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Review of the Hagfishes (Myxinidae, Myxiniformes) of the Northwestern Pacific Ocean, with Descriptions of Three New Species, *Eptatretus fernholmi*, *Paramyxine moki*, and *P. walkeri*

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Charmion B. McMillan and Robert L. Wisner (2004) Review of the hagfishes (Myxinidae, Myxiniformes) of the northwestern Pacific Ocean, with descriptions of three new species, *Eptatretus fernholmi*, *Paramyxine moki*, and *P. walkeri*. *Zoological Studies* **43**(1): 51-73. Sixteen known species of Asian hagfishes are reviewed and 3 new species are described: *Eptatretus fernholmi*, *Paramyxine moki*, and *P. walkeri*. The study area includes the coastal waters of Japan, South Korea, Taiwan, China, and Luzon Island, the Philippines. We present keys to the identification of genera and species, and discuss various characters useful in hagfish taxonomy. http://www.sinica.edu.tw/zool/zoolstud/43.1/51.pdf

Key words: Myxinidae, Hagfishes, *Eptatretus*, *Paramyxine*, *Quadratus*.

This study deals with the species of hagfishes found in the area of the northwestern Pacific Ocean bounded by about 13° to 45°N and 110° to 145°E (Fig. 1). Myxinids are of great phylogenetic importance because they are the most primitive of living vertebrates (Hubbs 1947). Hagfishes play an ecological role as scavengers of dead and dying fishes and invertebrates, and as food fish in Asian countries bordering the NW Pacific Ocean, and are of commercial importance for the "eelskin" trade. Commercial fishing has resulted in increased harvesting that has threatened the populations of some species as shown by greatly reduced catches from Korean and Japanese waters (Gorbman et al. 1990). Four genera, *Eptatretus* Cloquet, 1819, *Paramyxine* Dean, 1904, *Quadratus* Wisner, 1999, and *Myxine* Linnaeus, 1758 are known from the NW Pacific Ocean. Most species are found in Japanese and Taiwanese waters, possibly due to a greater collecting effort or more commercial fishing occurring here than elsewhere in the area. The only genera not reported from this region are *Notomyxine* Nani and Gneri, 1951, *Neomyxine* Richardson, 1953, and *Nemamyxine* Richardson, 1958; these are found only in the southern hemisphere. Little was known of Asian hagfishes until Jordan and Snyder (1901) described the species *Myxine garmani* and recognized *Eptatretus burgeri* (Girard, 1855). Dean (1904) described *E. okinoseanus* and erected a new genus *Paramyxine* with the description of *P. atami*, both new species from Japan. Strahan and Honma (1960 1961) and Strahan (1962) presented studies of *P. atami*. In Taiwan, Teng (1958) described *P. yangi* and Shen and Tao (1975) described 2 other new species, *P. cheni* and *P. taiwanae*. Kuo et al. (1994) provided a revision of the hagfishes of Taiwan and described 4 new species of *Paramyxine*. Kuo and Mok (1994) described *E. chinensis* from the South China Sea, and Huang et al. (1994) presented a study of Taiwan hagfish taxonomy as inferred from mitochondrial diversity. Honma (1998) reviewed the classification and distribution of 13 species of Asian hagfishes and presented a discussion of the hagfish industry. Kuo and Mok (1999) redescribed *P. nelsoni* and *P. yangi*, and Mok (2001) introduced 2 new diagnostic characters, nasal

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papillae and skeletal morphology. Mok and Chen (2001) reported on the distribution of hagfishes in Taiwan, and Mok and Kuo (2001) described *M. formosana*, the 1st species of *Myxine* known from Taiwan. Mok (2002) described *M. kuoi*, making a total of 16 known hagfish species in the NW Pacific Ocean. The purpose of this paper is to review these Asian hagfishes and to describe 3 new species.

MATERIALS AND METHODS

Material examined is listed in each species description; methods of counting, measuring and terminology generally follow Fernholm and Hubbs (1981), McMillan and Wisner (1984), and Wisner and McMillan (1988). All measurements are in milimeters (mm); body proportions are in percent (%) of total length (TL); body width is measured at the pharyngocutaneous duct (PCD), while body depth is measured at the deepest place, usually about mid-body. We have presented the original descriptions for 2 species, *E. chinensis* and *M. kuoi*, for which we have no study material. The data in the diagnoses and in the tables are the combined results of our studies with those of other authors in the literature. All other data in the descriptions are those of material examined by the authors, unless otherwise stated. Acronyms for repositories follow Leviton et al. (1985) with the addition of the following: CUMZ, Chinese Univ. Museum of Zoology; NTUM, National Taiwan Univ. Museum; NSYSU, National Sun Yat-sen Univ.; TUM, Tokyo Univ. Museum; and UPZM, Univ. of Philippines Zoology Museum. Although spelled "Tong Kong" on some maps, we have used the spelling "Tung Kong" from HK Mok (pers. comm.) for the name of the fishing village on the SW coast of Taiwan (47°46'26"E, 21°44'29"N), where so many hagfishes have been collected, and we believe that Fukan (on collection labels and in Kuo et al. (1994) is the same place as Fukang (Mok and Chen 2001) on the SE coast of Taiwan.

Frequently used abbreviations are: GP, gill pouches; GA, gill apertures; DM, dental muscle; PCD, pharyngocutaneous duct; VA, ventral aorta; VFF, ventral finfold; w/VFF, with ventral finfold; w/o VFF, without ventral finfold; CFF, caudal finfold; EBD, efferent branchial duct; PBR, prebranchial; BR, branchial; TR, trunk; TA, tail. We have followed Fernholm (1998) in the terms "fused cusps" for "multicusps," but have capitalized "auc" and "puc" as AUC and PUC for anterior (outer) and posterior (inner) unicusps. We use the term "1st" for the most anterior, "slender" for a body width of less than 1/2 its depth and "robust" for a specimen whose body width is greater than 1/2 body depth. In describing the VFF, "prominent" or "well developed" describes a finfold that is 3 mm or deeper, "low" or "poorly developed" for 1-2 mm, and "vestigial" if less than 1 mm. Species are considered "dwarfed" if specimens less than 300 mm in TL have developing testes or elongated eggs. Except for occasional notes and the description of new species, we have not given barbel lengths since they are usually curled, difficult to measure accurately, and so small compared with TL that any errors are magnified. We have treated the genera *Paramyxine* and *Quadratus* as separate from *Eptatretus*, and offer a key to each genus, followed by descriptions of the species in alphabetical order.

Key to the genera of *Myxinidae* of the NW Pacific Ocean

1a. One pair of gill apertures ..... *Myxine*
1b. More than 1 pair of gill apertures 2
2a. Efferent branchial ducts of about equal length; gill apertures widely spaced and in a straight line; 1st gill aperture

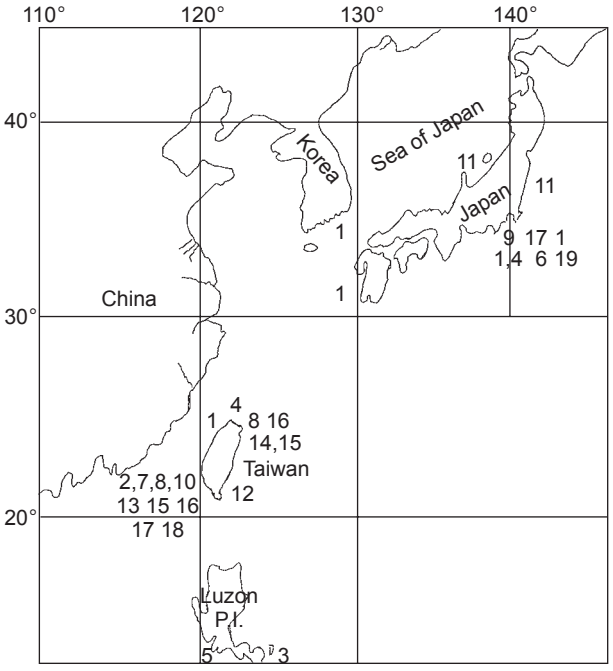

Fig. 1. Distribution of hagfish species of the northwestern Pacific Ocean: (1) *Eptatretus burgeri*, (2) *E. chinensis*, (3) *E. fernholmi*, (4) *E. okinoseanus*, (5) *E. strahani*, (6) *Paramyxine atami*, (7) *P. cheni*, (8) *P. fernholmi*, (9) *P. moki* sp. nov., (10) *P. sheni*, (11) *P. walkeri*, (12) *P. wisneri*, (13) *Quadratus nelsoni*, (14) *Q. taiwanae*, (15) *Q. yangi*, (16) *Myxine formosana*, (17) *M. garmani*, (18) *M. kuoi*, and (19) *M. paucidens*.

