Gape extends to near posterior half of eye. Snout plicate (Fig. 6A), three main plicae on each side of mid-line, outermost least developed. Outer margins of first and second plicae bear some four and eight papillae respectively, other minute papillae occur along all plical ridges. Tip of lower jaw also plicate (Fig. 6B), two main plicae on each side of mid-line, outermost least developed. Teeth conical, arranged in bands along maxillary, dentary and intermaxillary/vomer [Fig. 7]. Teeth not compound. Maxillary teeth in two to four rows (medially) reducing to one irregular row posteriorly, with anterior teeth somewhat enlarged. Dentary teeth in three to five irregular rows, with anterior ones (in two rows) larger. Intermaxillary teeth with 16–18 strong teeth concentrically arranged around tooth patch with inner teeth slightly larger. Vomerine teeth abutting intermaxillary tooth patch with two irregular rows anteriorly (with 10–11 teeth each) and converging to single row posteriorly (with three to four teeth), total number of vomerine teeth 24–25. Both intermaxillary and vomerine teeth surrounded by papillae. Cephalic lateralis pores (Fig. 5B): supraorbital pores three, first located between first and second plicae on snout, second on snout at level of the dorsal rim of anterior nostril, third on dorsal of snout above adnasal pore; infraorbital pores six, first (adnasal pore) just posterior to dorsal rim of anterior nostril, second on lip just posteroventral to base of anterior nostril, third on lip one third of the way between anterior and posterior nostrils, fourth on lip anteroventral to posterior nostril, fifth on lip just ventral to the anterior margin of the eye, sixth on lip slightly posterior to posterior margin of eye; preoperculo-mandibular pores eight to nine, first very small and located within plicae at tip of lower jaw, remaining 6–7 mandibular pores spaced progressively far apart along jaw, last mandibular pore located approximately below rictus, 1–2 preopercular pores located posteriorly in the opercular region. Only the paratype has 2 preopercular pores which are on the left side of the head and are set very close together in a pair. Lateral line incomplete, relatively long; pores extend to approximately 75% length of body. Three to six pores anterior to pectoral-fin base, 7–10 pores anterior to dorsal-fin origin, 29–32 pores anterior to anus, 88–94 total pores. Scales present all over body, except head, arranged broadly in classic basket-weave pattern (Fig. 8A–D). Number, shape, and disposition variable. Scales generally elongate in shape, but length may vary between 2–3 scale width [type  $\alpha$  scales (Fig. 8B) or 10–15 or more times scale width [type  $\beta$  scales (Fig. 8C–D). Disposition of scale types variable between specimens and not necessarily bilaterally symmetrical on an individual. Type  $\alpha$  scales present in only one specimen (Fig. 8A), one patch on left side on belly posterior to left pectoral fin and two patches on right side, one between lateral line and dorsal profile, posterior to right pectoral fin, and second on beginning of caudal region between lateral line and ventral profile. Type  $\beta$  scales are most common and present on all three specimens. Vertebral numbers: predorsal 8–9, preanal 31–32, total 131–134.



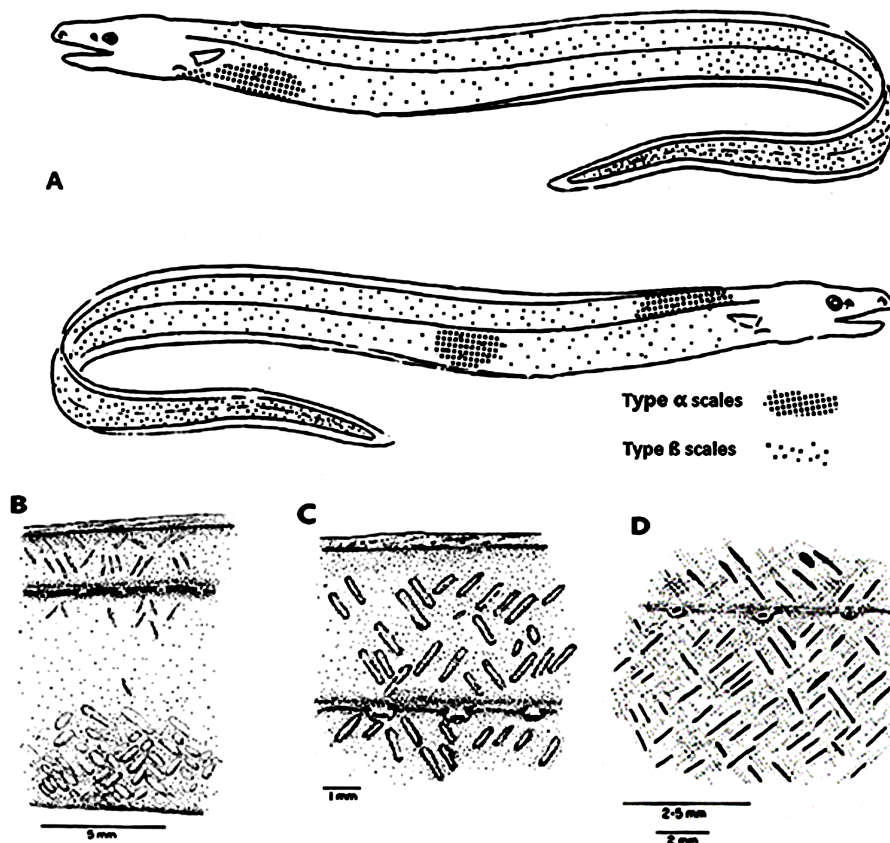
**FIGURE 5.** *Ilyophis maclainei* sp. nov. Referred Specimen, DISCOVERY Collection, Station 50517, 237 mm TL (A) Lateral view. (B) Head and cephalic lateralis system (from Merrett & Saldanha 1985)



**FIGURE 6.** *Ilyophis maclainei* sp. nov. Holotype, BMNH 1995.4.19.31 (DISCOVERY Collection, Station 50710), 240 mm TL (A) Snout ornamentation. (B) Lower jaw tip ornamentation (from Merrett & Saldanha 1985)



**FIGURE 7.** *Ilyophis maclainei* sp. nov. Referred Specimen, DISCOVERY Collection, Station 50517, 237 mm TL (A) Dentition of upper jaw. (B) Dentition of lower jaw (from Merrett & Saldanha 1985)



