Abstract.---Nine new species of hagfishes (Myxinidae, Myxine) from the Pacific and Atlantic coasts of North and South America are described and a key is offered to the new world hagfishes. New data are presented for Myzine circifrons from the eastern Pacific Ocean, M. limosa from the northwestern Atlantic Ocean, and M. affinis and M. australis from in and near the Straits of Magellan. Myxine limosa is removed from the synonymy of M. glutinosa. The nine new species occur as follows: M. hubbsi along the Pacific coast from San Francisco, California, to Valparaiso, Chile; M. hubbsoides and M. pequenoi near Valdivia, Chile; M. mccoskeri and M. robinsi in the southern portion of the Caribbean Sea: M. fernholmi, M. knappi, and M. dorsum near the Falkland Islands, and M. debueni in the Straits of Magellan. Myxine mccoskeri and M. pequenoi are regarded as dwarfed, containing nearly mature eggs or testes at total lengths of 230 and 175 mm, respectively. Hermaphroditism is often found in individuals of M. hubbsi, M. limosa, and M. affinis.

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# Review of new world hagfishes of the genus *Myxine* (Agnatha, Myxinidae) with descriptions of nine new species

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Hagfishes (slime eels) are cartilaginous, eel-like, abundant bottomdwelling scavengers occurring at depths ranging from a few to at least 2,400 meters. Myxine is one of the six recognized genera in the "agnathan" family Myxinidae (Nelson, 1994). In the new world it comprises eight species in the Atlantic Ocean and six in the Pacific (references in this study); species occurring in the Straits of Magellan also may occur in either ocean. The genus Myxine, which presently contains 19 species including those in this study, is characterized principally by all the efferent gill pouch ducts discharging into a single aperture on each side, the left being confluent with the pharyngocutaneous duct. This character is shared by the genera Neomyxine Richardson, 1953, and Nemamyxine Richardson, 1958. Neomyxine is further characterized by having paired lateral finfolds in the prebranchial region, as well as the usual ventral finfold posterior to the gill apertures. In *Nemamyxine*, the body is extremely slender and the ventral finfold extends far forward nearly to the anteriormost prebranchial slime pores. In all other myxinids the ventral finfold does not extend anterior to the pharyngocutaneous duct. Head grooves ("lateral lines" of earlier authors) are lacking in genus

Myxine as are the external eyespots common in genus Eptatretus (McMillan and Wisner, 1984). Hermaphroditism does not occur in our material of M. circifrons but is not uncommon in M. limosa, M. affinis, M. australis, and M. hubbsi and occurs in two of the three specimens of M. hubbsoides. The remaining new species have too few specimens to state with certainty whether or not hermaphroditism occurs among them. Great variation in developmental stages of eggs occurs among specimens of the same length and possibly age, which supports a widely held belief that hagfishes spawn throughout the year. As eggs mature, the polar caps enlarge into dome-like structures containing anchor filaments that are connected to the eggs when they are extruded. With one exception (a female M. limosa discussed below), eggs of all specimens examined here were not fully mature; polar caps were not visible, nor were they still encapsulated.

This study of new world hagfishes, the latest by us in a series on the family Myxinidae begun by Carl L. Hubbs (deceased), includes all 14 known species of *Myxine* from the Pacific and Atlantic coasts of North and South America. We have added old world *M. glutinosa* to all tables for comparison with the closely related *M. limosa*. Of the other four known species, M. ios from the eastern Atlantic and M. capensis from South Africa are compared briefly with the new world species M. pequenoi. Both M. garmani, and M. paucidens Regan, 1913 are known only from Japan and are not closely related to any new world species. The number of new species (nine) from near the coasts only, suggests a need for further and more intensive collecting throughout the world.

#### Methods

Methods of counting and measuring generally follow those of Fernholm and Hubbs (1981) and McMillan and Wisner (1984). All measurements are in mm, and body proportions (Table 1) are in percent of total length. Features used in measuring and counting are shown in Figures 1 and 2, and geographic distribution in Figure 3. Counts of slime pores (Tables 2–5) and unicusps (Table 6) represent the left side only because we have found no significant differences between the left and right sides. Occasionally one extra gill pouch occurs, usually on one side only and much smaller than normal; one less pouch rarely occurs on either side. The one to three slime pores which may occur over the pharyngocutaneous duct are included in the prebranchial pore count. In all species of Myxine only two fused cusps (a multicusp) occur on the posterior set of cusps (inner row of Fernholm and Hubbs, 1981) in contrast to either two or three on the anterior set. This latter character is used to group species (Tables 1-7). Some terms have appeared previously in myxinid accounts without clear definition. We offer precise definition of these and some new terms used in this study: rostrum, rounded to pointed, fleshy extension lying over the nasal orifice between the

anteriormost pairs of barbels; head, from tip of rostrum to a vertical from wrinkled tissue below the mouth; face, ventral aspect of head; mouth, the elongate slit in face which opens to permit extrusion of cusps for feeding (Fig. 2A); multicusp, a unit of two or three cusps (teeth of other authors), fused together at bases (Fig. 2B); unicusp, a single unfused cusp (Fig. 2C); pores (slime pores), the small openings along the ventral aspect of body which emit mucus; gill aperture (GA), the opening through which water discharges to the exterior after passing through the gill pouches; PCD, the external opening of the pharyngocutaneous duct, always on the left side and usually confluent with the left gill aperture in Myxine (or posteriormost GA in Eptatretus); ventral finfold (VFF), a band of thin, fleshy tissue extending along ventral midline of body between PCD and origin of cloaca (Fig. 1); cloaca, the slit-like ventral opening anterior to tail through which body wastes and sexual products discharge; and caudal finfold (CFF), the band of thin fleshy tissue extending around tail, ending dorsally about over origin of cloaca (Fig. 1).

Colors are determined after scraping away the coating of coagulated slime (mucus). Although given in the descriptions, color is subjective and may change greatly with preservation; therefore, the use of counts is preferred as a more distinguishing character. Because eggs are similar in all species, we have not used them as a species character. They vary widely in length and diameter and in developmental stages, ranging from tiny to nearly mature in females of the same length. Accurate measurement of diameter is hindered in eggs deformed because of crowding in life or during preservation; many are somewhat flattened and diameters may vary as much as 1.5 mm in the same specimen. We have not provided photographs or drawings of individual species since



there are no distinguishing external features other than those characters given in the key. A list of the materials examined and of the collections where these materials were obtained follows the Acknowledgment section. Institutional abbreviations are listed as in Leviton, et al. (1985).

## Key to new world hagfishes (Genus Myxine)

	A 3-cusp multicusp on anterior set, a 2-cusp multicusp on posterior set of cusps
	Gill pouches 6, rarely 7       3         Gill pouches 5       4
3b	VFF well developed, 3-7 mm high, mounted on thick triangular base extending from the ventral surface; last few prebranchial pores in an uneven line, resembling the letter W; total pores 112-121
	Anterior unicusps 6-9; total cusps 36-48; total pores 77-92; color light brown, often         lighter dorsally than ventrally
	Anterior unicusps 11–13; total cusps 56–58; total pores 92–100; VFF usually low (3–6 mm); head and barbels pale
	Gill pouches 7; anterior unicusps 4; posterior unicusps 5–6; total cusps 26–28
7a 7b	CFF extending forward dorsally 2-3 times tail length; total pores 108-109; VFF low, (3-5 mm)
8a 8b	Prominent whitish band on ventral surface; VFF usually well developed
	Ventral whitish band not extending above line of trunk pores, but often extending to face; color dark reddish-brown; total cusps 38-46
	VFF moderately to well developed
	Color bluish gray to brownish, head pale; whitish mid-dorsal narrow stripe extending forward a variable distance; total cusps 42–48; total pores 101–119
	VFF nearly vestigial, 1–3 mm high; color pinkish to bluish; head pale; prebranchial pores31–32; trunk pores 61–65; total pores 108–110VFF vestigial; color brown to purplish-black; prebranchial pores 18–31; trunk pores 58–72;total pores 91–11613
	Color light to dark purplish-brown; occasional pale blotches ventrally; total pores 101-109;VFF variably vestigial to 8 mm highColor dark brown to blackish; no pale blotches ventrally; head only slightly pale; total pores111-116; VFF vestigial, intermittently absentM. hubbsoides

## **Systematics**

#### Myxine circifrons Garman, 1899

Myxine circifrons Garman, 1899: 344 "Albatross Station 3395; 7°30'36"N, 78°W; 730 fm (1,336 m) temperature  $38.5^{\circ}F$ ; bottom rocky."

**Diagnosis** A 3-cusp multicusp on anterior sets of cusps; five gill pouches each side; color blackish to dark reddish-brown, anteriormost portion of head pale.