about opposite first or second gill pouch ..... *Eptatretus*
2b. Efferent branchial ducts of unequal length, the first one 2-3 times longer than the last 3
3a. Gill apertures close together in a straight, or slightly irregular line; the 1st gill aperture opposite gill pouches 3-5 .... *Paramyxine*
3b. Gill apertures non-linear, closely crowded together in a pattern that may vary from a very irregular line to a rectangular or rhomboidal shape ..... *Quadratus*

Key to the species of *Eptatretus* from the NW Pacific Ocean

1a. Gill pouches 6 2
1b. Gill pouches 7 or 8 3
2a. Fused cusps 3/2; white mid-dorsal stripe; total cusps 40-42, total slime pores 81-92 ..... *E. burgeri*
2b. Fused cusps 3/3; no white dorsal stripe; total cusps 46-52; total pores 72-83 ..... *E. chinensis*
3a. Gill pouches 7; fused cusps 3/3 ..... *E. strahani*
3b. Gill pouches 8; fused cusps 3/2 4
4a. Total cusps more than 50; ventral finfold vestigial; eyespots absent ..... *E. fernholmi* sp. nov.
4b. Total cusps fewer than 50; ventral finfold well developed; eyespots present ..... *E. okinoseanus*

Eptatretus burgeri (Girard, 1855)

(Table 1; Fig. 2)

Heptatrema cirrhatum Temminck and Schlegel, 1850 (description)[misidentified]; *Bdellostoma burgeri* Girard 1855: 199 (description based on Temminck and Schlegel 1850); *Homea burgeri* Jordan and Snyder 1901: 37, 126 (review of hagfishes of Japan); *Heptatretus burgeri* Regan, 1912: 524 (brief description).

Materials examined: SIO 80-212, 2, 518, 623 mm TL, collected by M-J Yu off Ta-Chi, NE Taiwan, 121°53'41"E, 24°56'35"N, 12 Feb. 1977; SIO 80-217, 1, 370 mm TL, from NE Taiwan by L. Chen, by otter trawl, 13 Apr. 1977; SIO 00-33, 1, 290 mm TL, 24°52.5'N, 121°52.5'E, collected by H.-K. Mok, 28 Mar. 1977, trap at 98-170 meters; SIO 80-223, 1, 297 mm TL, caught by commercial fishermen off Ta-Chi, collected by L. Chen, 30 June 1977; SIO 88-12, 2, 378, 484 mm TL, collected by MJ Yu from Su-ao, NE Taiwan, before July 1972; SIO 00-94, 1, 309 mm TL, off NE Taiwan, 24°52.5'N, 121°50-55'E, by H.-K. Mok, by trap, 28 June 1977, UMMZ 190386, 3, 139-365 mm TL, collected by K. Aoki near Misaki, Sagami Bay, Japan, Apr. 1929.

Diagnosis: Six pairs of gill pouches and apertures; prominent eyespots and white mid dorsal line; fused cusps 3/2, total cusps 40-42; total slime pores 81-92.

Description: Gill pouches and apertures 6 (rarely 5), well spaced in a linear pattern, the last left GA usually confluent with PCD; the 1st EBD

Table 1. Cusps, slime pores and body proportions of NW Pacific Ocean *Eptatretus*

	E. burgeri	*E. chinensis*	*E. strahani*	*E. fernholmi*	*E. okinoseanus*
Capture depth (m)	10-270	600	189	560	300-1020
Maximum TL (mm)	690	375	520	373	800
Gill pouches	6	6	7	8	8
Fused cusps	3/2	3/3	3/3	3/2	3/2
AUC	6-8	10-10	9-11	11-11	7-10
PUC	7-9	10-10	8-10	9-10	7-10
Total cusps	35-42	46-52	47-52	51	40-49
Slime pores:					
Prebranchial	18-23	15-19	13-15	15	13-17
Branchial	4-5	4-5	6	7	6-8
Trunk	45-51	42-45	45-48	50	54-61
Caudal	11-14	11-14	10-12	9	10-14
Total pores	81-92	72-83	76-80	81	87-97
Body proportions in % of TL:					
Prebr. length	25.2-29.6	25.0-25.7	21.0-23.1	21.2	19.2-22.6
Branchial length	6.2-7.8	7.4-8.0	5.2-8.7	8.0	6.2-9.2
Trunk length	47.6-55.0	51.7-52.0	48.2-56.4	56.3	50.4-59.4
Tail length	13.2-17.0	[5.2]-14.8	17.4-20.2	14.9	12.7-15.5
Depth w/VFF	4.7-8.5	-------	10.1-12.5	8.0	5.7-8.1
Depth w/oVFF	4.0-8.3	-------	10.1-12.5	8.0	5.5-7.9
Tail depth	5.1-8.5	7.7-8.5	10.9-12.5	8.6	6.2-9.0

about twice length of last one; 1 or 2 GP at end of dental muscle; ventral aorta splitting at 3rd or 4th GP, first GA about opposite second GP. Fused cusps 3/2, AUC 6-8, PUC 7-9, total cusps 36-41. Slime pores: PBR 19-22, BR 5, TR 46-49, TA 10-12, total pores 81-92. Body proportions for the SIO specimens: PBR 27-28%, BR 5.0-5.5%, TR 52-53%, TA 14-15%; body width at PCD 3.2-3.7%, body depth w/VFF 4.7-6.0%, w/o VFF 4.0-5.8%, depth at cloaca 4.5-5.8%, tail depth 5.6- 6.1%. Body brownish grayish tan dorsally, lighter ventrally, with a prominent pale stripe along dorsal midline; rostrum bluntly rounded; eyespots prominent; no pale margins on GA, PCD, or slime pores; VFF and CFF well developed. Dean (1904) wrote that in a collection of several hundred *E. burgeri*, the largest specimen was a 600 mm female; the longest male was 545 mm, and the "average length of 100 specimens was 41-42 cm." The larger SIO specimen is a 623 mm male, exceeding the maximum TL "60 cm" of Fernholm (1998). The skin of both SIO specimens was leathery, and they had shrunk some 3 to 4 mm in TL since first measured by the senior author in 1977. The ventral and caudal finfolds differ in these 2 specimens: the VFF of the male is about 3 mm and CFF also well developed while the VFF and CFF of the female are only about 1 mm, and tail depth is only about 1 mm more than cloacal depth. We have found great variation in tail shapes of *Eptatretus* specimens in the same collection, not related to the sex of the individual (McMillan and Wisner 1984: 260). Thus, these differences in VFF and CFF of the 2 SIO *E. burgeri* specimens are probably normal variation, rather than sexual dimorphism. Dean (1904) found the last GA on the left side to be in front of the PCD in as many as 10% of the 642 specimens he examined. He reported that most were taken "at depths of 3 to 4 fathoms" and were seen in shallow water near the steps of the Misaki Marine Laboratory. Strahan (1962) presented an intensive study of freshly collected specimens of *E. burgeri*; his data are included with our results and those of Fernholm (1998) in table 1.

Fig. 2. *Eptatretus burgeri*, UMMZ 190386, 365 mm TL.

Distribution: *Eptatretus burgeri* is known from Japan, South Korea, China, and Taiwan at various depths from about 5-8 meters in Japan (Dean 1904) to 450 meters off Taiwan (Kuo et al. 1994).

Remarks: Since *E. burgeri* was the 1st species of hagfish described from this region and is easily caught in shallow water, probably more is known about its habits and behavior than any other hagfish from the NW Pacific Ocean. It is of economic importance because of the demand for the "eel-skin" leather industry in Korea, the damage to fishes in nets, and its use as food in Taiwan, China, and Japan. It has been so intensively fished off Korea and Japan that populations are threatened, as shown by greatly reduced catches in fish size and number over the last 20 yr. Fernholm (unpubl. notes) collected 60 specimens of *E. burgeri* from Sagami Bay, Japan, with the ranges of characters all within those of the Korean and Chinese specimens, but found that those collected off NE Taiwan had "significantly higher numbers of cusps."