**FIGURE 8.** *Ilyophis maclainei* sp. nov. (A) Referred Specimen, DISCOVERY Collection, Station 50517. Distribution of type  $\alpha$  and  $\beta$  squamation on left and right side of specimen. (B) Same specimen. Detail of squamation from area of trunk region (scales of type  $\alpha$  ventrally). (C) Same specimen. Detail of squamation from anal region (scales of type  $\beta$ ). (D) Holotype, BMNH 1995.4.19.31. Detail of squamation from region of end of caudal (scales of type  $\beta$ ) (modified from Merrett & Saldanha 1985)

**Remarks.** The Referred Specimen listed above (Discovery Collection Station 50517) was one of the original three specimens described by Merrett & Saldanha (1985). This specimen was also examined by Sulak & Shcherbachev (1997). Since then, most of the specimen has apparently been lost. Only the gonads of this female specimen are still in existence and are cataloged at the Natural History Museum as BMNH 1996.3.8.2. However, since much of the data on the northeastern Atlantic population provided by Merrett & Saldanha (1985) was based on this specimen, we have included it in the description. If the body of this specimen is ever found, it should be reunited with BMNH 1996.3.8.2.

**Comparative remarks.** *Ilyophis maclainei* can be distinguished from all members of the genera *Atractodenchelys*, *Dysomma* *Dysommina*, and *Linkenchelys* by the lack of compound teeth in the dentition (versus at least vomerine teeth compound). *Ilyophis maclainei* is distinguished from *Meadia abyssalis* and *M. roseni* by its head length shorter than its trunk (versus head length longer than trunk). Finally, it can be distinguished from a third species in the genus *Meadia*, *M. minor*, by its higher vertebral number (131–134 versus 118–122 in *M. minor*).

Morphometric, meristic, and morphological data for all described species of the genus *Ilyophis* are presented in Table 2. The presence of scales distinguishes *I. maclainei* from other members of the genus *Ilyophis* except *I. brunneus*, *I. blachei* and *I. nigeli*. *Ilyophis maclainei* is differentiated from those three species by its lower vertebrae number (131–134 versus 145–151 in *I. brunneus*, 177–188 in *I. blachei* and 140–152 in *I. nigeli*). *I. maclainei* can be distinguished from *I. arx* with which it had previously been confused not only by the presence of scales (versus no scales in *I. arx*), but also by its longer lateral line (ca. 70–76% TL versus ca. 35–46% TL in *I. arx*), the correlated higher number of lateral line pores (88–94 versus 31–47 in *I. arx*), and a lower number of preanal fin vertebrae (33–34 versus 37–42 in *I. arx*).

**Etymology.** We take pleasure in naming this new species after our colleague James Maclaine, Senior Curator of Fishes at The Natural History Museum, United Kingdom, for his dedication to the collections under his care,

and especially his hard work in incorporating the collections of the Institute of Oceanographic Sciences/National Oceanography Centre into the Natural History Museum, United Kingdom.

**Distribution.** *Ilyophis maclainei* is known only from the three specimens which were collected in the vicinity of the Porcupine Sea-Bight and Goban Spur areas, off SW Ireland at a depth range of 1785 to 4788 m (Fig. 9).

Whether the species is endemic to this area or might be more widely distributed in the slope region of the eastern North Atlantic is unknown.

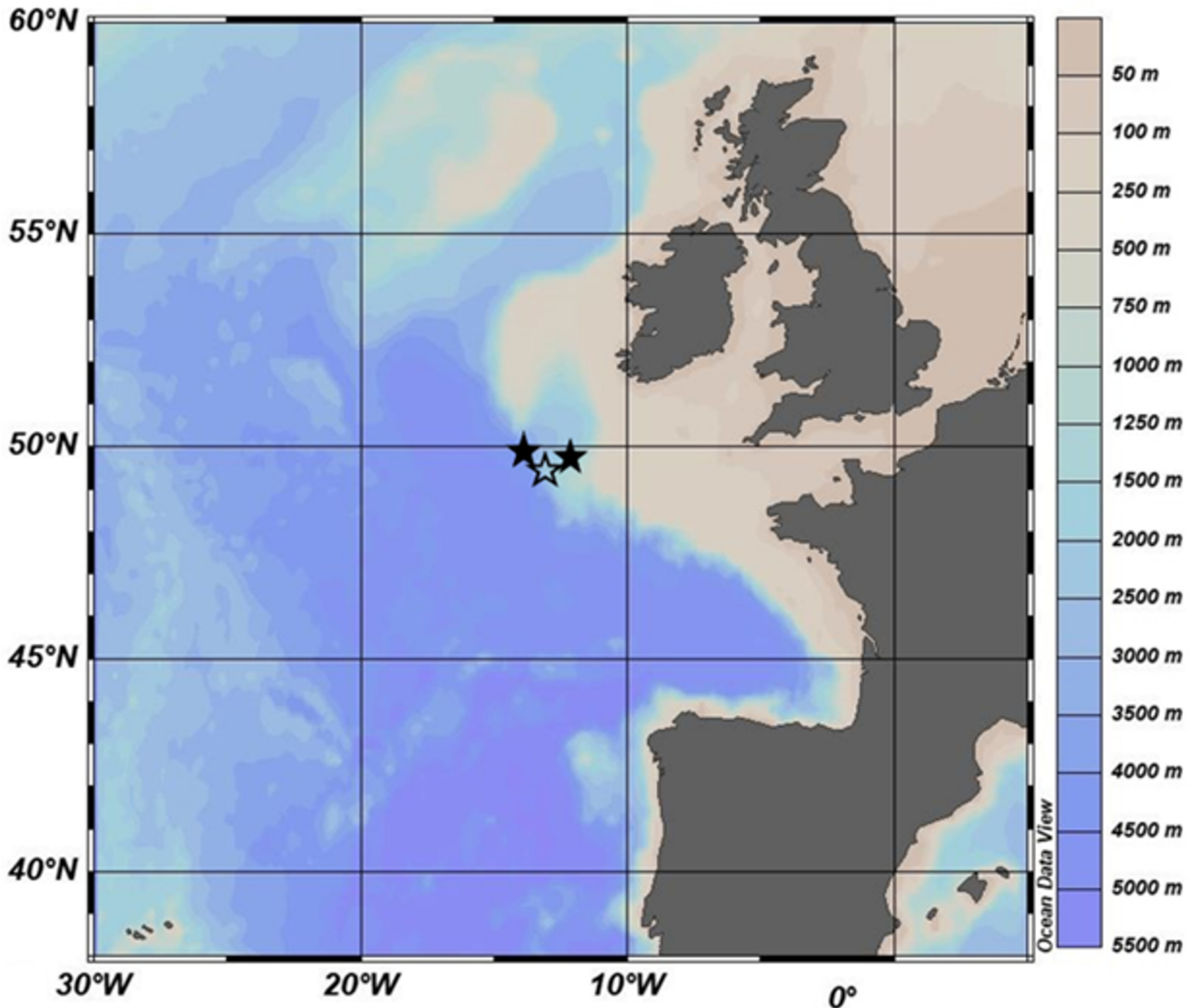


FIGURE 9. Distribution of *Ilyophis maclainei* in the eastern North Atlantic Ocean. Open star is the type locality. Closed stars are other study material.