**Description** Counts and proportions are given in Tables 1–7. Body robust, slightly deeper than wide; snout bluntly pointed, rostrum short, variably triangular to bluntly rounded; cusps short, stout; anterior multicusps bulbous at bases, the free tips about equal in length to bulbous portion; tail length about 13% of TL, its depth about 40% of its length; VFF usually well developed, but may be vestigial, ranging in height from 1 to 12 mm, averaging about 5 mm; CFF high, extending around tail to about over cloaca, thickened dorsally; body color dark, gravishblack to reddish-brown; anterior portion of head paler, often whitish to near vertical from margin of face, occasionally extending into the prebranchial region; barbels color of head; VFF and CFF same color as body, without pale margins; GA and slime pores often with narrow pale margins; total cusps 43-56; total slime pores 80–102; numbers of large eggs (20 mm and longer) range from 15 to 18 in females of 435 mm TL, largest egg  $28 \times 7$  mm.

**Distribution** From near San Francisco, California, to north-central Chile at depths of about 700 to 1,860



(A) sketch of ventral aspect of a myxinid head, identifying the terms used in the text: (B) and (C), sketches of a 3cusp and a 2-cusp multicusp, with two adjacent unicusps. m (Fig. 3). We find no significant differences in counts or proportions throughout this extensive range of about 11,000 kilometers.

**Comments** Sex ratios in our material are equal off southern California (n=220) but unequal near the mouth of the Gulf of California (n=136), 66% female to 34% male, and Costa Rica to northern Chile (n=54), 59% female to 41% male. We find no hermaphrodit-



Areas of occurrence of new world species of Myxine: 1 = M. circifrons, from near San Francisco, California, to north-central Chile; 2 = M. hubbsi, from near San Francisco, California, to near Valparaiso, Chile; 3 = M. hubbsoides and 4 = M. pequenoi, off south-central Chile; 5 = M. fernholmi, from near Valdivia, Chile to Falkland Islands, S.E. Atlantic Ocean; 6 = M. dorsum and 7 = M. debueni, Straits of Magellan; 8 = M. australis, principally in Straits of Magellan; 10 = M. knappi, near the Falkland Islands; 11 = M. mccoskeri, 12 = M. robinsi, and 13 = M. mcmillanae, southern Caribbean Sea; 14 = M. limosa, Davis Strait, Greenland, southerly to eastern portion of the Gulf of Mexico.

ism in 320 specimens exceeding 350 mm TL, a minimum length arbitrarily chosen as offering reliable sex determination.

#### Myxine mccoskeri new species

**Holotype** SIO70-363, female, 201 mm, taken at 09°39'N, 78°60'W, 530-560 m, 1 October 1970.

**Paratypes** SIO70-363, 2 (117, 170 mm), taken with the holotype; SIO90-117, 1 (235 mm), 11°46'N, 67°05'W, 1, 100–1,174 m (formerly UMML 29269); USNM 325212, 2 (170, 235 mm), 11°30'N, 72°26'W, 530–567 m (formerly UMML 28722); CAS 79537, 2 (170, 235 mm), 12°13'N, 75°50'W, depth unknown (formerly UMML 29884); MCZ 48809, 2 (218, 264 mm), 11°35'N, 62°52'W, 512–547 m; MCZ 41634, 1 (254 mm), 11°35'N, 62°59'N, 439–476 m.

**Diagnosis** A 3-cusp multicusp on anterior sets of cusps; five gill pouches each side; VFF weakly developed, often nearly vestigial, 0–5 mm high; color dark brown, often lighter dorsally than ventrally; a dwarf species, mature at about 300 mm TL.

**Description** Counts and proportions are given in Tables 1–7. Body slender, slightly deeper than wide, its width about 75% of its depth; tail narrow, its length about 15% of TL, its depth about 33% of its length. VFF usually low, ranging in height from 0-5 mm, average 2 mm; CFF prominent, its margins thin, the internal supporting rays visible; snout rather sharply pointed, rostrum elongate, bluntly pointed; cusps long, slender, sharp, the bases of multicusps slightly bulbous; body variably pale to medium or dark brown, the head and ventral aspects anterior to GA lighter than body; posterior to GA the ventral aspect is notably darker toward end of tail, a pale band extends dorsally to over the cloaca, the general aspect being reverse countershading; VFF and CFF color of body, usually without, or with faintly expressed, pale margins; barbels very slightly or not at all pigmented; GA with narrow pale margins, slime pores without; total slime pores 77-92; total cusps 36-48. A 264-mm-TL paratype (MCZ 48809) contains only four large eggs, each about 18×7 mm; in addition, two other females (218, 222 mm) contain four and five eggs, about 15×5 mm. We consider this species dwarfed because of the short length of females with such large eggs.

**Etymology** We name this species for John E. McCosker, Director, Steinhart Aquarium, San Francisco, for his work on Caribbean and Panamanian fishes, and for making the first specimens of this species available to us. **Distribution** Known only from the southern Caribbean Sea (Fig. 3).

**Comments** Shimizu (1983) reported as *Myxine* sp. three specimens (273–320 mm TL) from off Suriname at 310 m, with 3-cusp multicusps on anterior sets of cusps, 38 total cusps, and 87–90 total slime pores; number of gill pouches and sexual maturity not stated. Color was described as "Body color white on snout, gradually becoming blackish, and uniformly black behind posterior half of head." The cusp and slime pore counts agree well with *M. mccoskeri*; however, the white snout as described and shown in the color photo from Shimizu, is whiter than those on our specimens of *M. mccoskeri*. This feature and the blackish body are more like those of *M. robinsi* (described below); however, the latter has more total cusps (56–58) and total pores (94–104).

#### Myxine robinsi new species

Holotype SIO90-149, ripe female, 475 mm TL, taken at 11°37'N, 60°50'W, in a 40-ft otter trawl between 783 and 1281 m (formerly UMML 29270, date of capture not recorded).

**Paratypes** SIO90-149, 1 (510 mm) taken with the holotype; USNM 325213, 1 (540 mm); 11°37'N, 60°59'W (formerly UMML 29877); MCZ 101239, 1 (460 mm), 10°03'N, 7620'W, (formerly UMML 22807), 675–966 fm [1,235–1,768 m].

**Diagnosis** A 3-cusp multicusp on anterior set of cusps; five gill pouches each side; whitish on head and continuing to first few prebranchial pores, and light dorsally to about over GA; body light to medium brown.

**Description** Counts and proportions are given in Tables 1–7. Body rather robust, slightly deeper than wide; tail length about 13% of TL, its depth about 38% of its length; VFF moderately well developed. 3-6 mm high; CFF prominent, extending around tail to about over cloacal origin, thickening dorsally; rostrum variably rounded to bluntly conical; anterior unicusps long, slender, sharp, curved near tips; bases of anterior multicusps slightly bulbous; color light to medium brown; head whitish continuing to first few prebranchial pores; a decreasingly paler area, often blotchy, extends posteriorly along dorsal surface and often laterally to near GA; slime pores and GA with no or very pale margins; VFF and CFF color of body, without pale margins. One female 475 mm TL contains six large eggs, 29–31 mm long by 11–12 mm wide, arranged in a single row.

**Etymology** We name this new species for both C. Richard and Catherine Robins, University of Miami Rosenstiel School of Marine and Atmospheric Sciences, for their works on the marine fauna of the tropical western Atlantic, particularly the Caribbean area.

**Distribution** Known only from the type material from the southern Caribbean Sea (Fig. 3).

**Discussion** Myxine circifrons, M. mccoskeri, and M. robinsi may be closely related. Each has a 3-cusp multicusp on the anterior sets of cusps and are the only species of *Myxine* known to have only five gill pouches each side. Counts and most body proportions overlap, which invites speculation that prior to the permanent establishment of the Panamanian land barrier, M. circifrons may have occupied the Caribbean area. If true, M. robinsi evolved primarily to a lighter color and M. mccoskeri to a dwarfed state, with fewer anterior unicusps, trunk and total slime pores, as well as a strikingly different color pattern. All counts for M. robinsi are similar to those for M. circifrons. However, despite these similarities, we hold M. mccoskeri and M. robinsi to be specifically distinct from M. circifrons. Although Myxine mcmillanae is also from the same area (see below). we do not consider it related because it has a 2-cusp multicusp on both anterior and posterior sets of cusps and six gill pouches rather than five. One other species with 3-cusp multicusps on anterior row is M. garmani, known only from Japan and distinct from the three species described above that have six gill pouches rather than five and a wide geographical separation.

#### Myxine fernholmi new species

**Holotype** ISH 257-1978, female, 555 mm TL, taken at 49°29'S, 58°56'W, 200-ft bottom trawl, 400 m, 6 June 1968.

**Paratypes** SIO90-138, 1 (790 mm), 53°00'S, 64°00'W (formerly ISH 108–1971); SIO90-139, 1 (575 mm), 33°39'S, 72°09'W, 1,170–1,480 m; ZIL 791–966, 1 (665 mm), 54°35'S, 57°30'W, 135–145 m.