Temminck and Schlegel (1850) misidentified *E. burgeri* as *Heptatrema cirrhatum*, but Jordan and Snyder (1901) gave credit for the authorship to Charles Girard (1855) who published the following description in the *Proceedings of the Academy of Sciences*, *Philadelphia*: "We find mentioned in the Fauna Japonica, a species under the name of *Heptatrema cirrhatum*, which is another Bdellostoma (Bd. Burger), judging of it by the figure given on Plate CXLIII which exhibits a similar aspect of the head, the same shape of the mouth and cephalic tentacles. A singular circumstance is mentioned by Mr. Burger, by whom it was collected, and who states that during the summer months these fishes "generally a foot and some inches long," are caught in great numbers on mud bottoms in the Bay offshore near Samara, at some distance from Nagasaki, and that the Japanese usually ate them raw." Authors have since credited Girard with naming the species *E. burgeri* based on this brief description.

Eptatretus chinensis Kuo and Mok, 1994
(Table 1)

No specimens were available to us for this study; data and description below are from Kuo and

Mok (1994) with additional notes obtained from H.K. Mok by pers. commun. (5 Sept. 2001). The original description was based on 5 specimens, NSYSU 2866, 348 mm TL, and NSYSU 2867, 335 to 353 mm TL, from the continental slope in the South China Sea, SW of Taiwan, at 19°37'N, 113°14'E, 600 m depth.

Diagnosis: Six pairs of gill pouches and apertures, GA in a straight line, not crowded; eyespots prominent; fused cusps 3/3, 8-10 unicusps each row, total cusps 46-52; slime pores: PBR 15-19 + BR 4-5 + TR 42-45 + TA 11-14.

Description: Gill pouches and apertures 6, GA well separated in a straight line; last left GA confluent with PCD; 2-3 GP along end of DM; VA splits at 5th or 6th GP 5, just anterior to the heart. The following counts and body proportions are from the original description: Fused cusps 3/3, 10 unicusps in each row, total cusps 52. Slime pores: PBR 15-19 + BR 4-5 + TR 42-45 + TA 11-14. Body proportions: PBR 25.0-26.7%, BR 7.4-8.0%, TR 51.7-52.0%, TA 5.2-14.8%, tail depth 7.7-8.5%. Body brownish gray; eyespots prominent; deepest at mid-body; margins of VFF, GA, and PCD usually lighter than surrounding area; slime pores without pale margins. VFF low to vestigial; CFF thick ventrally, thinner around tail, ending dorsally over cloacal origin. The range for total slime pores (in diagnosis above) was not given in Kuo and Mok (1994); the hypothetical range of 72-83 was obtained by Honma (1998: 50) by adding the lower and upper ranges of each pore count. He also gave the maximum body length as "40 cm," but did not list any specimens examined; the largest specimen of Kuo and Mok (1994) was 353 mm. *Eptatretus chinensis* differs from *E. burgeri* in having 3/3 rather than 3/2 fused cusps and no white mid-dorsal line. It is distinguished from the other 3 Asian species of *Eptatretus* by having 6 rather than 7 or 8 pairs of GP.

Distribution: *Eptatretus chinensis* is known only from the type locality in the South China Sea, east of Hainan I., China and SW of Taiwan, at about 600 m depth.

Remarks: The lower figure (5.2%) of the range for tail length is unusually low, possibly a data processing error, as it is less than that of tail depth when it should be about twice as great. We could not check this measurement since we had no specimen of *E. chinensis* for study.

***Eptatretus fernholmi* sp. nov.**

(Table 1; Fig. 3)

Holotype: USNM 207761, tag 8686, 373 mm TL, taken at 12°43'51''N, 124°58'50''E by R/V Albatross, Station D 5444, by Agazzi trawl at 563 m, 3 June 1909, off Batag I., 5.1 miles [about 8.2 km] off Atalaya Pt, E of the southern end of Luzon I., the Philippines.

Diagnosis: Gill pouches and apertures 8, fused cusps 3/2, total cusps 51; total slime pores 81; eyespots absent; VFF vestigial.

Description: Gill pouches and apertures 8, well spaced in a straight line; VFF vestigial, CFF well developed, tail depth slightly more than mid-body depth. Lengths of barbels are unusual (1.0, 1.5, and 1.6 mm), since the 1st 2 pairs around the nasal orifice are usually about equal, while the 3rd pair may be up to twice the length of 1st 2 pairs. Fused cusps 3/2, anterior unicusps 11-11, posterior unicusps 9-10, and total cusps 51. Slime pores: PBR 5 + BR 7 + TR 50 + TA 9, total pores 81. Body proportions: PBR 21%, BR 8%, TR 56%, TA 15%, body depth 8%, depth at cloaca 6%, tail depth 9%. Body is slender, medium brown, badly deteriorated, with most skin missing; eyespots not visible. *Eptatretus fernholmi* is somewhat similar in numbers of cusps and slime pores to *E. strahani* (also from the Philippine I.), but differs in having 3/2 instead of 3/3 fused cusps and 8 rather than 7 GP. It is easily distinguished from *E. chinensis*, which has 6 GP. *Eptatretus fernholmi* with a slender body, no eyespots, and vestigial VFF, differs from *E. okinoseanus* (also with 8 GP), which has a wide body, prominent eyespots and well developed VFF. There are 4 other 8-gilled species of *Eptatretus* outside the study area: *E. indrambaryai* Wongratana, 1983 from the Andaman Is., Indian Ocean, *E. octatrema* Barnard, 1923 from South Africa, and 2 species from the Galapagos Is., *E. mccoskeri* McMillan, 1999 and *E. wisneri* McMillan, 1999.

Fig. 3. Holotype of *Eptatretus fernholmi*, USNM 207761, 373 mm TL.

Etymology: We are pleased to name this new species for Bo Fernholm for his many important contributions to the knowledge of hagfishes and for the discovery of this new species.

Distribution: *Eptatretus fernholmi* is known only from the type locality, 5.1 miles [about 8.2 km] off Atolaya Point, Batag I., E of the southern end of Luzon I., the Philippines.

Remarks: Data for the type specimen are from unpublished notes by Fernholm, who discovered this specimen in the U.S. National Museum of Natural History about 30 years ago. He planned to describe it as a new species "*E. luzonica*" with Carl L. Hubbs, to whom he gave the data and photo, but apparently abandoned the idea when Hubbs died a few years later. The notes and photo came into our possession with other hagfish data when Hubbs' lab was closed, and the specimen was left in the National Museum of Natural History. HK Mok (pers. commun.) reported that it could not be found at USNM when he wished to study it there in 2001.

***Eptatretus okinoseanus* (Dean, 1904)**

(Table 1; Fig. 4)

Homea okinoseana Dean, 1904 (original description); *Heptatretus okinoseanus* Regan, 1912.

Materials examined: CAS-SU 23552, 1, 410 mm TL collected in 1904 by K. Aoki from the fishing banks off the mouth of Tokyo Bay at about 730 m; FMNH 22654, 1, 620 mm TL, and FMNH 71701, 1, 690 mm TL, both specimens from Misaki Marine Biological Station, Sagami Bay, eastern coast of Honshu, Japan.

Diagnosis: Eight pairs of gill pouches and apertures, GA well spaced in a straight line; 3/2 fused cusps, total cusps 44-49; total slime pores 87-97; eyespots present; VFF well developed; CFF well developed only from tip of tail dorsally to above origin of cloaca.

Fig. 4. *Eptatretus okinoseanus*, FMNH 71701, 699 mm TL.

Description: Gills and apertures 8; GA well spaced in a straight line; last left GA confluent with PCD; 2-3 GP on left side and 1-2 on right side, along end of dental muscle; VA dividing opposite 7th or 8th GP. Fused cusps 3/2, unicusps 9-10 each row, total cusps 46-49. Slime pores: PBR 16-17 + BR 7 + TR 55-61 + TA 10-12, total pores 88-95. Dean (1904) described the body as robust, "its color dark purplish-brown in life", but body color is medium brown after many years in preservative. Eyespots present, but small and not prominent; GA and slime pores inconspicuous, without pale margins; VFF and CFF well developed, CFF extending dorsally to a vertical from cloacal origin. Body proportions for the small specimen of *E. okinoseanus* from the east coast of Taiwan (Kuo et al. 1994) are shown in brackets following those of the SIO and CAS specimens: PBR 19.2%-22.6% [21.9%], BR 8.3%-9.1% [8.7%], TR 56.5%-59.4% [56.4%], TA 12.9%-13.8% [15.5%], body width 5.0% [6.4%], body depth w/VFF 7.5% [10.0%], depth w/o VFF 6.2%, cloacal depth 6.0%, tail depth 7.6% [9.0%]. Dean (1904) gave no slime pore counts or body proportions, but stated that the figure (Fig. 2B) was drawn to scale. The proportions may be correct, but the number of slime pores on the artist's sketch is not accurate when compared with our data and those of Fernholm (1998). We omitted data for body proportions of the larger specimen of *E. okinoseanus* from Taiwan, since they only add up to 85.5%.