**Comparative Specimens Examined.** *Ilyophis brunneus*: USNM 44403 (holotype, 380 mm TL), Eastern Pacific Ocean, Galápagos Islands, Near San Cristóbal Island [Chatham Island], 0° 36' 30" S, 89° 19' 00" W, Albatross station 2808, depth 634 fathoms (1160 m). USNM 185665 (1, 312 mm TL), Gulf of Mexico, off Mississippi Delta, 28° 58' N, 88° 11' W, Oregon station 2822, depth 1143 m. USNM 195901 (1, 414 mm TL), Gulf of Mexico, off Alabama, 28° 55' N, 87° 49' W, Oregon station 2022, depth 1646 m. USNM 197115 (1, 403 mm TL) North Atlantic Ocean, Straits of Florida, north of Cay Sal Bank. 24° 24' N, 80° 00' W, depth 400–400 fathoms. USNM 212185 (1, 262 mm TL), Southern Caribbean Sea, off western Venezuela, 11° 44' N, 68° 43' W, depth 1006 m. *Ilyophis saldanhai*: MMF 27080 (2, 354–382 mm TL), MMF 27081 (1, 409 mm TL); North Atlantic Ocean, Mid-Atlantic Ridge, Broken Spur Hydrothermal Vent Field. 29° 08' N, 43° 13' W. 3020 m.

## Synopsis of the subfamily Ilyophinae Jordan & Davis, 1891

**Ilyophidae** Gilbert 1891:351. Type genus *Ilyophis*.

Dysommidae Gill 1893:132. Type genus *Dysomma* [type genus inferred from the stem].

Nettodaridae Whitley 1951:407. Type genus *Nettodarus*.

Dysomminidae Böhlke & Hubbs 1951:10. Type genus *Dysommina*.

Todaridae Greenwood, Rosen, Weitzman & Myers 1966:393. Type genus *Todarus*.

### Genus **TRACTODENCHELYS**

*Atractodenchelys* Robins & Robins, 1970: 296. Type species *Atractodenchelys phrix* Robins & Robins, 1970 by original designation. Feminine.

#### *Atractodenchelys brevitrunca* Vo & Ho, 2020

*Atractodenchelys brevitrunca* Vo & Ho, 2020: 589, Figs. 1–4. Holotype: OIM E.55743. Type locality: off Nha Trang City, southern Vietnam, western South China Sea, ca. 280–350 m.

#### *Atractodenchelys phrix* Robins & Robins, 1970

*Atractodenchelys phrix* Robins & Robins, 1970: 297, Fig. 1A. Holotype: ANSP 114437. Type locality: eastern Caribbean, 11° 36' N, 62° 52' W, 385–425 m.

#### *Atractodenchelys robinsorum* Karmovskaya, 2003

*Atractodenchelys robinsorum* Karmovskaya, 2003: 441. Holotype: MNHN 1997-3794. Type locality: SW Pacific, Chesterfield Is., 19° 43' S, 158° 48' E, 710 m.

### Genus **DYSOMMA**

*Dysomma* Alcock 1889: 459. Type species *Dysomma bucephalus* Alcock, 1889 by monotypy. Neuter.

*Dysommopsis* Alcock 1891: 137. Type species *Dysommopsis muciparus* Alcock, 1891 by monotypy. Feminine.

*Todarus* Grassi & Calandruccio 1896: 349. Type species *Nettastoma brevirostre* Facciola, 1887 by monotypy. Masculine. Name preoccupied.

*Sinomyrus* Lin 1933: 93. Type species *Sinomyrus angustus* Lin, 1933 by original designation. Masculine.

*Nettodarus* Whitley 1951. Replacement for *Todarus* Grassi & Calandruccio. Masculine.

#### *Dysomma achiropteryx* Prokofiev, 2019

*Dysomma achiropteryx* Prokofiev 2019: 317, Fig. 1. Holotype: PMBC [no number]. Type locality: Andaman Sea off Phuket Is., 508–518 m.

#### *Dysomma alticorpus* Fricke, Golani, Appelbaum-Golani & Zajonz, 2018

*Dysomma alticorpus* Fricke *et al.* 2018: 2, Figs. 1–2. Holotype: HUI 17054. Type locality: Red Sea, Gulf of Aqaba, 29° 30' 45" N, 34° 56' 30" E, 350m.

### ***Dysomma anguillare* Barnard, 1923**

*Dysomma anguillaris* Barnard 1923:443. Holotype: SAM 12744. Type locality: off Tugela River mouth, KwaZulu-Natal, South Africa, 63 fm (115 m).

*Sinomyrus angustus* Lin 1933: 94, Fig. 1. Holotype: FESC [now PRFRI] 405. Type locality: Hoitow, Hainan, China.

*Dysomma aphododera* Ginsburg 1951: 452, Fig. 7. Holotype: USNM 154992. Type locality: Gulf of Mexico, 26° 30' N, 96° 26' W, 50 fm (92 m).

*Dysomma japonicus* Matsubara 1936: 961, Fig. unnumb. Holotype: FAKU 1941. Type locality: Japan, Kumano-Nada, SE of Kii Peninsula, 150 fm (275 m).

*Dysomma zanzibarensis* Norman 1939: 44, Fig. 17. Holotype: BMNH 1939.524.651. Type locality: western Indian Ocean, 5° 38' 54" S, 39° 15' 42" E, 183–194 m.

### ***Dysomma brachygnathos* Ho & Tighe, 2018**

*Dysomma brachygnathos* Ho & Tighe 2018: 59, Figs.4–5. Holotype: USNM 444742. Type locality: South China Sea, Dong-gang fishing port, SW Taiwan.