**Diagnosis** A 3-cusp multicusp on anterior sets of cusps, total cusps 34-37; six gill pouches each side; tail length 10% or less of TL; last four prebranchial pores forming an irregular line which resembles the letter W.

**Description** Counts and proportions are given in Tables 1–7. Body moderately robust, slightly deeper than wide; tail short, 8–10% of TL, its depth about half its length; VFF extending 3–7 mm, and mount-

ed on a prominent fleshy triangular extension along the ventral surface; CFF thin, high, extending around tail to about over cloacal origin; reddish supporting rays visible on most specimens; rostrum triangular, the tip slightly rounded; unicusps long, slender, sharp, slightly curved at tips; bases on anterior multicusps bulbous, posterior multicusps not bulbous; last four prebranchial slime pores anterior to GA in an irregular line forming a pattern resembling the letter W; all slime pores tiny; tail pores 7–9, total slime pores 112–121; color variably pale, yellowish, or light bluish-pink; GA with prominent pale margins, slime pores with less prominent; females with only immature eggs, 2–8 mm long.

**Etymology** We name this species for Bo Fernholm, Museum of Natural History, Stockholm, for his work on the physiology, anatomy, and systematics of Myxinidae.

**Distribution** Known only from the type material taken off south- central Chile and near the Falkland Islands, southwestern Atlantic Ocean (Fig. 3).

#### Myxine debueni new species

Holotype SIO90-140, male, 570 mm TL, taken at 53°39'S, 70°14'W, 300 m, 27 April 1970, Straits of Magellan.

**Paratype** SIO90-140, male 545 mm TL, taken with the holotype.

**Diagnosis** A 3-cusp multicusp on anterior sets of cusps; six gill pouches each side; VFF absent; tail short, 8–9% of TL; rostrum triangular, the tip pointed; prebranchial slime pores in a straight line anterior to GA.

**Description** Counts and proportions are given in Tables 1–7. Body slender, nearly cylindrical; tail short, 8-9% of TL; depth about 40% of length; VFF absent; CFF prominent, thickened at margin, extending around tail to over cloacal origin; head narrow, pointed, rostrum triangular, the tip pointed; unicusps long, slender, sharp, slightly curved; bases of multicusps not bulbous; prebranchial slime pores in a straight line anterior to GA. The two specimens appear to have been "dry-burned" from insufficient preservative, causing the skin to harden and become a dark reddish-brown color on damaged portion. mostly dorsally. Undamaged part of body is pale bluish-gray anterior to GA; posteriorly a pale pinkish color continues to tail; CFF with narrow pale margins, slime pores with very narrow ones.

**Etymology** We name this species for Fernando DeBuen in recognition of his extensive work on fishes of South America.

**Distribution** Known only from the two specimens from the Straits of Magellan (Fig. 3).

**Comments** This species and M. fernholmi (described above) are similar in that each has a tail length of 10% or less of TL and a somewhat longer trunk length than other species treated here. Each has a 3-cusp multicusp on the anterior sets of cusps; they differ primarily in M. debueni lacking a VFF (prominent in M. fernholmi); also, the last four prebranchial pores lie in a straight line not forming the letter W.

#### Myxine hubbsi new species.

**Synonymy** Myxine circifrons Chirichigno, 1968:383 (description; a 2-cusp multicusp on anterior set of cusps; northern Peru to Gulf of Panama).

**Holotype** SIO65-452, female, 515 mm TL, taken at 32°38'N, 118°08°4'W, 25 September 1965, bottom trap, 2,009 m.

**Paratypes** SIO65-452, 82 (209–522 mm), taken with the holotype; SIO68-60, 36 (120-484 mm), 23°07'N, 109°16'W, 1,830 m; SIO68-61, 2 (350, 400 mm), 23°06'N, 109°13'W, 2,196 m; SIO73-293, 16 (230-480 mm), 09°24'N, 85°06'W, 1,107 m; SIO92-114, 7 (260-450 mm), 03°41'S, 81°36'W, 2,440 m; SIO92-115, 7 (290-420 mm), 08°26'S, 80°36'W, 1,830-1,930 m; SIO72-176, 8 (326-473 mm), 21°37'S, 70°55'W, 2,114 m; CAS 79536, 10 (280-445 mm), taken with the holotype, CAS 77360, 3 (322-410 mm), 31°00'N, 118°06'W, 1,739 m (formerly SIO65-451); LACM 45786-1, 18 (222-456 mm), 32°40'N, 118°12'W, 1,742 m (formerly SIO65-451); USNM 325214, 16 (258-486 mm), 32°39'N, 118°11'W, 1,830 m, (formerly SIO68-676); MCZ 101240, 6 (275-460 mm), 32°41'N, 118°12'W, 1,823 m.

**Diagnosis** A 2-cusp multicusp on both anterior and posterior sets of cusps; six gill pouches each side (very rarely 5 or 7); body nearly cylindrical; VFF low to vestigial; rostrum rounded; color light to dark brownish-purple to nearly black; head and barbels pale.

**Description** Counts and proportions are given in Tables 1–7. Body nearly cylindrical, its width narrowing posteriorly; tail length about 10% of TL, its depth about 38% of its length; VFF weakly developed, often vestigial or absent. Of 205 specimens,

155 (75%), VFF ranges in height between 3 and 4 mm, and between 6 and 8 mm in only 4 specimens; CFF well developed, often thick at margin, ending over cloacal origin; head bluntly pointed, rostrum short, rounded; multicusps small, short, bulbous at bases; unicusps slender, sharp; body color variably light to dark purplish-black, rarely with pale blotches; head usually pale anteriorly; all barbels pale; VFF and CFF color of body; GA with narrow pale margins; slime pores only occasionally with pale margins. From 7 to 15 large eggs, ranging between 17×6 and 24×8 mm, occur in eight females (415–450 mm TL); all other females have small eggs. The largest number of eggs (15) occur in a female of 440 mm TL.

**Etymology** We name this species for our deceased friend and mentor Carl L. Hubbs, primarily for his foresight in instigating the worldwide study on hagfishes.

**Distribution** Known from  $33^{\circ}N$  to  $34^{\circ}S$ , at depths from about 1,100 to 2,440 m (Fig. 3). As in *M. circifrons* (discussed above), we find no significant differences in counts or proportions over this range of about 9,000 km.

**Comments** The sex ratio in our material is extremely unbalanced; of 150 specimens, 114 (76%) are female, 35 (23%) hermaphroditic, and 6 (0.4%) male. Although there were few large eggs (7–15), no eggs were lost since no specimens were opened prior to our examination. Bichromatism is rare; only five of 36 specimens from near Cape San Lucas, Baja California, Mexico (SIO68-60), are notably bichromatic with colors generally bluish-purple ventrally and laterally, the dorsal areas pinkish. Most bodies are pale anterior to GA, with occasional small to large bluish blotches; similar bichromatism occurs in five of nine specimens off San Diego, California.

#### Myxine hubbsoides new species

**Holotype** SIO90-143, hermaphroditic female, 826 mm TL, taken at 34°00'S, 72°14'W, 880 m, formerly MNHMC 80047).

**Paratypes** SIO90-141, hermaphroditic female, 702 mm TL, 34°21'S, 78°18'W, 820 m (formerly MNHMC 80043); SIO90-142, female, 651 mm TL, 34°14'S, 72°21'W, 735 m (formerly MNHMC 80044).

**Diagnosis** A 2-cusp multicusp on both the anterior and posterior sets of cusps; six gill pouches each side; VFF vestigial or nearly so, often absent; total pores 111-116.

**Description** Counts and proportions are given in Tables 1-7. Body slender, cylindrical; tail length about 12% of TL, its depth about 35% of its length; VFF very low, portions intermittently absent; CFF variably well developed, ranging between thick at cloaca and around tail to thin dorsally, ending about over cloaca; rostrum broadly rounded at tip; all cusps in anterior sets bulbous at bases, those of posterior sets not bulbous; all unicusps straight or only slightly curved; body color blackish-brown with no pale areas or spots; head only slightly paler; face pale to slightly past mouth; barbels almost entirely pale; GA and slime pores with very narrow pale margins. The 702-mm paratype (SIO90-141) has 49 dark brown eggs as large as 17×5 mm, with many tiny round eggs scattered among them; the holotype has many eggs to about 11 mm, but was not opened fully for count; well-developed testicular tissue present posterior to eggs; the 651-mm paratype is spent or immature and has very few tiny eggs present.