Distribution: For many years, *Eptatretus okinoseanus* was known only from the fishing banks of the mouth of Tokyo Bay at about 730 m depth. Two specimens were collected off Taiwan during 1988, one from the east coast at 300 m and a larger one from the SW coast at 1020 m, reported by Kuo et al. (1994).

Remarks: When originally described, *E. okinoseanus* was the largest known myxinid with specimens of 700-800 mm reported from Japan. The length of our largest specimen was 690 mm even with the shrinkage that occurred after many years in preservative. Dean (1904) studied several hundred specimens collected off Okinose, Honshu I., Japan; unfortunately he did not preserve very many, as there are very few in museums. His original description was of 3 specimens, 2 of which were placed in the Imperial Tokyo Museum and 1 sent to Columbia Univ., New York City. Dean (1904) reported that the eggs were

large and numerous, and "an 80 cm female had 44 well-developed eggs," with an average size of 35 x 12 mm. The body was described as "robust," its body width greater than that of *E. burgeri*.

Eptatretus strahani McMillan and Wisner, 1984
(Table 1)

Materials examined: USNM 227442, ♂, 465 mm TL, MNHN 1968462, ♀, 520 mm TL, SIO 81-116, 2, 265, 450 mm TL, collected at 14°00'N, 120°18.2'E, at 189 m, 21-22 Mar. 1976, near Lubang I. SW of Luzon I. the Philippines.

Diagnosis: Gill pouches and apertures 7; body brown, eyespots absent; VFF well developed; fused cusps 3/3, total cusps 47-52; total slime pores 76-80.

Description: Gill pouches and apertures 7, GA widely spaced in a straight line; 3-4 GP along end of DM; VA splitting at 7th GP just anterior to the heart. Fused cusps 3/3, AUC 9-11, PUC 8-10, total cusps 47-52. Slime pores PBR 13-16 + BR 6-7 + TR 45-48 + TA 10-12, total pores 76-80. Body proportions: PBR 22%, BR 8%, TR 50%-52%, TA 18%-20%, depth about 11% at mid-body and 12% at tail. Body brown, without eyespots; VFF well developed; slime pores and VFF without pale margins; CFF with very narrow pale margin, well developed only around end of tail and dorsally to above the origin of the cloaca. *Eptatretus strahani* is readily distinguished from the other species of Asian *Eptatretus* by having 7 rather than 6 or 8 pairs of gill pouches.

Distribution: *Eptatretus strahani* is known only from Lubang I., SW of Luzon, the Philippines at 189 m.

Remarks: In *E. strahani*, as in the other 4 species of Asian *Eptatretus*, bifurcation of the ventral aorta is just anterior to the heart at the last or next-to-last gill pouch. This same condition was also noted in *E. indrambaryai* (Wongratana 1983: 139, fig. 1C), *E. cirrhatus* (McMillan and Wisner 1984: 254, figs. 3-5), *E. polytrema*, and *E. bischoffi* (Wisner and McMillan 1988: 229, 231, figs. 2, 3).

Key to the species of *Paramyxine* from the NW Pacific Ocean

1a. Fused cusps 3/3 2
1b. Fused cusps 3/2 4
2a. Gill pouches 5; total cusps 50-53; prebranchial pores 24-27, total pores 76-81 ..... *P. cheni*
2b. Gill pouches 6 3
3a. Body dark brown dorsally, slightly lighter ventrally; 3-4 gill pouches along tip of dental muscle; ventral aorta splitting at gill pouch 4 or 5; separate pale rings around each gill aperture, not a white rectangular area; total cusps 49-53; total slime pores 62-74 ..... *P. sheni*
3b. Body uniformly dark purplish-brown with prominent pale rectangular area around branchial area apertures; 1-2 gill pouches at tip of dental muscle; ventral aorta splits at gill pouch 5 or 6; total cusps 47-52; total slime pores 71-78 ..... *P. atami*
4a. Ventral finfold well developed, with wide pale margin; total cusps 38-42; total pores 75-82 ..... *P. moki* sp. nov.
4b. Ventral finfold low to vestigial 5
5a. Body light brown or tan dorsally, gray or white ventrally 6
5b. Body uniformly medium to dark brown; eyespots usually absent or very faint; total cusps 38-44; total pores 69-79 ..... *P. walkeri* sp. nov.
6a. Branchial length over 4% of total length; last left GA confluent with PCD; ventral 1/2 of body grayish tan; ventral finfold with white margin ..... *P. wisneri*
6b. Branchial length less than 3% of TL; last left GA not confluent with PCD; ventral 1/2 of body white ..... *P. fernholmi* sp. nov.

Paramyxine atami Dean, 1904
(Table 2; Fig. 5)

Materials examined: TUM 9696, 1, 430 mm TL (no collection data); CAS-SU 23480, 1, 400 mm TL, collected by Aoki from Misaki, Sagami Bay, east coast of Honshu I., Japan. Our counts and measurements are combined in table 2 with those of Strahan (1962:806), data from 19 specimens from Fernholm (1998:34,38), and data from 1 specimen from Sagami Bay, USNM 161442 (Bigelow and Schroeder 1952).

Diagnosis: Six pairs of gill pouches with gill apertures closely spaced in a fairly straight line; 1-2 GP at end of dental muscle; ventral aorta splitting at about GP 5-6; fused cusps 3/3, total cusps 47-52; prebranchial slime pores 12-19, total pores 71-78; eyespots faint or absent; VFF low to vestigial.

Description: Six pairs of gill pouches and apertures; GA closely spaced in a fairly straight

Fig. 5. *Paramyxine atami*, TUM 9696, 430 mm TL.

line; 1-2 GP along end of DM; VA branching at about 5th or 6th GP, near the heart. Fused cusps 3/3, AUC 9-10, PUC 8-10, total cusps 47-52. Slime pores: PBR 17-19 +BR 0-1 + TR 43-47 + TA 9-12, total pores 71-78. Body proportions: PBR 26.6%-30.2%, BR 2.0%-3.2%, TR 53.9%-55.5%, TA 11%-14.2%, body depth w/VFF 8.1%-9.0%, depth w/oVFF 7.9%-8.0%, cloacal depth 6.3%-8.8%, tail depth 7.4%-8.8%. Body uniformly dark purplish-brown except for the GA area, which appears as a prominent white rectangle caused by the merging of the pale rings around the very closely spaced GA; eyespots absent or very faint; slime pores color of body. Prebranchial and caudal pores conspicuous, but trunk pores small and difficult to count; branchial region usually without pores; no pale margins on barbel tips, slime pores, ventral, or caudal finfolds. Ventral finfold low to vestigial, only about 1 mm deep at mid-body, tapering to a line at cloaca. Caudal finfold thin, but well developed around tail, continuing dorsally to a vertical above cloacal origin where it becomes a distinct fleshy ridge along dorsal mid-line to about 1/3 third of trunk length. Neither Dean (1904) nor Fernholm (1998) noted this fleshy ridge extending forward on the dorsal midline from the caudal finfold; however, Bigelow and Schroeder (1952) said that the "dorsal finfold" on the 500 mm specimen of *P. atami* (USNM 161442) continued forward as a "definite though low dermal ridge to the last pair of gill openings." Shen and Tao (1975) compared their new species *P. taiwanae* with specimens identified as *Paramyxine atami*, ranging from 100 to 500 mm in total length, but did not state date or location of collection. They could have been dealing with the Taiwanese *Paramyxine* with 6 GP and 3/3 fused cusps, later described as *P. sheni*, but it has not been found to exceed 450 mm in total length. *Paramyxine atami* and *P. sheni* are similar in most counts and body proportions and have the same number (34) of somatic chromosomes (Kitada and Tagawa 1975). *Paramyxine atami* has a few more trunk and total pores, 43-47 and 71-78 compared to *P. sheni* with 39-46 and 62-67, respectively. There are also small differences in the color pattern of the branchial area; with pale rings around each GA of *P. sheni* and a solid white rectangular area in *P. atami* since the gill apertures are closer together. Further DNA and biochemical studies may prove them to merely be different populations of the same species, but until new material and studies prove differently, we will consider *P. atami* and *P. sheni* as separate species. Unfortunately Dean (1904) gave no slime pore counts, and those derived by Bigelow and Schroeder (1952) from Dean's figure were not accurate. Strahan and Honma (1961: 336) also noted the unusually high number of "abdominal