### ***Dysomma brevirostre* (Facciola, 1887)**

*Nettastoma brevirostre* Facciola 1887: 166, Pl. 3 (Fig. 3). Holotype: lost. Type locality: Mediterranean Sea.

*Leptocephalus telescopicus* Schmidt 1913: 11, Pl. 1 (fig. 8). Holotype: ZMUC (lost). Type locality: Mediterranean, Tyrrhenian Sea.

### ***Dysomma bucephalus* Alcock, 1889**

*Dysomma bucephalus* Alcock 1889: 459. Holotype: ZSI F11675. Type locality: Bay of Bengal, 20° 17' 30" N, 88° 51' E, 193 fm (353 m).

### ***Dysomma bussarawiti* Prokofiev, 2019**

*Dysomma bussarawiti* Prokofiev 2019: 319, Fig. 2. Holotype: PMBC [no number]. Type locality: Andaman Sea, off Phuket Is., 520–532 m.

### ***Dysomma dolichosomatum* Karrer, 1983**

*Dysomma dolichosomatum* Karrer 1983: 93, Figs. 28A–B. Holotype: MNHN 1979-0004. Type locality: Indian Ocean off Madagascar, 22° 25' S, 43° 04.5' E, 550–555 m.

### ***Dysomma formosa* Ho & Tighe, 2018**

*Dysomma formosa* Ho & Tighe 2018: 54, Figs. 1–3. Holotype: NMMP 23172. Type locality: South China Sea, SW Taiwan, Dong-gang fishing port.

### ***Dysomma fuscoventrale* Karrer & Klausewitz, 1982**

*Dysomma fuscoventralis* Karrer & Klausewitz 1982: 199, Figs. 1–3. Holotype: SMF 15660. Type locality: Red Sea, 21° 26.50' N, 38° 38.30' E, 799–801 m.



***Dysomma goslinei* Robins & Robins, 1976**

*Dysomma goslinei* Robins & Robins 1976: 261, Figs. 3, 6, 7c, 8. Holotype: ANSP 133805. Type locality: Bay of Bengal, 14° 52' N, 96° 39' E, no depth given.

***Dysomma intermedium* Vo & Ho 2024**

*Dysomma intermedium* Vo & Ho in Vo, Ho, Dao & Tran (2024). Holotype: OIM-E.55838. Type locality: Quy Nhon, Bình Định, southeast coast of Vietnam, ca. 13° 46' 24" N, 109° 14' 48" E, ca. 50–80 m.

***Dysomma longirostrum* Chen & Mok, 2001**

*Dysomma longirostrum* Chen & Mok 2001: 79, Figs. 1A, 2A–C. Holotype NSYU 2732. Type locality: Taiwan, Nan-fang-au fish market.

***Dysomma melanurum* Chen & Weng, 1967**

*Dysomma melanurum* Chen & Weng 1967: 84, Fig. 63. Holotype: NMMBP 5284 [ex THUP 1687]. Type locality: South China Sea, Taiwan, Tung-kang [=Dong-gang].

***Dysomma muciparus* (Alcock, 1891)**

*Dysommopsis muciparus* Alcock 1891: 137. Lectotype: ZSI F13106 (designated by Robins & Robins, 1976: 260). Type locality: Bay of Bengal, 15° 56' 50" N, 81° 33' 30" E, 240–246 fm (439–505 m).

***Dysomma opisthoproctus* Chen & Mok, 1995**

*Dysomma opisthoproctus* Chen & Mok 1995: 927, Fig. 1. Holotype: NSYSU 2701. Type locality: Taiwan, Nan-fang-ao, 24° 51' 24" N, 121° 58' 30" E, 200 m.

***Dysomma phukutense* Prokofiev, 2019**

*Dysomma phukutensis* Prokofiev 2019: 319, Fig. 3. Holotype: PMBC [no number]. Type locality: Indian Ocean, Andaman Sea, off Phuket Is., 464–467 m.

***Dysomma polycatodon* Karrer, 1983**

*Dysomma polycatodon* Karrer 1983: 89, Figs. 27A–B. Holotype: MNHN 1979-0003. Type locality: Indian Ocean off NW Madagascar, 15° 21' S, 46° 11' E, 170–175 m.

***Dysomma robinsorum* Ho & Tighe 2018**

*Dysomma robinsorum* Ho & Tighe 2018: 61, Figs. 6–7. Holotype: NMMBP 26327. Type locality: South China Sea, SW Taiwan, Dong-gang fishing port.

***Dysomma taiwanense* Ho, Smith & Tighe, 2015**

*Dysomma taiwanensis* Ho *et al.* 2015: 87, Figs. 1–2. Holotype: NMMBP 11115. Type locality: Daxi, Yilan, NE Taiwan.

***Dysomma tridens* Robins, Böhlke & Robins, 1989**

*Dysomma tridens* Robins, Böhlke & Robins in Robins & Robins 1989: 250, Figs. 237–240. Holotype: USNM 193563. Type locality: Caribbean Sea, off Belize, 16° 44' N, 87° 55' W, 190 fm (348 m).

## Genus *DYSOMMINA*

*Dysommima* Ginsburg, 1951: 450. Type species *Dysommima rugosa* Ginsburg 1951 by original designation. Feminine.

### *Dysommima brevis* Vo & Ho, 2024

*Dysommima brevis* Vo & Ho in Vo, Ho, Dao & Tran (2024). Holotype: OIM-E.55839. Type locality: Luong Son, Nha Trang, Khánh Hòa, southeast coast of Vietnam, ca. 12° 20' 7" N, 109° 12' 14" E, ca. 120–180 m.

### *Dysommima orientalis* Tighe Ho, & Hatooka, 2018

*Dysommima orientalis* Tighe *et al.* 2018: 44, Figs. 1–3A. Holotype NMMBP 11131. Type locality: SW Taiwan, Dong-gang fishing port.

### *Dysommima rugosa* Ginsburg, 1951

*Dysommima rugosa* Ginsburg 1951: 450, Fig. 6. Holotype: USNM 131594. Type locality: western North Atlantic off Georgia, 30° 53' 00" N, 79° 42' 30" W, 273 fm (500 m).

## Genus *ILYOPHIS*

*Ilyophis* Gilbert, 1891:351. Type species *Ilyophis brunneus* Gilbert, 1891 by original designation. Masculine.

### *Ilyophis arx* Robins, 1976

*Ilyophis arx* C.H. Robins in Robins & Robins 1976: 245, Figs. 4, 6, 7b, 8. Holotype: ANSP 133808. Type locality: Southeastern Pacific, Galapagos Islands, 01° 48' S, 90° 19' W, 3522 m.