**Etymology** The name *hubbsoides* refers to the similarity to *Myxine hubbsi* described above.

**Distribution** Known only from off central Chile between Coquimbo and Punta Topocalma (Fig. 3).

#### Myxine pequenoi new species.

**Holotype** SIO90-145, 183 mm TL, maturing female, taken at  $41^{\circ}29$ 'S,  $74^{\circ}09$ 'W, 185 m.

**Paratype** SIO90-146, 175 mm TL, mature male, taken at 40°44'S, 74°14'W, 215 m.

**Diagnosis** A 2-cusp multicusp on both anterior and posterior sets of cusps; total cusps 26–28; seven gill pouches each side; VFF nearly vestigial; total slime pores 81–85; a dwarfed species.

**Description** Counts and proportions are given in Tables 1–7. Body slender, slightly deeper than wide; tail about 12% of TL, its depth about 30% of its length; VFF very low; CFF thick at margin, thinner around tail, ending well behind a vertical from origin of cloaca; rostrum short, sharply pointed; barbels small, pale; all cusps have bulbous bases, with sharp, slender points; seven gill pouches; head and body medium brown, lighter ventrally; GA and slime pores with narrow pale margins; VFF and CFF with pale margins; holotype with 10 maturing eggs to 10×4 mm; most eggs in a single row; paratype with well-developed testes. We regard this species as dwarfed because of the advanced sexual development of these two small specimens, 175 and 183 mm TL (even smaller than *M. mccoskeri* described above).

**Etymology** We name this species for German Pequeño R., Instituto de Zoologia, Universidad Austral de Chile, Valdivia, for his work on the fishes of Chile and for making specimens available to us.

**Distribution** Known only from the type specimens taken south of Valdivia, Chile, about 41°S, 74°W (Fig. 3).

**Discussion** Within the genus *Myxine*, only three species have seven gill pouches (except rarely in M. hubbsi and M. mcmillanae). These three are M. capensis Regan, 1913, from off South Africa (22° to 25°S, 16°17°W), M. ios Fernholm, 1981, from southwest of Ireland (40° to 41°N, 12° to 13°W) and M. pequenoi (described above) from off Chile. Proportions of the three species are quite similar despite the dwarfed condition of M. pequenoi, but significant differences occur in certain counts. Those for M. pequenoi are given first followed in parentheses by those for M. capensis and M. ios. Total cusps 26-28 (36-43, 44-49); prebranchial slime pores 22-23 (26-28-28-36); total slime pores 81-88 (92-110, 103-117). Body colors are similar in all three species except that *M. ios* from near Ireland has a white head; the others do not. Myxine paucidens (known only from Japan) has the same number of unicusps as M. pequenoi (4 on anterior and 5 on posterior sets of cusps) but is distinctly different with six gill pouches, as well as having wide geographical separation.

#### Myxine dorsum new species

Holotype ISH 99-1971, 440 mm female, taken at 54°25'S, 59°42'W, 140-ft bottom trawl, 112 m.

**Paratype** SIO92-21 (formerly ZIN 722–966), 490 mm female, taken at 49°16'S, 57°02'W, bottom trawl, 630–650 m.

**Diagnosis** A 2-cusp multicusp on both the anterior and posterior sets of cusps; six gill pouches; VFF low, 2.0 mm high; CFF extending forward dorsally as a ridge beyond a vertical from cloacal origin three to four times the length of tail; total slime pores 108– 113; color light pinkish-brown.

**Description** Counts and proportions are given in Tables 1–7. Body moderately slender, slightly deeper than wide; tail about 13% of TL, its depth 40% of its length; VFF low, 2.0 mm, mounted on a prominent fleshy narrow triangular base extending 4–7 mm from body and defined by an intermittent suture-like line below the rows of pores; a structure similar to that of *M. fernholmi* (described above) but much less strongly developed; CFF wide, thick ventrally, thin-

ning around tail and dorsally; prominent dorsal ridge extending anteriorly as a finfold to 4.3 times tail length in holotype and 3.2 times in paratype; body light pinkish-brown, the original label states "lifelong color pink"; VFF and CFF pale; GA and slime pores with narrow pale margins; holotype with 9 welldeveloped eggs to  $19\times5$  mm; paratype with 8 similar eggs to  $18\times6$  mm; eggs widely and irregularly spaced; only a few paired.

**Etymology** The name *dorsum*, from Latin meaning "ridge," refers to the far forward extension of the CFF dorsally as a ridge to three or four times length of tail.

**Distribution** Southwestern Atlantic Ocean between 112 and 650 m (Fig. 3).

**Discussion** Although the two specimens are slightly wrinkled and hardened, the integuments cannot be stretched laterally and down far enough to eliminate the dorsal ridges. In addition, a suture-like line parallels the base of these ridges, ending at the point where downward stretching fails to eliminate them. This feature is not previously reported in species of *Myxine;* in all others, CFF extends dorsally little more than half a tail length forward of a vertical from cloacal origin.

#### Myxine knappi new species

Holotype SIO90-144, 565-mm female, taken at 49°16'S, 57°02'W, 24 March 1965, 630-650 m.

**Paratypes** SIO90-144, 2 (510,560 mm TL) taken with the holotype.

**Diagnosis** A 2-cusp multicusp on both the anterior and posterior sets of cusps; six gill pouches each side; tail slime pores 11–14; rostrum broadly rounded; VFF nearly vestigial; color pinkish-blue, head and barbels slightly paler than body; total slime pores 116–123.

**Description** Counts and proportions are given in Tables 1–7. Body slender, slightly deeper than wide; tail length about 13% of TL, its depth about 33% of its length; VFF low and variably developed; in the holotype it is 2.5 to 3.5 mm high; in a paratype (510 mm TL) it is less than 1.0 mm high to about 60 mm anterior to cloaca where it increases to 3.0 mm high, continuing to cloaca; CFF prominent around tail, thickened ventrally; in the 510 mm paratype CFF extends forward of a vertical from cloacal origin about half the tail length; rostrum broadly rounded at tip; cusps robust, bluntly pointed, bases of multicusps slightly bulbous; 1–2 slime pores over GA; body color pinkish to bluish, one paratype more pink than blue; head pale to about over mouth; barbels pale; VFF entirely pale; CFF color of body, without pale margin; GA and slime pores with narrow pale margins; a label in the package containing the bluish specimen states "life-long color blue." The pinkish specimen was packaged separately with label stating "lifelong color pink"; holotype with 15 large eggs to  $26\times7$ mm; pink paratype with 12 eggs as large as  $18\times6$ mm.

**Etymology** We name this species for Leslie W. Knapp, Director, Department of Fishes, Smithsonian Sorting Center, primarily for supplying us with study material.

**Discussion** This species and M. dorsum appear to be closely related, differing primarily in far forward extension of CFF in M. dorsum; this feature is weakly expressed in a paratype of M. knappi by an extension of about half the tail length.

**Distribution** Known only from near the Falkland Islands (Fig. 3).

**Comments** A discrepancy exists in recorded dates of capture. The "life-long pink" specimen has a label stating the date of capture as "March 24, 1935"; the label with the two "life-long blue" specimens (packaged separately) states "March 24, 1965." All other data, handwriting, and label paper are identical; therefore we assume the date of 1935 to be in error because we know of no Russian research vessel collecting near the Falkland Islands in 1935. Because of the poor condition of one of the paratypes, it was not possible to obtain accurate body measurements or slime pore counts; however, we were able to count the cusps.

#### Myxine australis Jenyns, 1842

Myxine australis Jenyns, 1842:159 (description: "colored like an earthworm but more leaden, beneath yellowish, head purplish; Tierra del Fuego").

**Synonymy** Myxine acutifrons Garman, 1899:347 (from original description: rostrum acute, resembling a barbel; color dark brown, lighter ventrally; anterior two teeth of each series confluent to bases).

**Diagnosis** 2-cusp multicusp on both anterior and posterior sets of cusps; six gill pouches each side; head pointed, rostrum variably acute to rounded at tip; VFF low, averaging less than 2 mm; CFF narrow; a wide yellow ventral band extends slightly above rows of slime pores, continuing in a variably wide band to the yellow face.

**Description** Counts and proportions are given in Tables 1–7. Body slightly deeper than wide; tail slender, width about 33% of its length, its length 15% of TL; head narrow, pointed; tip of rostrum variably acute to rounded; a 2-cusp multicusp on both the anterior and posterior sets of cusps; VFF usually low, 0–6 mm, averaging 1.6 mm; CFF thin and wide around slender tail; body color reddish to dark brown, top of head dark; prominent yellow band ventrally extending slightly above rows of slime pores, continuing forward and widening into large blotches anterior to GA and to yellow face; large eggs range in numbers and sizes between 9 (24×8 mm) in a 330 mm female, and 16 (21×7 mm) in one of 345 mm TL.

**Distribution** Principally in and near the Straits of Magellan; however, three collections are from farther north (two off Argentina: 48°18'S, 65°06'W, and 50°00'S, 68°30'W, and one off Chile at 48°29'S, 78°46'W). Frequently taken with *M. affinis* (Fig. 3).