Table 2. Cusps, slime pores and body proportions of the NW Pacific Ocean *Paramyxine*

	P. cheni	*P. sheni*	*P. atami*	*P. moki*	*P. walkeri*	*P. wisneri*	*P. fernholmi*
Capture depth (m)	180-268	200-619	300-536	100	75-120	200	300-412
Maximum TL (mm)	386	436	610	470	518	388	359
Gill pouches	5	6	6	6	6	6	6
Fused cusps	3/3	3/3	3/3	3/2	3/2	3/2	3/2
AUC	9-11	9-12	9-10	6-8	6-8	7-10	8-10
PUC	8-11	8-11	8-10	7-9	6-9	7-9	8-10
Total cusps	50-53	48-53	47-52	38-42	38-44	36-44	38-44
Slime pores:							
Branchial	0-0	0-2	0-1	0	0	0-1	0
Trunk	41-47	39-47	43-47	44-50	40-48	36-44	38-44
Caudal	7-10	8-12	9-12	10-14	9-14	6-11	5-11
Total pores	75-81	62-74	71-78	75-82	69-79	63-72	64-71
Body proportions in % of total length:							
Prebr. length	33.3-35.5	24.5-30.7	26.6-30.2	26.8-30.9	26.5-32.0	28.-30.7	29.8-32.5
Branchial length	2.2-3.4	2.4-4.2	1.3-4.2	1.4-3.0	2.0-3.1	4.6	2.0-2.9
Trunk length	45.9-50.8	53.2-56.2	53.9-56.1	49.2-55.1	52.6-57.7	49.4	49.8-52.0
Tail length	13.2-16.7	14.4-16.7	11.1-14.2	15.4-19.5	13.0-15.6	13.6	3.4-16.3
Depth w/VFF	8.1-9.9	7.3-10.0	8.1-9.0	6.7-10.3	6.4-8.4	9.6	6.4-10.4
Depth w/oVFF	7.7-9.9	6.9-9.2	7.9-8.0	5.2-8.2	6.2-8.2	9.3	5.6-8.0
Tail depth	7.6-10.2	8.3-10.0	7.4-8.8	7.7-9.7	7.1-8.3	10.5	7.0-10.5

slime glands."

Distribution: *Paramyxine atami*, known only from the east coast of Honshu I., Japan, was first collected at about 486 m off Cape Manazuru near Atami (W coast of Sagami Bay), and has also has been taken from Hyalonema Grounds, and Suruga Bay from 300-536 m (Fernholm 1998).

Remarks: Strahan and Honma (1961: 335) obtained 5 specimens of *P. atami* from Suruga Bay, just S of Sagami Bay and Atami, and found that they had significantly higher numbers of cusps than in their *Paramyxine* specimens from the Sea of Japan. Some 6-gilled *Paramyxine* from Taiwan, formerly identified as *P. atami*, were described as 3 new species by Kuo et al. (1994); those with 3/3 fused cusps were described as *P. sheni*, and those with 3/2 fused cusps became either *P. fernholmi* or *P. wisneri*.

***Paramyxine cheni* Shen and Tao, 1975**
(Table 2)

Materials examined: SIO 88-14, 2, 280, 386 mm TL, Taiwan, by Fernholm, 1 June 1976; SIO 99-91, 1, 333 mm TL, from 22°23.3'N, 120°15.5'E, at 225 m depth, collected in a shrimp trap 9 Jan. 1998 by H.-K. Mok; SIO 00-31, 2, 147, 209 mm TL, found by H.-K. Mok in the Tung-Kong fish market, collected from about 22°35.6N, 120°14.1'E at 156 m depth, 15 Nov. 1996; NTUM 27212, 1, 357 mm and NTUM 7502714, 1, 361 mm TL, caught off Tung Kong at 20°28'N, 120°26.3'E, by trawling net at about 180 m, 10 Feb. 1975.

Diagnosis: Five pairs of gill pouches and apertures; GA closely spaced in a straight line, the last GA not confluent with PCD. Fused cusps 3/3, total cusps 50-53; prebranchial slime pores 24-27, total pores 75-81; eyespots absent; ventral finfold vestigial.

Description: Five pairs of GP and GA, closely spaced in a straight line, last GA slightly anterior to PCD, no branchial slime pores; 1 or 2 GP along tip of DM; ventral aorta branching after the 3rd GP. Fused cusps: 3/3, AUC 9-11, PUC 8-11, total cusps 50-53. Slime pores PBR 24-27 + BR 0 + TR 41-46, TA 7-10, total pores 75-81. Body proportions: PBR 33.3%-35.5%, BR 2.2%-3.4%, TR 45.9%-50.8%, TA 13.2%-16.7%, body width 4.8%-6.3%, depth w/VFF 8.1%-9.9%, depth w/oVFF 7.7%-9.6%, cloacal depth 7.8%-9.9%, tail depth 7.6%-10.2%. Originally described as "light brown in formalin," body color in alcohol is now grayish-brown dorsally, lighter ventrally; eyespots absent; GA, PCD and slime pores without pale margins. VFF vestigial or absent, without pale margin; tail rounded, depth of CFF slightly deeper than mid-body depth. Maximum length for this species is probably about 400 mm, and it is fully adult at little more than 300 mm TL; one 333 mm male had developing testes and a 313 mm female had eggs to 4 mm. *Paramyxine cheni* is easily distinguished from the other Asian 6-gilled *Paramyxine* since it has 5 GP and very high numbers of prebranchial pores (24-27), about 5 to 10 more than in the other Asian *Paramyxine*.

Distribution: *Paramyxine cheni* has been reported from the SW coast of Taiwan, at 156-400 m, at 20°25.0'N, 120°26.3'E. It was also collected at several stations from about 22°10'-24'N, 120°14'-37'E at depths of 156 to 268 m (Mok and Chen 2001).

Remarks: The pattern of fused cusps was given as 3/2 by Shen and Tao (1975), but later corrected to 3/3 by Kuo et al. (1994: 132). The original description of this species stated that 26 prebranchial pores was "the highest number of prebranchial pores in any *Paramyxine*," but we found 27 in one of our SIO *P. cheni* specimens.

***Paramyxine fernholmi* Kuo, Huang and Mok, 1994**
(Table 2)

Materials examined: SIO 00-183, 1, 325 mm TL, collected by H.-K. Mok by trap, from 22°23' 25"N, 120°14'08"E, 5 Oct. 1996, at 330 m (photo in Kuo et al. 1994:138, fig. 9); 2 collections taken by otter trawl, off Tung Kong, SW Taiwan by L. Chen: SIO 80-206, 1236 mm TL, 20 Oct. 1976 and SIO 00-207, 1180 mm TL, at 384 m, 6 Nov. 1976.

Diagnosis: Six pairs of gill pouches and apertures, GA very close together in a fairly straight line; last left EBD not confluent with PCD; branchial length less than 3% of total length; fused cusps 3/2, total cusps 42-50; prebranchial slime pores 16-23, total pores 64-71; VFF poorly developed.

Description: Six pair of gill pouches and apertures, GA close together in a fairly straight line, 1 to 3 GP along end of DM; VA branching at 3rd or 4th GP. Fused cusps 3/2, unicusps 8-10 in each row, total cusps 42-50. Slime pores: PBR 16-23 + BR 0 +TR 38-44 + TA 6-11, total pores 64-71. Body proportions: PBR 29.8%-32.5%, BR 2.0%-2.9%, TR 49.8%-51.3%, TA 14.4%-16.3%, body depth w/VFF 6.2%-8.0%, depth w/oVFF 5.6%-8.0%, cloacal depth 5.2%-6.3%, tail depth 7.0%-9.0%. Body light brown dorsally and grayish white ventrally; eyespots absent; GA area pale, but not obvious against light body; VFF poorly developed,

1 mm or less at deepest point, tapering to little more than a white line along ventral midline; CFF well developed. *Paramyxine fernholmi* and *P. wisneri* are similar in size, color and counts, but are easily distinguished by the branchial length, less than 3% of TL in the former and more than 4 % in the latter.