### *Ilyophis blachei* Saldanha & Merrett, 1982

*Ilyophis blachei* Saldanha & Merrett, 1982: 624, Figs. 2–3. Holotype: BMNH 1981.3.17.1. Type locality: Porcupine Sea Bight, Northeastern Atlantic, 51° 04.4' N, 11° 59.3' W, 1494–1572 m.

### *Ilyophis brunneus* Gilbert, 1891

*Ilyophis brunneus* Gilbert, 1891: 352. Holotype: USNM 44403. Type locality: Southeastern Pacific, Galapagos Islands, 0° 36' 30" S, 89° 19' 00" W, 634 fm (1159 m).

### *Ilyophis maclainei* Tighe, Smith & Merrett (this paper)

*Ilyophis maclainei* Tighe, Smith & Merrett in Tighe *et al.* (this paper) Holotype: BMNH 1995.4.19.31. Type locality: Goban Spur, off SW Ireland, northeastern Atlantic Ocean, 49° 30' 06" N, 13° 19' 54" E; 1800–2000 m.

### *Ilyophis nigeli* Shcherbachev & Sulak, 1997

*Ilyophis nigeli* Shcherbachev & Sulak in Sulak & Shcherbachev, 1997: 1172, Figs. 1C, 2B, 4C. Holotype: ZIN 45274. Type locality: Northwestern Pacific, Japan, 42° 27' N, 144° 27' E, 1160 m.

### *Ilyophis robinsae* Sulak & Shcherbachev, 1997

*Ilyophis robinsae* Sulak & Shcherbachev, 1997: 1171, Figs. 3C, 4B. Holotype ZMMU P-14759. Type locality: Western Pacific, 7° 39.3' N, 121° 32' E, 4800 m.

***Ilyophis saldanhai* Karmovskaya & Parin, 1999**

*Ilyophis saldanhai* Karmovskaya & Parin, 1999: 316, Figs. 1–6. Type locality: Mid-Atlantic, 29° 08' N, 43° 13' W, 3020 m.

***Ilyophis singularis* Tashiro & Chen, 2022**

*Ilyophis singularis* Tashiro & Chen, 2022: 2, Figs. 1–3. Holotype: NTUM 13381. Type locality: Northeastern South China Sea, 21° 39' N, 118° 20' E – 21° 36' N, 118° 16' E, depth 1,665–1,612 m.

**Genus *LINKENCHELYS***

*Linkenchelys* Smith, 1989: 78. Type species *Linkenchelys multipora* Smith, 1989 by original designation. Feminine.

***Linkenchelys multipora* Smith, 1989**

*Linkenchelys multipora* Smith, 1989: 78, Figs. 70–73. Holotype: ANSP 156814. Type locality: western Atlantic, Bahamas, San Salvador, 238 m.

**Genus *MEADIA***

*Meadia* Böhlke, 1951: 6. Type species *Dysomma abyssale* Kamohara, 1938 by original designation. Feminine.

***Meadia abyssalis* (Kamohara, 1938)**

*Dysomma abyssale* Kamohara, 1938: 12, Fig. 3. Neotype: FMNH 76869, designated by Robins & Robins, 1976: 256. Type locality: Sagami Sea, Japan.

***Meadia minor* Vo & Ho, 2021**

*Meadia minor* Vo & Ho in Vo, Ho, Dao & Tran 2021:182, Figs. 1–2. Holotype: OIM-E.55801. Type locality: off Quy Nhon, Binh Dinh, central coast of Vietnam, South China Sea, ca. 13° 44' N, 109° 15' E, ca. 100–120 m.

***Meadia roseni* Mok, Lee & Chan, 1991**

*Meadia roseni* Mok *et al.*, 1991: 39, Figs. 1–3. Holotype: NSYU 2582. Type locality: SW Taiwan, off Dong-gang, 22° 21' 05" N, 120° 12' 46" E, 1020 m.

**ARTIFICIAL KEY TO THE SPECIES OF ILYOPHINAE**

- 1a. Vomerine teeth compound, uniserial . . . . . 2
- 1b. Vomerine teeth simple, in one or more rows . . . . . 23
  
- 2a. Pectoral fins absent . . . . . 3
- 2b. Pectoral fins present . . . . . 9
  
- 3a. Trunk very short, about half head length . . . . . *Dysomma brachygnathos*
- 3b. Trunk longer, about twice head length . . . . . 4
  
- 4a. Three large intermaxillary teeth projecting downward from tip of snout in front of lower jaw . . . . . *Dysomma tridens*
- 4b. Two intermaxillary teeth, not projecting from snout . . . . . 5