**Comments** The sex ratio of our material is unbalanced: of 86 specimens, 71 are female, 12 male, and 3 hermaphroditic. Although the multicusp pattern and number of gill pouches is the same as *M. affinis*, *M. australis* may be distinguished by fewer unicusps, fewer trunk and total pores, and shorter TL of mature specimens.

#### Myxine affinis Günther, 1870

**Synonymy** Muraenoblenny olivacea Lacépède, 1803: 6524 ("olive without spots, ventral surface whitish; no pectoral fins, no appearance of other fins; copious slime production"); presumably from the Straits of Magellan [nomen dubium].

Myxine affinis Günther, 1870, Catalog 8:511 ("Eleven rather stout teeth in each of two series, the foremost strongest and more confluent at the base than the others. Hab.\_\_\_\_? Twelve inches long") Norman, 1937:2-8 (examination of type; 11 teeth in each series; body too dried and hardened for slime pore counts).

**Diagnosis** A 2-cusp multicusp on both the anterior and posterior sets of cusps; six gill pouches each side; VFF variably developed; color reddish-brown to purple.

**Description** Counts and body proportions are given in Tables 1–7. Body slightly deeper than wide; rostrum triangular, tip rounded; barbels dark at base, pale distally; VFF yellowish , usually low, averaging 3 mm, but ranging from 0.5 to 13 mm, only 3 specimens with VFF between 8 and 13 mm; CFF wide, rarely with pale margin; tail about 15% of TL, its depth about 38% of its length; body reddish-brown to purple, head region somewhat lighter; narrow yellow band ventrally limited to below the lines of pores, often extending as intermittent patches to the yellowish face; GA and slime pores with narrow pale margins; numbers and sizes of large eggs range from 36 (20×6 mm) in a female of 550 mm TL to 17 (26×9 mm) in one of 475 mm TL.

**Distribution** Within or closely adjacent to the Straits of Magellan (Fig. 3).

**Comments** Frequently taken with *M. australis* but distinguished by higher unicusp and trunk slime pore count, as well as by generally larger eggs and a longer body. Sex ratio of our material is unbalanced; of 256 specimens sexed, 171 (67%) are female, 48 (19%) male and 37 (14%) hermaphroditic.

#### Myxine mcmillanae Hensley, 1991

Myxine mcmillanae Hensley, 1991:1040-1043.

**Diagnosis** A 2-cusp multicusp on both the anterior and posterior sets of cusps; six gill pouches (rarely seven) each side; color dark bluish-gray to brown; head whitish to first slime pores.

**Description** Counts and proportions are given in Tables 1–7. Body slightly deeper than wide; tail length 13% of TL, its depth 40% of its length; of 43 specimens two have seven pouches on the left side, one has seven on right side; VFF 3–6 mm high; body dark bluish-gray to brown; head pale to first slime pores; rostrum triangular, rounded at tip; VFF, CFF and margins of PCD, GA and slime pores pale; 7 to 11 large eggs (27–36 by 8–9 mm); the polar caps weakly developed.

**Distribution** Known only from the Caribbean Sea, west and southwest of Puerto Rico and from St Croix, U.S. Virgin Islands (Fig. 3).

**Comment** Hensley (1991) did not report on the sex of his material. The 10 specimens available to us (SI090-21) were all females. No hermaphroditism was noted.

#### Myxine limosa Girard, 1858

Myxine limosa Girard, 1858:223–224. (abundance: Grand Manan Isle; Bay of Fundy; 50 fm).

**Synonymy** Myxine atlanticus Regan, 1913:398 (Western North Atlantic, 44°27'N, 58°10'W; 120 fm; counts, proportions).

**Diagnosis** A 2-cusp multicusp on both the anterior and posterior sets of cusps; six gill pouches each side; head rather pointed, rostrum triangular, bluntly pointed; color reddish-brown to dark purple; head often pale; occasional ventral blotches; VFF variably low to high; a narrow pale streak on dorsal midline usually present.

**Description** Counts and body proportions are given in Tables 1–7. Body slender, nearly cylindrical; tail slender, 12–17% of TL, its depth about 30% of its length; VFF low, 0–4 mm (average 1.6 mm); CFF prominent, thin, thickening dorsally; head pointed, rostrum bluntly triangular; body color varying shades of reddish-brown to blackish-purple; head only slightly pale; occasional pale blotches ventrally; VFF and CFF usually with pale margins; GA and slime pores with prominent pale margins; a narrow pale streak of variable length usually present on dorsal midline; females (368–385 mm TL) contain 12 to 20 large eggs, 17×5 to 27×8 mm; a 385 mm female contains 14 fully developed eggs, 16×6 to 17×8 mm, all linked by anchor filaments.

**Distribution** Between Davis Strait (66°N) and south to Florida, between 75 and 1,006 m; one specimen (383 mm TL) from Campeche Bank, Gulf of Mexico, at 24°25'N, 87°38'W.

**Discussion** Since its description, *M. limosa* has often been identified as M. glutinosa L. (1758) from the eastern North Atlantic (ENA), but we find two characters involving coloration that distinguish the two. All descriptions and our findings on ENA material indicate a grayish-pink color; in contrast, all our western North Atlantic (WNA) material is reddishbrown to blackish-purple. Girard (1858) indicated reddish to dark brown or black. In addition to the much darker coloration, most WNA specimens have a narrow pale streak along the dorsal midline extending forward from CFF an average of 46% (18-80% of TL). This pale streak is not mentioned by any author offering color descriptions of WNA material, and it is not present in ENA material available to us (180 from Skagerrak, Denmark; SIO59-50). This streak appears to result from white connective tissue binding skin to the dorsal midline in conjunction with an overlying unpigmented streak in the skin. Removal of the overlying skin and examination with the aid of strong backlighting shows this band to be present only in WNA material. Also, a difference in maximum lengths exists between mature specimens of *M. limosa* and. *M. glutinosa*. Of 250 specimens of the former, the longest is 510 mm TL, and 133 exceed 400 mm, averaging 445 mm TL. Tambs-Lyche (1969:283) reported "maximum 450 mm" for ENA material. Conel (1917:78) recorded a maximum length of 79 cm from off South Harpswell, Maine, and stated that of 20 specimens, only three were between 31 and 36 cm; all others were from 50 to 79 cm. We have not seen any that large, and no further description of the 20 specimens was given.

**Comments** Apparently all previous authors have assumed that *M. glutinosa* occurs across the North Atlantic Ocean, but Saemundsson (1949) did not include it in his list of fishes from Iceland. However, Konstantinov and Shchegelov (1958:1745) stated "On June 16, 1956, near the eastern coast of Iceland, at the depth of 940 m, a *M. glutinosa* L., 28.5 cm long, was caught in a Sigsbee trawl." We consider these two species closely related, and have included *M.glutinosa* in all the tables for comparison with *M. limosa*.

## Discussion

Owing to the absence of a fossil record, we are unable to state with certainty whether or not the new world species treated herein are monophyletic or polyphyletic. However, monophyly is assumed, based on the synapomorphic character of having all branchial ducts on either side combined into one single external opening posterior to the gill pouches. Also, monophyly of *Myxine* is supported by allozyme studies of hagfish from three continents.<sup>1</sup>

Relationships among these 14 species are in general somewhat obscure on the basis of body proportions and most counts. Although some means differ (Tables 1–7), considerable overlap in ranges of counts tends to mask significance. Only two species (both new) differ notably in body proportions (Table 1); all 12 others are very similar. *M. fernholmi* has a shorter prebranchial length and a correspondingly longer trunk length and shorter tail. *Myxine debueni* also has somewhat shorter prebranchial and tail lengths, but the trunk length is similar to that of other species, except for *M. fernholmi*. The few specimens available (2 to 4) in 7 of the 14 species inhibits speculation as to relationships, geographical separation notwithstanding. Most counts are similar for most

<sup>&</sup>lt;sup>1</sup> Fernhom, B. Swedish Museum of Natural History, Section for Vertebrate Zoology, P.O. Box 50007, 5-110405, Stockholm, Sweden. Personal commun., May 1994.