Distribution: *Paramyxine fernholmi* has been collected from the SW coast of Taiwan, usually at depths of 200-400 m (Kuo et al. 1994). Mok and Chen (2001) list 3 stations off of the SW coast of Taiwan where *P. fernholmi* was taken: 122 specimens at 384 m, 11 at 412 m, and 1 at 400 m.

Paramyxine moki sp. nov.
(Table 2; Fig. 6)

Holotype: SIO 87-104, 1, 470 mm TL, collected by B. Fernholm, 21 Nov. 1972 at about 100 m., from Koajiro-wan off Kanagawa-ken, Sagami Bay, 10 meters north of Misaki Marine Biological Station, E. coast of Honshu I., Japan.

Paratypes: SIO 87-104, 8, 368-460 mm TL, taken with the holotype.

Diagnosis: Six pairs of gill pouches and apertures, GA closely spaced in a nearly straight line, closely spaced but not crowded; fused cusps 3/2, total cusps 38-43; prebranchial slime pores 18-21; total pores 75-82; ventral finfold well developed with wide pale margin; eyespots faint or absent.

Description: Gill pouches and apertures 6; GA in a straight or slightly irregular line; the first GA opposite the 5th or 6th GP; 1 GP on right and 2 GP on left side along end of DM; VA splitting at 3rd or 4th GP. Fused cusps 3/2, AUC 6-8, PUC 7-9, total cusps 38-43. Slime pores: PBR 18-21 + BR 0 + TR 44-50 + TA 10-14, total pores 75-82. Body proportions: PBR 26.8%-30.9%, BR 1.4%-3.0%, TR 49.2%-55.1%, TA 15.4%-19.5%, body width at PCD 4.6%-5.7%, depth w/VFF 6.7%-10.3%, depth w/oVFF 5.2%-8.2%, cloacal depth 5.8%-8.2%, tail depth 7.7%-9.7%. Body dark brown, slightly lighter ventrally; rostrum bluntly rounded, small pale area around mouth and on labial barbels; the other 3 pairs of barbels the same color as body; slime pores without pale margins; eyespots faint or absent; pale rings around GA; VFF well developed with wide pale margin; CFF well developed, without pale margin. *Paramyxine moki* is distinguished from *P. atami* by its 3/2 fused cusps, and from *P. walkeri* (described below) by its well-developed VFF with pale margin. It matures at a much greater total length than the Taiwanese *Paramyxine*, and the VFF is very deep, about 1% to 2 % of the TL compared to 0.2%-0.5% in the other 2 species of Japanese *Paramyxine*.

Fig. 6. *Paramyxine moki* sp. nov., SIO 87-104, 470 mm TL.

Etymology: We are pleased to name this species for our friend Hin-kiu Mok of National Sun Yat-Sen Univ., Taiwan for his many outstanding contributions to the knowledge of hagfishes.

Distribution: *Paramyxine moki* is known only from Misaki, Sagami Bay, Honshu I., Japan.

Remarks: Former references to *Paramyxine* specimens with 3/2 fused cusps that had been collected in the Sagami Bay area were probably this new species, *P. moki*.

Paramyxine sheni Kuo, Huang and Mok, 1994
(Table 2)

Materials examined: SIO 80-207, 1, 180 mm TL, from Tung Kong, SW Taiwan, collected by L. Chen, Nov. 1976; 2 collections by H.-K Mok: SIO 99-90, 2, 380, 399 mm TL, NW of Hsinchu, Taiwan, 25°08.9'N, 121°47.1'E by trap at 427 m, 25 Sept. 1977; SIO 00-34, 2, 195, 201 mm TL, from SW coast of Taiwan, 22°22.9'N, 120°22.9'E, at 585 m, 8 Mar. 1998.

Diagnosis: Six pairs of gill pouches and apertures; GA in a straight line, closely spaced, but not crowded; eyespots prominent; ventral finfold low; fused cusps 3/3, total cusps 48-53; prebranchial slime pores 13-19, total pores 62-74.

Description: Six GP and GA, apertures in a fairly straight line; 3-4 GP along end of DM; VA splitting at 4th or 5th GP. Fused cusps 3/3, AUC 9-12, PUC 8-11, total cusps 48-53. Slime pores: PBR 12-18 + BR 0-2 + TR 39-46 + TA 8-12, total pores 62-74. Body proportions: PBR 24.5%-27.4%, BR 3.0%-4.2%, TR 53.2%-56.0%, TA 14.4%-16.7%, body width 5.6%-6.6%, body depth w/VFF 7.3%-10.0%, depth w/oVFF 6.9%-9.2%, cloacal depth 7.9%-9.2%, tail depth 8.3%-10.0%.

Body dark brown dorsally, very slightly lighter ventrally; eyespots prominent; VFF low; slime pores, VFF, and CFF without pale margins. *Paramyxine sheni* is easily distinguished from *P. cheni* by having 6 rather than 5 pairs of GP, and its 3/3 fused cusps distinguish it from *P. fernholmi* and *P. wisneri*. *Paramyxine sheni* is very similar to *P. atami* in most counts and body proportions. They differ in maximum length; *P. atami* attains a greater total length, 610 mm, compared to about 450 mm for *P. sheni* (Fernholm, 1998), and there are also slight differences in color patterns. *Paramyxine sheni* has a brown body with prominent eyespots and GA separated enough so that the pale margins appear as rings around each one, while in *P. atami*, the eyespots are faint or absent, and the body is dark purplish-brown all over except for a sharply contrasting white rectangle in the branchial area. Kuo et al. (1994) stated that these 2 species differed in the higher trunk pore count (58-59) for the "type" of *P. atami* using the counts from Bigelow and Schroeder (1952: 3, Table 1). We agree with Strahan and Honma (1961: 336) that this figure was not accurate, since it was obtained by counting the pores on the artist's sketch (Dean 1904: 11, fig. 2D). This figure is obviously not true to life, as the slime pores begin too far forward, are too close together, and continue in a straight line from the PCD all the way to the end of the cloaca, with no tail pores. Trunk pores usually commence a little higher and slightly posterior to the PC, and always terminate well ahead of the cloacal origin, with a smooth space before the caudal pores begin higher and curve downward at the end of the cloaca, continuing for about 2/3 of the tail length. Bigelow and Schroeder (1952) also gave the trunk pores for the left and right sides (47, 47) of the USNM specimen, which are in the range we obtained (43 to 47) from counting the TUM and CAS specimens. Thus, there is a slight overlap in trunk pores for *P. sheni* (39-46) and *P. atami* (43-47). Kuo et al. (1994) reported the reproductive season as Jan. to Mar., the smallest female with developing eggs was 355 mm TL, and the largest eggs were about 39 mm long.

Distribution: Known from the SW and NE coasts of Taiwan, with a depth range of 200 to 800 m (Kuo et al. (1994). Mok and Chen (2001) reported 27 specimens from 276 to 427 m and 38 from various traps at 585 to 619 meters from the SW coast of Taiwan.

Remarks: *Paramyxine sheni* is apparently the largest species of *Paramyxine* known from Taiwan; Mok and Chen (2001) reported one 436 mm specimen at 283 m depth off NE Taiwan at 24°50'43"N, 122°01'08"E.

***Paramyxine walkeri* sp. nov.**

(Table 2; Fig. 7)

Holotype: SIO 76-257, 450 mm TL, taken off Choshi, E coast of Honshu I., Japan, at 75 m, 26 June 1973.

Paratypes: SIO 76-257, 9, 350-518 mm TL, taken with the holotype.

Non type materials: The following collections from the W coast of Honshu I., Sea of Japan: SIO 02-102 [formerly UMMZ 190390], 1, 305 mm TL, from 37°30'N, 139°0'E, in 1906, depth unknown, SIO 94-140, 7, 364-446 mm TL, collected by Fernholm, 21 Aug. 1973 from Izumosaki near Sado I., at 120 m; MCZ 40766, 6, 225-440 mm TL, collected by R. Strahan and Y. Honma, at 100 m, 8 mi offshore from Teradomari-machi, E of Sado I. and S of Niigata, 22 Oct. 1959; UMMZ 190391, 1, 315 mm TL [322 mm in 1972], collected by K. Aoki for the No Fishery School, at Niigata-ken, in 1906.