5a.	Tip of snout and chin bulbous, with conspicuous papillae and ridges; vertebrae greater than 190	<i>Dysomma brevirostre</i>	6
5b.	Snout only modestly ornamented, papillae not obvious; vertebrae less than 165		6
6a.	Lateral line complete		7
6b.	Lateral line incomplete, ca. 8–12 pores only		8
7a.	Supraorbital pores 3; trunk about 2 times head length; peritoneum black	<i>Dysomma achiropteryx</i>	
7b.	Supraorbital pores 4; trunk about 3 times head length; peritoneum pale	<i>Dysomma bussarawati</i>	
8a.	Infraorbital pores 5; trunk about 2 times head length	<i>Dysomma muciparus</i>	
8b.	Infraorbital pores 4; trunk about 3 times head length	<i>Dysomma dolichosomatum</i>	
9a.	Intermaxillary teeth absent		10
9b.	Intermaxillary teeth present		18
10a.	Vomerine teeth consisting of 7–8 long, needle-like compound teeth	<i>Linkenchelys multipora</i>	
10b.	Vomerine teeth consisting of 3–5 heavy, conical compound teeth		11
11a.	Head length greater than trunk		12
11b.	Head length less than trunk		14
12a.	Total vertebrae 137–141	<i>Dysommima orientalis</i>	
12b.	Total vertebrae less than 135		13
13a.	Predorsal vertebrae 12–13, preanal vertebrae 23–25	<i>Dysommima brevis</i>	
13a.	Predorsal vertebrae 14–15, preanal vertebrae 28–31	<i>Dysommima rugosa</i>	
14a.	Lower jaw longer than upper, jaws not closing completely	<i>Dysomma melanurum</i>	
14b.	Jaws equal or upper jaw longer; jaws close completely		15
15a.	Snout slender, elongate (ca. 26–32% of HL), jaw length long (ca. 42–52% HL); supraorbital pores 5, infraorbital pores 8, preoperculomandibular pores 9	<i>Dysomma longirostrum</i>	
15b.	Snout and jaws not notably slender and elongate); supraorbital pores 3, infraorbital pores 4–6, preoperculomandibular pores 6–8		16
16a.	Dorsal-fin origin anterior to pectoral-fin base	<i>Dysomma goslinei</i>	
16b.	Dorsal-fin origin above or posterior to pectoral-fin base		17
17a.	Lateral line complete; dorsal fin origin lightly behind pectoral-fin base	<i>Dysomma phuketensis</i>	
17b.	Lateral line incomplete, vertebrae 122–124; dorsal fin origin above pectoral-fin base	<i>Dysomma robinsorum</i>	
18a.	Trunk long, about twice head length		19
18b.	Trunk short, less than head length		21
19a.	Two intermaxillary teeth, arranged transversely	<i>Dysomma opisthoproctus</i>	
19b.	Intermaxillary teeth in a rounded patch		20
20a.	Total vertebrae 186–199	<i>Atractodenchelys robinsorum</i>	
20b.	Total vertebrae 168–173	<i>Atractodenchelys phrix</i>	
20c.	Total vertebrae 155–158	<i>Atractodenchelys brevitrunca</i>	
21a.	Dentary teeth numerous, 24–40; total vertebrae 107–109	<i>Dysomma bucephalus</i>	
21b.	Dentary teeth fewer than 25; total vertebrae 119 or more		22
22a.	Lateral line pores 57–75; dentary teeth 6–11; total vertebrae 119–128	<i>Dysomma anguillare</i>	
22b.	Lateral line pores 17–33; dentary teeth 14–22; total vertebrae 128–133	<i>Dysomma formosa</i>	
22c.	Lateral line pores 20–49; dentary teeth 6–15; total vertebrae 134–140	<i>Dysomma taiwanense</i>	
22d.	Lateral line pores 57–58; dentary teeth 8; total vertebrae 115	<i>Dysomma alticorpus</i>	
22e.	Lateral line pores 57–63; dentary teeth 16–21; total vertebrae 119–124	<i>Dysomma fuscoventralis</i>	
22f.	Lateral line pores 65–84; dentary teeth 23–25; total vertebrae 128–140	<i>Dysomma polycatodon</i>	
22g.	Lateral line pores 70–79, dentary teeth 8–9; total vertebrae 118–124	<i>Dysomma intermedium</i>	

23a.	Head length greater than trunk	24
23b.	Head length less than trunk	25
24a.	Vomerine teeth biserial; vertebrae 173–178	<i>Meadia abyssalis</i>
24b.	Vomerine teeth triserial; vertebrae 198–206	<i>Meadia roseni</i>
25a.	Full complement of head pores: supraorbital 5, infraorbital 7–8, preoperculomandibular 10–11, 1–2 frontal, 2–3 supratemporal	26
25b.	Head pores reduced: : supraorbital 3, infraorbital 4–7, preoperculomandibular 6–10, no frontal or supratemporal	27
26a.	Body partially scaled or naked; gill slit noticeably oblique; preanal Lateral line pores 37–44; total vertebrae 177–188	<i>Ilyophis blachei</i>
26b.	Body completely scaled; gill slit nearly horizontal; preanal Lateral line pores 32–37; total vertebrae 141–147	<i>Ilyophis nigeli</i>
27a.	Scales present	28
27b.	Scales absent	29
28a.	Preanal lateral line pores 33–38; total vertebrae 145–151	<i>Ilyophis brunneus</i>
28b.	Preanal lateral line pores 26–30; total vertebrae 131–134	<i>Ilyophis maclaunei</i>
29a.	Head slender and conical, snout pointed; total vertebrae 141	<i>Ilyophis robinsae</i>
29b.	Head shorter, snout blunt; total vertebrae 116–135	30
30a.	Total vertebrae less than 125	31
30b.	Total vertebrae greater than 125	32
31a.	Lateral line almost complete, extending nearly to caudal fin base; cephalic lateralis pores reduced: SOC 3, IO 4, POM 7; total vertebrae 118–122	<i>Meadia minor</i>
31b.	Lateral line incomplete (66–80% TL); cephalic lateralis pores: SOC 3, IO 7–8 (extending behind eye), POM 8–10; total vertebrae 116–118	<i>Ilyophis singularis</i>
32a.	Lateral line incomplete; pored lateral line, limited to anterior third of body (ca. 35–45% TL); total lateral line pores 31–47	<i>Ilyophis arx</i>
32b.	Lateral line incomplete; pored lateral line longer, extending further along total length of body (ca. 55–62 % TL); total lateral line pores 66–75	<i>Ilyophis saldanhai</i>

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## References

- Alcock, A.W. (1889) Natural history notes from H. M. Indian marine survey steamer 'Investigator,' Commander Alfred Carpenter, R. N., D. S. O., commanding.—No. 13. On the bathybial fishes of the Bay of Bengal and neighbouring waters, obtained during the seasons 1885-1889. *Annals and Magazine of Natural History*, Series 6, 4 (24), 450–461.  
<https://doi.org/10.1080/00222938909460563>
- Alcock, A.W. (1891) Class Pisces. In: II.—Natural history notes from H.M. Indian marine survey steamer 'Investigator,' Commander R. F. Hoskyn, R. N., commanding. Series II., No. 1. On the results of deep-sea dredging during the season 1890–91. *Annals and Magazine of Natural History*, Series 6, 8 (43/44), 16–34 + 119–138, pls. 7–8.  
<https://doi.org/10.1080/00222939109460385>