	3-cu	sp multicu	sp on ant	erior set o	f cusps	2-cusp multicusp on both the anterior and posterior sets of cusps									
	M. circifrons	M. mccoskeri	M. robinsi	M. fernholmi	M. debueni	M. hubbsi	M. hubbsoides	M. pequenoi	M. dorsum	M. knappi	M. australis	M. affinis	M. mcmillanae	M. limosa	M. glutinoso
No. of specimens examined Size range (mm)	572 125–650	20 165–286	4 460–540	4 540–846	2 540–570	136 209–522	3 655–820	2 175–183	2 440–490	3 510–565	131 91–394	271 141–659	43 271–473	78 117501	143 227–387
Prebranchial lengt	n 29 29–30	31 27–34	30 2 <del>9</del> 32	22 20–25	 2425	26 25–28	27 27–28	 24–26	 28–29	27 27–28	27 2632	28 26–31	29 26–31	28 23–30	27 24–30
Trunk length	57 55–58	51 52–56	59 57–60	70 67–72	 66–69	61 58–65	61 61–62	 57–59	 58–60	61 59–62	58 53–60	59 56–62	59 56–61	58 55–62	58 54-62
Tail length	13 10–15	15 13–17	12 11–14	9 8–10		11 10–12	12 12–12	 1112	 13–13	13 12–13	15 11–19	13 11–15	13 11–14	11 12–17	15 13–17
Body width	5 46	4 3–5	4 35	4 3–5	 45	4 3–5	3 2–4		_ 4_4	4 4-4	4 2–5	4 3–5	4 46	4 2–5	5 3–6
ody depths															
Including ventral finfold	7 6–8	6 5–9	6 5–7	5 47	 5–6	5 4–6	4 44		 66	4 45	6 48	5 47	6 48	6 47	7 5–9
Excluding ventral finfold	5 4–7	5 4–7	5 4–6	5 46	 56	5 4–5	4 4-4		 4–5	4 4-4	5 5—7	5 3–7	5 47	7 3–7	5 5–8
Over cloaca	5 3–5	5 4—7	4 45	4 3–5	 4_4	4 3–5	4 3–4	 4-4		4 44	5 46	4 45	5 4—6	4 3–5	5 4–6
Tail	5 5–6	6 4-7	5 45	4 4-6	 44	4 3–5	4 44	 4_5	 56	4 4-5	5 <sup>·</sup> 4—7	5 46	5 4-6	4 36	5 46

				Number	s of prebra	unchial sli	Table 2 me pores for	new world	species o	of Myxine					
	3-cus	p multicusp	on ante	rior set of c	usps	2-cusp multicusp on both the anterior and posterior sets of cusps									
No. of prebranchial slime pores	M. circifrons	M. mccoskeri	M. robinsi	M. fernholmi	M. debueni	M. hubbsi	M. hubbsoides	M. pequenoi	M. dorsum	M. knappi	M. australis	M. affinis	M. mcmillanae	M. limosa j	M. glutinoso
18	1					2									
19	8					4									
20	26					3									1
21	58				2	24									1
22	76	1				45		1			3			1	2
23	90	3		2		39		1						2	6
24	75	5				35					2				15
25	56	5	1	1		23	•				3			1	17
26	25	4		1		13					4	1	1	8	16
27	14	2				7					9	6		10	25
28	10		1			5					14	13	3	6	13
29	1										10	29	5	10	15
30	2		1				1				7	35	7	10	13
31							2		1	1	12	39	10	7	8
32	2		1						1	1	5	30	8	9	8
33	1										6	39	6	6	1
34											7	22	1	7	
35											1	19	2	5	1
36											6	16		2	1
37											3	12		2	
38											2	8		1	
39											7	9			
40											1	5		1	
41											3	3			
 42											1	2			
 n=	445	20	4	4	2	200	3	2	2	2	106	288	43	88	143
<del>x</del> =	23.24	24.70	-			23.23		-	-	-	31.25	36.62		<b>29.88</b>	28.85

				Num	bers of tru	nk slime	Table 3 pores for new	v world spe	cies of <i>M</i>	yxine.					
	3-cu	sp multicus	p on ant	erior set of a	cusps		2-c	usp multic	usp on bo	oth the ar	terior and	posterio	or sets of cus	ps	
No. of Trunk slime pores	M. circifrons	M. mccoskeri	M. robinsi	M. fernholmi	M. debueni	M. hubbsi	M. hubbsoides	M. pequenoi	M. dorsum	M. knappi	M. australis	M. affinis	M. mcmillanae	M. limosa	M. glutinosa
43 44 45 46 47 48 49 50 51 52 53 56 57 58 59 50 51 55 55 56 57 58 59 50 51 55 55 56 57 58 59 50 51 55 55 56 57 58 59 70 71 72 73 74 77 77 78 79 90 31 33 34 35 55 56 57 58 59 70 71 77 77 77 77 78 79 90 30 31 33 34 35 55 55 56 56 57 58 59 70 51 52 53 54 55 55 56 57 58 59 70 51 52 55 55 56 57 58 59 70 51 52 53 54 55 55 56 57 58 59 70 71 72 77 8 77 78 77 78 77 77 77 77 77 77 77 7	1 2 5 22 51 83 86 79 51 29 19 4 3 1	1 1 2 4 2 1 4 4 1	1 1 2	2	1	$1 \\ 2 \\ 2 \\ 5 \\ 5 \\ 16 \\ 21 \\ 31 \\ 34 \\ 17 \\ 13 \\ 10 \\ 5 \\ 1 \\ 2 \\ 2$	1 1 1	1	2	1	1 2 5 4 7 7 14 14 9 13 8 4 1 3 1 2 3	1 2 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7 7	1 5 4 5 5 7 5 6 2 1 2	1 1 4 8 10 6 10 8 7 5 3 5 4 3 6 6 1	2 4 5 14 17 14 20 12 26 12 9 3 3 2
6 97 9=	438 55.20	20 48.50	4	1 4	2	201 65.14	3	2	2	2	98 58.46	295 65.75	43 5 64.65	88 60.74	143 56.29

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					Numbers	of tail pore	Table 4 es for new wo	rld species	of Myxin	e.					
	3-cu	sp multicus	p on ant	erior set of c	rusps	2-cusp multicusp on both the anterior and posterior sets of cusps									
No. of Tail slime pores	M. circifrons	M. mccoskeri	M. robinsi	M. fernholmi	M. debueni	M. hubbsi	M. hubbsoides	M. pequenoi	M. dorsum	M. knappi	M. australis	M. affinis	M. mcmillanae	M. limosa	M. glutinose
7	7		1	1	2		•								_
8	48			2		4		1			1			1	1
9	108	1	9	1		17		1			2	7	3	3	2
10	127	5	1			<b>59</b>					23	29	22		16
11	116	8	1			70			2	1	34	93	15	25	22
12	33	5				40	2				22	102	3	20	47
13	2					9	1			1	5	38		25	37
14		1				1					1	11		10	16
15															2
16														4	
n=	441	20	4	4	2	200	3	2	2	2	88	280	43	88	143
$\overline{x}$ =	10.00	11.05				10.78					11.06	11.67	10.50	12.26	11.50

				Tot	al number	s of slime	Table 5 pores for new	world spe	cies of M <sub>j</sub>	vxine.					
	3-cus	o multicusp o	on ante:	rior set of c	rsba		2-c	usp multic	usp on bo	th the an	terior and	posterio	sets of cus	ps	
No. of Total slime <i>pores</i>	M. circifrons	M. mccoskeri re	M. obinsi	M. fernholmi	M. debueni	M. hubbsi	M. hubbsoides	M. pequenoi	M. dorsum	M. knappi	M. australis	M. affinis	M. mcmillanae	M. limosa	M. glutinosa
77 78 79 80 81 82 83 84 85 86 87 88 89 90 91 92 93 94 95 96 97 98 99 90 100 101 102 103 104 105 106 107 108 109 110 110 111 112 113 114 115 116 117 118 119 120 121 122 123	3 2 14 19 25 28 45 56 52 44 39 38 15 21 5 10 3 1 3 1	1 2 1 1 4 1 1 4 1 1 1 1	1 1 1	1 1 1	11	2 2 2 17 12 14 20 26 17 16 27 12 6 5 7 2 4 6 2 2 2 2	1 1 1	1	1	· 1 1	1 12 2 1 3 3 4 7 6 11 4 3 6 3 2 4 8 3 3 1 4 2 1 1 1 1 1 1	$\begin{array}{c}2&1&4&6&8&5\\&&10&2&2&2&2&2\\&&&15&2&2&2&2&2\\&&&&&&&&\\&&&&&&&&\\&&&&&&&&&\\&&&&&&$	3 5 1 3 8 3 1 5 8 2 2 2 12	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	2 1 2 2 9 8 9 9 11 10 11 6 14 9 7 9 10 5 5 1 1 2
$\frac{123}{124}$ $n=$ $\overline{x}=$	442 89.69	20 84.46	4	4	2	200 100.40	3	2	2	2	88 102.00	4 279 111.50	43 106.83	91 103.50	143 96.54