Diagnosis: Six pairs of gill pouches and apertures, closely spaced in a linear or slightly irregular pattern, each GA with pale margin; fused cusps 3/2, total cusps 38-44, prebranchial slime pores 16-20, total pores 69-79; VFF poorly developed to vestigial; eyespots faint or absent.

Description: Six (rarely 5) pairs of GP and apertures; GA closely spaced but not crowded, in a linear or slightly irregular pattern, last left GA usually confluent with PCD, each GA with pale margin; 1-2 GP at end of DM; VA splitting at 3rd or 4th GP. The following counts and body proportions are the data from the Choshi specimens (SIO 76-257) followed by those from the Sea of Japan collections in brackets: Fused cusps 3/2 [3/2], AUC

Fig. 7. *Paramyxine walkeri* sp. nov., SIO 76-257, 450 mm TL.

7-8 [7-9] PUC 7-8 [7-9], total cusps 38-42 [39-44]. Slime pores: PBR 16-23 [17-20] + BR 0 [0] + TR 42-48 [40-47] + TA 10-14 [10-13], total pores 69-79 [71-75]. Body proportions: PBR 26.5%-31.6% [26.5%-32.0%], BR 2.0%-3.6% [2.1%-3.2%], TR 52.6%-57.7% [54.2%-55.7%], TA 13.0%-15.6% [13.9%-15.6%], body width 4.9%-5.8% [4.1%-5.0%], body depth w/ VFF 6.4%-8.4% [6.9%-8.4%], depth w/o VFF 6.2%-8.2% [6.6%-8.2%], cloacal depth 5.6%-6.8% [5.6%-6.8%], tail depth 7.1%-8.3% [7.4%-8.2%]. Body brown; eyespots very faint or absent; rostrum bluntly rounded; slime pores small and inconspicuous; GA with pale margins. Ventral finfold low to vestigial at mid-body, tapering to a line at cloaca, slightly lighter color than body with very narrow pale margin. CFF absent from ventral part of tail, but well developed around end of tail and dorsally to a vertical above cloacal origin; some specimens with very narrow pale margin around posterior edge of tail. This appears to be a fairly large species at maturity; the smallest specimen in our study material is 350 mm TL, and a 390-mm male has testes not well developed. Two females at 446 and 460 mm had eggs only up to 4 mm in length without empty sacs indicating previous mature eggs. All other females, including one 362 mm long, had only round eggs less than 1 mm. *Paramyxine walkeri* differs from *P. atami* in having 3/2 rather than 3/3 fused cusps, 38-42 rather than 45-50 total cusps, and slightly shorter trunk length. The type specimens of *P. walkeri* were taken off Choshi on the E coast of Honshu I., and non type materials were collected off the W coast of Honshu in the Sea of Japan. The body color of the specimens in collection SIO 94-140 from Izumosaki, near Sado I., is very light brown, with very smooth, slippery skin, without the usual wrinkles, which could have been caused by too strong a preservative or exposure to sunlight. Because of the different color and somewhat distant capture location, as well as Fernholm's label, we had assumed that the Sea of Japan collection (SIO 94-140) was a different species from the Choshi collection. However, we recently obtained 7 more specimens collected near Sado I. In the Sea of Japan that are darker than those from Izumosaki, about the same color brown as those of SIO 76-256 from Choshi. Further comparison of the cusps and slime pores showed almost complete overlap with no significant differences in the figures for counts and body proportions of these 4 collections. The only difference was in the slightly lower average branchial length of SIO 94-140, caused by aberrant branchial configuration in 3 of the 7 specimens where there are fewer GA because 2-3 EBD combined to discharge through 1 aperture or the PCD. We shall consider the specimens from the Sea of Japan (MCZ, UMMZ, SIO 94-140) collections as *P. walkeri* until further material is obtained and DNA or other studies prove that specimens taken from the Sea of Japan actually differ from those taken off Choshi Pt.

Etymology: We have named this new species for H.J. Walker Jr. for his valuable assistance in providing us with hagfish specimens and data, and for his contributions to ichthyology.

Distribution: Known from Choshi Pt., E Honshu I., and from Izumosaki to Niigata on the W coast of Honshu I., Sea of Japan.

Remarks: The 6 MCZ specimens collected from Teradomari, Sea of Japan, were originally considered to be *Paramyxine atami* by Strahan and Honma (1961: 334), but they apparently had doubts since they found that their specimens had significant differences in some characters, especially in the cusps, from the type specimen of *P. atami*. The range for the TL of their 140 specimens was 130-583 mm. Strahan and Honma (1961: 329) also remarked on variation in the number of gill apertures, "one individual with 7 GA" where the 6th EBD was not confluent with PCD, and sometimes only 4 or 5 instead of 6 GA, "having one of the apertures shared by two adjacent ducts." We noted this same aberrant condition of the branchial ducts in 3 of the 7 specimens in the collection from Izumosaki, Sea of Japan. For many years 6-gilled Japanese *Paramyxine* with 3/2 fused cusps were misidentified as *P. atami*, including those from the Sea of Japan. Such references are as follows: Matsubara (1937), Okada et al. (1948), Okada (1955), Honma (1960), Lindberg and Legaza (1967), Strahan and Honma (1960).

Paramyxine wisneri Kuo, Huang and Mok, 1994

(Table 2)

Material examined: SIO 02-76, 1, 198 mm TL [former NSYSU 2869, paratype] from the coastal waters of Fukang, SE Taiwan, at about 200 m, 28 Sept. 1990, about 22°45'N, 121°10'E.

Diagnosis: Six pairs of gill pouches and apertures, GA closely spaced in a straight line; branchial length more than 4% of TL; fused cusps 3/2, total cusps 38-46; prebranchial slime pores 15-20, total pores 63-72; eyespots present but not prominent; VFF low to vestigial, with white margin.

Description: Six pairs of GP and GA, gill aper-

tures in a straight line, closely spaced, but not crowded, each with a pale margin, last left GA usually confluent with PCD; 2-4 GP along end of DM; VA splitting between the 3rd and 4th GP. We only had 1 specimen (former paratype, NSYSU 2869) for study material, so we have included the data of Kuo et al. (1994) with our counts and body proportions to obtain a meaningful range: Fused cusps 3/2, AUC 7-10, PUC 7-9, total cusps 36-48. Slime pores: PBR 15-20 + BR 0-1 + TR 36-44 + TA 6-11, total pores 63-72. Body proportions: PBR 28.0%, BR 4.6%, TR 49.4%, TA 13.6%, body width 5.1%, body depth w/VFF 9.6%, depth w/oVFF 9.3%, cloacal depth 8.1%, tail depth 10.5%. Color of preserved specimens light brown dorsally, lighter ventrally; eyespots present but not prominent. Gill apertures with pale rings, last left GA confluent with PCD; VFF low to vestigial, with pale margin obvious against slightly darker body. Ranges of counts and most body proportions are very similar to those of *P. wisneri* and *P. fernholmi*, suggesting that these 2 species may be closely related. The original description (Kuo et al. 1994) stated that the VFF is "prominent" and white in *P. wisneri*, while the entire ventral surface of *P. fernholmi* is white, but the specimens we have are very similar in color, light brown on the dorsal 1/3, and gray to white on the ventral part. Also, the VFF in both species are very low to vestigial. These 2 species are distinguished mainly by the difference in the branchial length, 4.5%-4.6% in *P. wisneri*, and 2.0%-2.9% in *P. fernholmi*, caused by the much closer crowding of the GP and GA in the latter species.

Distribution: Known only from the coastal waters off SE Taiwan at about 330-412 m depth.

Remarks: The location of collection SIO 02-76 [former NYSU 2869] was spelled "Fukan" by Kuo et al. (1994), but is shown as "Fukang" on the map in Mok and Chen (2001: 234, fig. 1).