- Barnard, K.H. (1923) Diagnoses of new species of marine fishes from South African waters. *Annals of the South African Museum*, 13 (Pt 8, No. 14), 439–445.
- Biscoito, M., Segonzac, M., Almeida, A.J., Desbruyères, D., Geistdoerfer, P., Turnipseed, M. & Van Dover, C. (2002) Fishes from the hydrothermal vents and cold seeps - An update. *Cahiers de Biologie Marine*, 43 (3 & 4), 359–362.
- Biscoito, M., Almeida, A.J. & Segonzac, M. (2006), Preliminary biological characterization of the Saldanha hydrothermal field at the Mid-Atlantic Ridge (36°34'N, 32°26'W, 2200 m). *Cahiers de Biologie Marine*, 47 (4), 421–427.
- Böhlke, E.B. (1982) Vertebral formulae for type specimens of eels (Pisces: Anguilliformes). *Proceedings of the Academy of Natural Sciences, Philadelphia*, 134, 31–49.
- Böhlke, E.B. (1984) Catalog of type specimens in the ichthyological collection of the Academy of Natural Sciences of Philadelphia. *Academy of Natural Sciences of Philadelphia Special Publication*, 14, 1–246.
- Böhlke, E.B. (1989) Methods and terminology. In: Böhlke, E.B. (Ed.), *Fishes of the Western North Atlantic. Memoir of the Sears Foundation for Marine Research*, 1 (Part 9), pp. 1–7.  
<https://doi.org/10.2307/j.ctvbc0dm.4>
- Böhlke, J.E. (1951) *Meadia*, a new genus for the West Pacific dysommid eel, *Dysomma abyssale* Kamohara. *Stanford Ichthyological Bulletin*, 4 (1), 6.
- Böhlke, J.E. and Hubbs, C.L. (1951) *Dysommia rugosa*, an apodal fish from the North Atlantic, representing a distinct family. *Stanford Ichthyological Bulletin*, 4 (1), 7–10.
- Barnard, K.H. (1923) Diagnoses of new species of marine fishes from South African waters. *Annals of the South African Museum*, 13 (Pt 8, No. 14), 439–445.
- Causse, R., Biscoito, M. & Briand, P. (2005) First record of the deep-sea eel *Ilyophis saldanhai* (Synaphobranchidae, Anguilliformes) from the Pacific Ocean. *Cybium*, 29 (4), 413–416.
- Chen, J.T.-F. & Weng, H.T.-C. (1967) A review of the apodal fishes of Taiwan. *Biological Bulletin of Tunghai University, Ichthyology Series*, 6, 135–220. [also appeared as a separate, pp. 1–86]
- Chen, Y.-Y. & Mok, H.-K. (1995) *Dysomma opisthoproctus*, a new synaphobranchid eel (Pisces, Synaphobranchidae) from the northeastern coast of Taiwan. *Copeia*, 1995, 927–931.  
<https://doi.org/10.2307/1447041>
- Chen, Y.-Y. & Mok, H.-K. (2001) A new synaphobranchid eel, *Dysomma longirostrum* (Anguilliformes: Synaphobranchidae), from the northeastern coast of Taiwan. *Zoological Studies*, 40 (2), 79–83.
- Facciola, L. (1887) Intorno a due Lepadogastrini ed un nuovo *Nettastoma* del mare di Sicilia. *Il Naturalista Siciliano, Giornale di scienze naturali*, 6, 163–167.
- Fricke, R., Golani, D., Appelbaum-Golani, B. & Zajonz, U. (2018) *Dysomma alticorpus*, a new species of cutthroat eel from the Gulf of Aqaba, Red Sea (Teleostei: Synaphobranchidae). *Comptes Rendus Biologies*, 341 (2), 111–119.  
<https://doi.org/10.1016/j.crvi.2017.10.005>
- Gilbert, C.H. (1891) Descriptions of apodal fishes from the tropical Pacific. In: Scientific results of explorations by the U. S. Fish Commission steamer Albatross. *Proceedings of the United States National Museum*, 14 (856), 347–352.  
<https://doi.org/10.5479/si.00963801.14-856.347>
- Gill, T.N. (1893) Families and subfamilies of fishes. *Memoirs of the National Academy of Science*, 6 (6), 127–138.  
<https://doi.org/10.5962/bhl.part.6303>
- Ginsburg, I. (1951) The eels of the northern Gulf Coast of the United States and some related species. *Texas Journal of Science*, 3 (3), 431–485.
- Grassi, G.B. & Calandruccio, S. (1896) Sullo sviluppo dei murenoidi. *Atti della Accademia Nazionale dei Lincei*, 5 (1), 347–349.
- Greenwood, P.H., Rosen, D.E., Weitzman, S.H. & Myers, G.S. (1966) Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bulletin of the American Museum of Natural History*, 131 (4), 341–455.
- Ho, H.-C., Smith, D.G. & Tighe, K.A. (2015) Review of the arrowtooth eel genera *Dysomma* and *Dysommia* in Taiwan, with the description of a new species (Anguilliformes: Synaphobranchidae Ilyophinae). *Zootaxa*, 4060 (1), 86–104.  
<https://doi.org/10.11646/zootaxa.4060.1.12>
- Ho, H.-C. & Tighe, K.A. (2018) Three new species of the cutthroat eel genus *Dysomma*, with comments on the variation of *D. taiwanense* (Anguilliformes: Synaphobranchidae). *Zootaxa*, 4454 (1), 52–67.  
<https://doi.org/10.11646/zootaxa.4454.1.7>
- Jordan, D.S. & Davis, B.M. (1891) A preliminary review of the apodal fishes or eels inhabiting the waters of America and Europe. *Report of the Commissioner, United States Commission of Fish and Fisheries*, 16 (Art. 9), 581–677. [for 1888]
- Kamohara, T. (1938) *On the offshore bottom-fishes of Prov. Tosa, Shikoku, Japan*. Maruzen Kobushiki Kaisha, Tokyo, 86 pp.
- Karmovskaya, E.S. (2003) New records of synaphobranchid eels (Synaphobranchidae, Anguilliformes) collected off New Caledonia and adjacent regions, with description of a new species of *Atractodenchelys*. *Voprosy Ikhtiologii*, 43 (4), 437–446. [in Russian, English translation in *Journal of Ichthyology*, 43 (7), 491–500]
- Karmovskaya, E.S. & Parin, N.V. (1999) A new species of the genus *Ilyophis* (Synaphobranchidae, Anguilliformes) from the Broken Spur Hydrothermal Vent Field (MidAtlantic Submarine Ridge). *Voprosy Ikhtiologii*, 39 (3), 316–325. [in Russian, English translation in *Journal of Ichthyology*, 39 (5), 353–362]
- Karrer, C. (1983) Anguilliformes du Canal de Mozambique (Pisces, Teleostei). *Faune Tropicale*, 23, 1–116.
- Karrer, C. & Klauswitz, W. (1982) Tiefenwasser- und Tiefseefische aus dem Roten Meer. II. *Dysomma fuscoventralis* n. sp., ein Tiefsee-Aal aus dem zentralen Roten Meer (Teleostei: Anguilliformes: Synaphobranchidae: Dysommiae).