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	3-cus	p multicusp	on ante	rior set of cu	lsps	2-cusp multicusp on both the anterior and posterior sets of cusps									
	M. circifrons	M. mccoskeri	M. robinsi	M. fernholmi	M. debueni	M. hubbsi	M. hubbsoides	M. pequenoi	M. dorsum	M. knappi	M. australis	M. affinis	M. mcmillanae	M. limosa	M. glutinoso
No. of a	aterior unicu	Sps													
4		-				1		2			1				1
5						2					21			2	28
6		4		2		15	1			2	92			25	184
7	1	5		2 2	2	115	. 2		1		11	31		40	11
8	5	9				65	-		1	1		294	7	8	
9	122	2				2						180	55		
10	269											7	27		
11	106		1												
12	11		1												
13	2		2												
n=	516	20	4	4	2	200	3	2	2	3	125	512	89	75	224
$\overline{x}$ =	10.00		0			6.50					5.50	8.50		6.50	
No. of p	osterior unicu	sps													
5						3		1			1			1	2
6				1		28		1			26			10	66
7		3		3	2	135	3			1	90	4		38	151
8	3 <del>9</del>	4				34			2	1	8	297	4	26	5
9	283	7								1		203	49		
10	175	6										8	33		
11	18		1										1		
12	1		3												
n=	516	20	4	4	2	200	3	2	2	3	125	512	87	75	224
x=	10.00		0			6.50					6.50	8.50	9.50	6.50	

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					Numbers	of total cus	Table 7	orld species	s of Myria	ne					
<u>.</u>	3-cus	o multicusp	on ante	rior set of cu		2-cusp multicusp on both the anterior and posterior sets of cusps									
Total cusps	M. circifrons	M. mccoskeri	M. robinsi	M. fernholmi	M. debueni	M. hubbsi	M. hubbsoides	M. pequenoi	M. dorsum	M. knappi	M. australis	M. affinis	M. mcmillana	M. e limosa	M. glutinos
26								1							
27															
28								1							
29											1				2
30											6			2	3
31											9			6	7
32						3					11			10	
33						3					19			5	12
34				1		19	1		1		56			24	63
35						18			_		11			17	3
36		1		2	1	54	3		3	1	12			29	1
30 37		1		1	-	46	U U		•	-	4			14	1
38		1		-	1	25				1	2	11		19	1
39		2			-	14				1	-	10		5	1
40		2				14				T		68		4	
		2				3						46		4 1	
41													0		
42		2				1						55	3	1	
43	4											25	4		
44	9	2										34	9		
45	14	3										5	10		
46	60	4										2	9		
47	60												6		
48	107	1											3		
49	77														
50 ·	85														
51	49														
52	30														
53	6														
54	10														
55	4														
56	1		2												
57			1												
58			1												
n=	516	20	- 4	4	2	200	4	2	4	3	131	256	43	137	93
<del></del>	49.50			-	-	36.00		-	-	-	33.68	42.00		36.00	

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species; numbers of trunk and total slime pores differ more widely, but there is frequent overlap. The total numbers of cusps (Table 7) show the greatest differences between species. The height of VFF shows considerable intraspecific variation; for example, in Myxine circifrons it varies between 1 and 12 mm. Both the numbers of fused cusps and the number of gill pouches are constant with only rare or aberrant variation and are extremely useful in separating the 14 species into groups. Five species have a 3-cusp multicusp on the anterior set of cusps. Of these five, M. circifrons, M. mccoskeri, and M. robinsi have 5 gill pouches and M. fernholmi and M. debueni have 6; the only new world species with 7 gill pouches is M. pequenoi. The remaining eight species have 6 gill pouches and a 2-cusp multicusp in both anterior and posterior sets of cusps. An additional, possibly diagnostic character is that Myxine mccoskeri and M. pequenoi mature at much smaller sizes than do the other species, and are here regarded as dwarfed. Prior to the permanent Panamanian land bridge, M. circifrons of the tropical Pacific, and M. mccoskeri and M. robinsi of the southern Caribbean Sea, may have represented the same species. Only these three species have five gill pouches; they also have in common the 3-cusp multicusp on the anterior row, and the anterior portions of the heads of M. circifrons and M. robinsi are notably and consistently whiter than in any of the other species. M. mccoskeri may have independently developed a dwarfed condition as well as a unique color pattern of reverse countershading, fewer trunk pores, and anterior unicusps. Hermaphroditism occurs frequently in all the large collections except in Myxine circifrons. The fact that in such a large number of hagfishes examined, only one specimen was found with fully developed filaments suggests that eggs are extruded very soon after becoming fully mature, regardless of time of year. We have found no indications of sexual dimorphism in color, body proportions, TL, or slime pore counts.

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## Material examined

#### Myxine circifrons

SIO67-118 (51), 38°00'N, 123°31'W, 732 m; SIO64-449 (38), 32°54'N, 117°38'W, 961 m; SIO59-257 (13), 32°35'N, 117°28'W, 1,208 m; SIO74-611 (65), San Diego Trough, 1,201 m; SIO66-7 (34), 32°32'N, 117°27'W, 1,190 m; SIO68-119 (34), 32°27'N, 117°27'W, 1,244 m; SIO69-227 (15), 31°35'N, 116°05'W, 1,202 m; SIO68-118 (110), 25°37'N, 109°43'W, 1,244 m; SIO68-59 (14), 23°07'N, 109°19'W, 1,281 m; SIO68-60 (6), 23°07'N, 109°11'W, 1,830 m; SIO68-119 (25), 25°36'N, 109°45'W, 1,491 m; SIO73-290 (4), 09°48'N, 85°42'W, 994 m; SIO73-293 (3), 09°23'N, 85°00'W, 1,107 m; SIO73-294 (17), 09°24'N, 85°06'W, 900 m; SIO69-148 (7), 02°02'S, 81°10'W, 1,000 m; SIO90-26 (1), 03°15'S, 80°53'W, 960 m; SIO90-27, (1), 03°15'S, 80°55'W, 960 m; SIO90-25, (2), 04°10'S, 81°27'W, 1,860 m; MCZ 49585 (1), 33°17'S, 77°05'W, 1,510 m. Twelve specimens from IMARPE, with incomplete data, taken between 08°S and 17°S, 71° and 81°W, between 800 and 1,500 m.

#### Myxine hubbsi

SIO92-127 (223),  $32^{\circ}40'N$ ,  $118^{\circ}12'W$ , 1,830 m; SIO65-451 (19),  $32^{\circ}40'N$ ,  $118^{\circ}12'W$ , 1,742 m; SIO65-452 (82),  $32^{\circ}38'N$ ,  $118^{\circ}08'W$ , 2,009 m; SIO68-676 (16),  $32^{\circ}39'N$ ,  $118^{\circ}11'W$ , 1,830 m; SIO71-116 (1),  $28^{\circ}52'N$  115°50'W, 2,004 m; SIO68-60 (37),  $23^{\circ}08'N$ ,  $109^{\circ}16'W$ , 1,830 m; SIO68-61 (2),  $23^{\circ}06'N$ ,  $109^{\circ}13'W$ , 2,196 m; SIO73-293 (16),  $09^{\circ}24'N$ ,  $85^{\circ}06'W$ , 1,107 m; SIO83-288 (1),  $09^{\circ}44'N$ ,  $85^{\circ}00'W$ , 2,181 m; SIO73-293 (1),  $09^{\circ}24'N$ ,  $85^{\circ}00'W$ , 1,102 m; SIO92-114 (11),  $03^{\circ}41'S$ ,  $81^{\circ}36'W$ , 2,440 m; SIO92-115 (7),  $08^{\circ}26'S$ ,  $80^{\circ}37'W$ , 1,930 m; SIO72-176 (8),  $21^{\circ}37'S$ ,  $70^{\circ}55'W$ , 2,114 m; MCZ-44897 (2),  $34^{\circ}12'S$ ,  $72^{\circ}76'W$ , 1,475 m. Examined, but not listed, are numerous collections of few specimens each from off southern California.

#### Myxine australis

SIO78-39 (8),  $45^{\circ}36$ 'S,  $74^{\circ}11$ 'W, 120 m; SIO78-40 (80),  $50^{\circ}30$ 'S,  $75^{\circ}20$ 'W, 80 m; SIO78-41 (2),  $54^{\circ}15$ 'S,  $70^{\circ}58$ 'W, 4 m; SIO78-43 (1),  $55^{\circ}03$ 'S,  $68^{\circ}10$ 'W, 30 m; SIO78-44 (3),  $55^{\circ}49$ 'S,  $67^{\circ}30$ 'W; SIO78-45 (2),  $55^{\circ}10$ 'S,  $65^{\circ}30$ 'W, 146 m; SIO78-49 (3),  $54^{\circ}46$ 'S,  $64^{\circ}03$ 'W, 23 m; SIO78-51 (18),  $54^{\circ}45$ 'S,  $64^{\circ}10$ 'W, 14 m; USNM 3939 (20),  $42^{\circ}29$ 'S,  $78^{\circ}46$ 'W; AMNH 4098 (2),  $51^{\circ}10$ 'S,  $69^{\circ}30$ 'W; FURG-? (4),  $48^{\circ}18$ 'S,  $65^{\circ}06$ 'W; the following collections lack stated depths but were taken in the area of the Straits of Magellan: MCZ 32518 (1); MCZ 38351 (6); MCZ 3836 (16); MCZ 3836 (16);

MCZ 8837 (22); MCZ 8839 (30); MCZ 8842 (10); MCZ 24972 (19); MCZ 35198 (1); USNM 103769 (1); USNM 117329 (1); USNM 153595 (1); USNM 267750 (1); AMNH 4098 (2); SU 22678 (1); IU 2124 (1); IU 4293 (1).

#### Myxine affinis

SIO78-39 (8),  $45^{\circ}36'S$ ,  $74^{\circ}11'W$ , 120 m; SIO78-40 (39), Isla Madre de Dios, Chile, 80 m; SIO78-41 (62),  $54^{\circ}14'S$ ,  $70^{\circ}06'W$ , 4 m; SIO78-42 (7),  $54^{\circ}52'S$ ,  $70^{\circ}58'W$ , 60 m; SIO78-43 (21),  $55^{\circ}03'S$ ,  $68^{\circ}10'W$ , 30 m; SIO 78-44 (15),  $54^{\circ}45'S$ ,  $64^{\circ}09'W$ ; SIO78-45 (4) Bahia Windhond, Chile, 146 m; SIO78-50 (3),  $54^{\circ}54'S$ ,  $64^{\circ}10'W$ , 14 m; SIO78-51 (31),  $54^{\circ}45'S$ ,  $64^{\circ}10'W$ , 14 m; SIO83-121 (2),  $54^{\circ}22'S$ ,  $71^{\circ}22'W$ . The following collections lack stated depths and coordinates but were taken in the area of the Straits of Magellan: MCZ 35198 (12); MCZ 8836 (3); MCZ 8837 (7); MCZ 8839 (1); MCZ 8840 (6); MCZ 8841 (11); MCZ 24972 (1); USNM 77377 (1); USNM 26715 (1); USNM 39039 (2); USNM 39140 (1); USNM 17418 (1); FMNH 9820 (3); SU 22678 (1).

#### Myxine limosa

SIO74-181 (28), 36°43.2'N, 74°38'W, 300 m; SIO74-185 (3), 37°05'N, 74°39'W, 280-360 m; SIO74-187 (4), 36°36'N, 79°42'W, 316 m; SIO74-188 (1), 38°18'N, 73°35'W, 215-250 m; SIO74-189 (4), 37°27'N, 74°30'W, 120-320 m; SIO74-190 (5), 36°19'N, 74°47'W, 310-400 m; SIO75-677 (5), 41°54'N, 69°50'W, 75 m; SIO75-678 (1), 41°53'N, 68°07'W, 183 m; SIO75-679 (2), 49°09'N, 66°56'W; SIO75-680 (5), 42°30'N, 66°04'W; SIO75-681 (3), 43°02'N, 64°32'W; SIO75-682 (1), 42°33'N,66°58'W, 293 m; SIO75-683 (6), 42°26'N, 68°44'W; SIO75-684 (1), 42°30'N, 69°20'W; SIO75-685 (2), 42°31'N, 69°42'W, 275 m; SIO75-686 (4), 42°33'N, 69°48'W, 275 m; SIO75-689 (3), 37°05'N, 74°40'W, 280-360 m; SIO77-101 (1), 39°35'N, 72°04'W, 201 m; SIO77-102 (1), 39°32'N, 72°22'W, 375-512 m; SIO77-103 (1), 41°32'N, 68°29'W, 86 m; SIO77-104 (1), 41°51'N, 68°05'W, 88 m; SIO77-105 (3), 39°12'N, 72°29'W, 302 m; SIO77-106 (1), 39°05'N, 72°43'W, 234 m; SIO77-107 (4), 38°30'N, 73°19'W, 220 m; SIO77-108 (1), 37°28'N, 74°24'W, 191 m; SIO77-119 (2), 37°54'N, 74°00'W, 261 m; ISH6-1965 (1), 45°06'N, 54°46'W; ISH42-1970 (1), 40°25'N, 68°10'W, 220-230 m; ISH-1987 (3), 66°38.6'N, 56°38.2'W, 540 m; ISH-7238-1982 (2), 66°04'N, 56°13.9'W, 323 m; ISH63-1987 (1), 63°05'N, 52°13'W, 127-155 m; ISH431-1986(1), 57°38'N, 18°13'W, 1,006 m; ISH5-1965 (1), 45°06'N, 54°48'W, 180-260 m; ISH2-1970 (1), 45°00'N, 54°47'W, 175 m; ISH23-1961 (33), 44°19'N, 54°27'W, 175 m; ISH42-1970 (1), 40°25'N, 68°10'W, 230 m; ISH3653-1979 (1), 33°45.8'N, 76°05.6'W, 608 m.

## Literature cited

Chirichigno, F. N.

1968. Nuevos registros para la ictiofauna marina del Peru. Instituto del Mar del Peru 1(8):37–503.

Conel, J. L.

**1917.** The urogenital system of myxinoids. J. Morph. 29 (1):75-164.

#### Fernholm, B.

1981. A new species of hagfish of the genus *Myxine*, with notes on other eastern Atlantic myxinids. J. Fish. Biol. 19:73-82.

Fernholm, G., and C. L. Hubbs.

**1981.** Western Atlantic hagfishes of the genus *Eptatretus* (Myxinidae) with descriptions of two new species. Fish. Bull. 79:69-83.

Garman, S.

1899. Reports of an exploration of the west coasts of Mexico, Central and South America and off the Galapagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer "Albatross," during 1891, Lieut. Cmdr. Z. L. Tanner, U.S.N. commanding. XXVI: The fishes. Mem. Mus. Comp. Zool. Harvard College 24:1-431.

Girard, C.

1858. Ichthyological notices. Proc. Acad. Nat. Sci. of Philadelphia (printed 1859):223-224.

Günther, A.

1870. Catalogue of the Physostomi, containing the families Gymnotidae, Symbranchidae, Muraenidae, Pegasidae, and of the Lophobranchii, Plectognathi, Dipnoi, Ganoidei, Chondroopterygii, Cyclostomata, Leptocarcdii in the British Museum. Catalogue of the Fishes in the British Museum, London, 549 p.

1991. Myxine mcmillanae, a new species of hagfish (Myxinidae) from Puerto Rico and the U.S. Virgin Islands. Copeia 1991 (4):1040-1043.

Jenyns, L.

1842. Fish. In C. Darwin (ed.), The zoology of the voyage of HMS *Beagle*, under the command of Captain Fitzroy, R.N. during the years 1832 to 1836, part 4. Smith, Elder, and Co., London.

Konstantinov, K. G., and V. D. Shchegelov.

1958. Myxine glutinosa of the Iceland Shores. Zoologicheskii Zhurnal. Vol. 37, Part 2, No. 1745. [In Russian, English summary.]

- Lacépède, B. G.
  - 1803. Histoire naturelle de poisssons. Vol. XI, 138–
     652. Chez Plasson, Paris.
- Leviton, A. E., R. H. Gibbs Jr., E. Heal, and C. E. Dawson.
  1985. Standards in herpetology and ichthyology. Part 1: Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985 (3):802–832.
  Linnaeus, C.

1758. Systema naturae. Regnum animali, 824 p.

McMillan, C. B., and R. L. Wisner.

**1984.** Three new species of seven gilled hagfishes (Myxinidae, *Eptatretus*) from the Pacific Ocean. Proc. Calif. Acad. Sci. 43 (16):249-267.

1994. Fishes of the world, 3rd ed. John Wiley and Sons, Inc., New York.

Norman, J. R.

1937. Coast fishes. Part II: The Patagonian region (including the Straits of Magellan). Discovery Reports 16:1–150. Regan, C. T.

1913. A revision of the myxinoids of the genus Myxine. Ann. and Mag. Nat. Hist. (Ser. 8) 11:395-398.

Richardson, L. R.

1953. Neomyxine n. s. (Cyclostomata) based on Myxine biniplicata Richardson and Jowett 1951, and further data on the species. Trans. R. Soc. N.Z. 81, (part 3):379–383.

Hensley, D. A.

Nelson, J. S.

<sup>1958.</sup> A new genus and species of Myxinidae (Cyclostomata). Trans. R. Soc. N.Z., 81 (Part 3): 283-287.

#### Saemundsson, B.

1949. The zoology of Iceland; marine pisces. Vol. 4, Part 72:72–150. E. Munksgaard, Reykjvik.

Shimizu, T.

1983. Myxinidae. *Myxine.* In T. Uyeno, K. Matsuura, and E. Fujii (eds.), Fishes trawled off Suriname and French

Guiana, 519 p. Japan Fishery Resource Center, National Science Museum, Tokyo. [In Japanese with English summaries.] Tambs-Lyche, H.

1969. Notes on the distribution and ecology of Myxine glutinosa. Fisk. Dir. Skr. Havunders 15:279-284.