*Senckenbergiana Biologica*, 62 (4/6), 199–203. [1981]

- Leitner, A.B., Durden, J.M., Smith, C.R., Klingberg, E.D. & Drazen, J.C. (2021a) Synphobranchid eel swarms on abyssal seamounts: largest aggregation of fishes ever observed at abyssal depths. *Deep Sea Research Part I: Oceanographic Research Papers*, 167, 103423.  
<https://doi.org/10.1016/j.dsr.2020.103423>
- Leitner, A.B., Drazen, J.C. & Smith, C.R. (2021b) Testing the seamount refuge hypothesis for predators and scavengers in the western Clarion-Clipperton Zone. *Frontiers in Marine Science*, 8, 636305.  
<https://doi.org/10.3389/fmars.2021.636305>
- Lin, S.-Y. (1933) A new genus and three new species of marine fish from Hainan Island. *Lingnan Science Journal, Canton*, 12 (1), 93–96.
- Matsubara, K. (1936) Studies on the deep-sea fishes of Japan. I. On a new apodal fish, *Dysomma japonicus*, with an emendation of the genus *Dysomma*. *Zoological Magazine Tokyo*, 48 (11), 960–962.
- Merrett, N.R. & Saldanha, L. (1985) Aspects of the morphology and ecology of some unusual deep-sea eels (Synphobranchidae, Derichthyidae and Nettastomatidae) from the eastern North Atlantic. *Journal of Fish Biology*, 27, 719–747.  
<https://doi.org/10.1111/j.1095-8649.1985.tb03216.x>
- Mok, H.-K., Lee, C.-Y. & Chan, H.-J. (1991) *Meadia roseni*, a new synphobranchid eel from the coast of Taiwan (Anguilloidea: Synphobranchidae). *Bulletin of Marine Science*, 48, 39–45.
- Norman, J.R. (1939) Fishes. The John Murray Expedition 1933–34. *Scientific Reports, John Murray Expedition*, 7 (1), 1–116.
- Prokofiev, A.M. (2019) Three new eels of the genus *Dysomma* Alcock, 1889 from off Phuket Island, Thailand (Teleostei: Anguilliformes: Synphobranchidae). *Munis Entomology & Zoology*, 14 (2), 317–325.
- Robins, C.H. & Robins, C.R. (1970) The eel family Dysommidae (including Dysommidae and Nettastomatidae), its osteology and composition, including a new genus and species. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 127, 249–280.
- Robins, C.H. & Robins, C.R. (1976) New genera and species of dysommidae and synphobranchine eels (Synphobranchidae) with an analysis of the Dysommidae. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 122, 293–335.
- Robins, C.H. & Robins, C.R. (1989) Family Synphobranchidae. In: Böhlke, E.B. (Ed.), *Fishes of the Western North Atlantic. Memoir of the Sears Foundation for Marine Research*, 1 (Part 9), pp. 207–253.  
<https://doi.org/10.2307/j.ctvbc0dm.12>
- Saldanha, L. & Merrett, N.R. (1982) A new species of the deep-sea eel genus *Ilyophis* Gilbert (Synphobranchidae) from the eastern North Atlantic, with comments on its ecology and intrafamilial relationships. *Journal of Fish Biology*, 21, 623–636.  
<https://doi.org/10.1111/j.1095-8649.1982.tb02866.x>
- Saruwatari, T., López, J.A. & Pietsch, T.W. (1997) Cyanine Blue: a versatile and harmless stain for specimen observation. *Copeia*, 1997 (4), 840–841.  
<https://doi.org/10.2307/1447302>
- Schmidt, J. (1913) On the identification of muraenoid larvae in their early ("prelptocephaline") stages. *Meddelelser fra Kommissionen for havundersøgelser, Serie Fiskeri*, 4 (2), 1–14.
- Smith, D.G. (1989) Family Chlopsidae. In: Böhlke, E.B. (Ed.), *Fishes of the Western North Atlantic. Memoir of the Sears Foundation for Marine Research*, 1 (Part 9), pp. 72–97  
<https://doi.org/10.2307/j.ctvbc0dm.9>
- Smith, D.G. (1999) Synphobranchidae. In: Carpenter, K.E. & Niem, V.H. (Eds.), *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Vol. 3. Batoid fishes, chimaeras and bony fishes. Part 1 (Elopidae to Linophrynidae)*. FAO, Rome, pp. 1658–1661
- Sulak, K.J. & Shcherbachev, Y.N. (1997) Zoogeography and systematics of six deep-living genera of synphobranchid eels, with a key to taxa and description of two new species of *Ilyophis*. *Bulletin of Marine Science*, 60 (3), 1158–1194.
- Tashiro, F. & Chen, W.-J. (2022) *Ilyophis singularis* (Synphobranchidae; Ilyophinae), a new deep-sea eel from the South China Sea. *Ichthyological Research*, 70, 332–336. [first published online, 18 August 2022]  
<https://doi.org/10.1007/s10228-022-00887-w>
- Tighe, K.A., Ho, H.-C. & Hatooka, K. (2018) A new species of the genus *Dysommia* (Teleostei: Anguilliformes: Synphobranchidae: Ilyophinae) from the Western Pacific. *Zootaxa*, 4454 (1), 43–51.  
<https://doi.org/10.11646/zootaxa.4454.1.6>
- Vo, Q.V. & Ho, H.-C. (2020) A new species of *Atractodenchelys* (Synphobranchidae, Anguilliformes) from Vietnam. *Zootaxa*, 4742 (3), 588–594.  
<https://doi.org/10.11646/zootaxa.4742.3.12>
- Vo, Q.V., Ho, H.-C., Dao, H.V. & Tran, H.H.T. (2021) A new arrowtooth eel of genus *Meadia* (Synphobranchidae: Ilyophinae) from Vietnam, South China Sea. *Zootaxa*, 4952 (1), 181–191.  
<https://doi.org/10.11646/zootaxa.4952.1.11>
- Vo, Q.V., Ho, H.-C., Dao, H.V. & Tran, T.C. (2024) New species of the eel genera *Dysomma* and *Dysommia* from Vietnam, South China Sea (Family Synphobranchidae). *Journal of Fish Biology*, 104 (4), 1067–1078 [first published on-line, 4 January 2024]  
<https://doi.org/10.1111/jfb.15638>
- Whitley, G.P. (1951) Studies in ichthyology. No. 15. *Records of the Australian Museum*, 22 (4), 389–408.