Key to the 3 species of *Quadratus* from the NW Pacific Ocean

1a. Gill pouches 5(rarely 4) 2
1b. Gill pouches 6; total slime pores 60-68..... *Q. taiwanae*
2a. Trunk slime pores 33-39, total pores 57-67 ..... *Q. nelsoni*
2b. Trunk slime pores 39-47, total pores 68-79 ..... *Q. yangi*

***Quadratus nelsoni* (Kuo, Huang and Mok, 1994)**

(Table 3; Figs. 8, 11a)

Paramyxine nelsoni Kuo, Huang and Mok, 1994 (original description).

Materials examined: Three collections taken by otter trawl by L. Chen: SIO 80-205, 15, 105-230mm TL, off TungKong, July 1973; SIO 80-208, 2, 165, 185 mm TL, from TungKong, 19 Dec. 1976; SIO 80-215, 1, 247mm TL, from the Taiwan Strait, 18 Mar. 1977; SIO 80-300, 5, 117-259 mm TL, 10 June 1980; SIO 00- 184, 1, 153 mm TL, collected by H.-K. Mok, at 22°24'42"N, 120°15' 8"E, by trap at 179 m, 31 Dec. 1997; SIO 91-139, 2, 235, 253 mm TL, collected by M.-J. Yu, off Tung Kong, prior to 1975; NTUM 1103528, 1, 194 mm TL, collected by H.-C. Yung, 21 Feb. 1958, 100-150 m depth.

Diagnosis: Five gill pouches and apertures, GA crowded together in an irregular pattern; fused cusps 3/2, anterior unicusps 5-8, posterior unicusps 5-7, total cusps 32-38; trunk slime pores 33-39, total pores 57-67.

Description: Five GP and GA, crowded together in an irregular pattern, each GA surrounded by a pale ring, so close that the branchial area appears white. Last left GA usually confluent with PCD, 1 to 2 GP at tip of DM, VA splitting at 3rd or 4th GP. Ventral finfold vestigial, CFF well developed, giving tail a rounded appearance; body depth at tail about the same as mid-body depth. Fused cusps 3/2, AUC 5-8, PUC 5-7, total cusps 32-38; slime pores: PBR 14-20 + BR 0 + TR 35-39 + TA 6-10, total pores 65(57-67). Body proportions: PBR length 30.5%-32.6%, BR 1.2%-2.8%, TR 49.5%-52.6%, TA 15.0%-15.5%, body width 8.9%-9.2 %, body depth w/VFF 15.0%-15.5%, depth w/oVFF 14.7%-15.3%, cloacal depth 6.4%-7.1%, tail depth 8.9%-10.1%. Body brownish-gray, eyespots absent, ventral finfold low to vestigial, CFF well developed. This is a dwarf species; males develop testes at about 200 mm and a 224 mm female had elongated eggs; a 268 mm specimen had eggs 24 mm long; and a 244 mm specimen had 11 eggs about 15 mm long with polar caps already forming. *Quadratus nelsoni* appears to be closely related to the other 2 *Quadratus* from Taiwan, with 3/2 fused cusps, similar coloring and small size at maturity. However, it is easily distinguished from *Q. yangi* by having about 10 fewer trunk and total slime pores, and a much deeper body, 15.0%-15.5% compared to 7%-10% in *Q. yangi*. *Quadratus nelsoni* is distinguished from *Q. taiwanae* by having 5 rather than 6 GP. Although similar in many characters, frequency distribution charts of Kuo and Mok (1999) clearly proved *Q. nelsoni* and *Q. yangi* to be 2 distinct species. The number of GP in the original description of this species (Kuo et al. 1994) was reported as 4, based on 1 small specimen with only 4 gill apertures.

When later dissected, it was found to have 5 gill pouches, with 2 EBD joined to discharge through the same GA. Kuo and Mok (1999) found that nine of 309 *Q. nelsoni* specimens varied from 5 pairs of GP and GA; 3 had 4-4 GP and GA, and the other 6 specimens had various combinations of 3-4 and 3-5, and 4-5 GP and GA.

Distribution: *Quadratus nelsoni* is known from the coastal waters off Tung Kong, SW Taiwan at depths of 82-250 m, and from the Taiwan Strait; sometimes collected with *Q. yangi* and *Q. taiwanae*.

Remarks: From Sept. 1996 through Oct. 1997 over 300 specimens were collected from the SW coast of Taiwan (Kuo and Mok 1999). However, only 8 specimens of *Q. nelsoni* were collected, at 22°24'25"N, 120°15'51"E, at 179 m depth among the many hundreds of hagfishes taken in a 4-yr survey (Mok and Chen 2001).

Quadratus taiwanae (Shen and Tao, 1975)

(Table 3; Figs. 9, 11c)

Paramyxine taiwanae Shen and Tao, 1975 (original description).

Materials examined: SIO 76-256, 4, 160-250 mm, caught by fishermen at 100-150 ft [31-46 m], off Ta-Chi, NE Taiwan, 26 May 1972, at about 24°56.5'N, 121°53'E, collected by S.C. Chen; SIO 88-13, 5, 178-285 mm TL, collected off Ta-Chi by Fernholm, 4 Mar. 1972; SIO 02-99, 1, 213 mm TL, collected off Ta-Chi by M.-J. Yu for Fernholm, 1 June 1972; SIO 80-215, 1, 247 mm TL, collected by L. Chen from the Taiwan Strait, 18 Mar. 1977; 3 collections by trawl off Ta-Chi by L. Chen: SIO 80-212, 6, 212-283 mm TL, 12 Feb. 1977, SIO 80-299, 1, 253 mm TL, 21 May 1977; SIO 88-11 [formerly NTUM 723401], 3, 178-262 mm TL, at 100-180 fath [183-329 m], 4 Mar. 1972. Data from our specimens are combined with those of the original description of 118 specimens and data from Kuo et al. (1994) to obtain ranges of counts in table 3.

Diagnosis: Six pairs of gill pouches and apertures, GA crowded together in irregular pattern; fused cusps 3/2, unicusps 6-8/ 5-9, total cusps 32-37; trunk slime pores 36-42, total pores 60-68.

Description: Six GP and apertures, GA crowded together in an irregular pattern; the 1st EBD about 3.2 times longer than the last one; 1 to 2 GP along end of DM; VA splitting at 4th or 5th GP. Counts and body proportions from SIO specimens: Fused cusps 3/2, unicusps 6-8 in each row, total cusps 32-36. Slime pores: PBR 16-19 + TR 36-42 + TA 6-9, total pores 60-68. Body proportions: PBR 28%-35%, BR 1.3%-2.7%, TR 51.8%-56 %, TA 12.1%-14.6 %, body depth w/VFF 9.4%-11.0%, w/oVFF 8.1-9.4%, cloacal depth 8.1%-10.0%, tail depth 8.1%-11.8%. Body light brown dorsally and gray ventrally; eyespots faint or absent; GA so close together that the entire branchial area appears as a white patch. Body depth greatest at mid-body, VFF low to vestigial, about 1 mm deep at mid-body, tapering to a white line, ending at cloaca. Ventral part of CFF is absent from cloaca to end of tail, where it is well developed and continues dorsally to above cloaca. *Quadratus taiwanae* is closely related to the other 2 species of *Quadratus* from Taiwan, but is easily distinguished by having 6 rather than 5 GP. This is a dwarf species maturing at less than 300 mm TL; the maximum length of 118 specimens was only 317 mm. Two females, 260 and 275 mm, contained 6 and 7 eggs, some as large as 17 x 6 mm, with weakly formed polar caps, and a 283 mm female had 8 eggs about 18 x 9 mm. Kuo et al. (1994) stated that 12% of specimens from the SW region had eggs in February, the largest egg of 20.6 mm, found in a 295 m female with 10 eggs.

Fig. 8. *Quadratus nelsoni*, SIO 80-215, 247 mm TL.

Fig. 9. *Quadratus taiwanae*, SIO 02-99, 213 mm TL.

Distribution: *Quadratus taiwanae* has been collected mainly off Ta-Chi, NE coast of Taiwan, by trawl at 24°46-56'N, 121°53-54'E, at about 31 to 46 m, and 1 collection is known from the Taiwan Strait. Mok and Chen (2001) reported several collections, including 74 specimens of *Q. taiwanae* (with 95 *Q. yangi* and 76 *E. burgeri*) off Ta-Chi at 120 m. In the original description (Shen and Tao 1975), 114 of the 118 specimens were from NE Taiwan and only 4 were collected from Tung Kong, SW Taiwan.

Remarks: Shen and Tao (1975) originally described *taiwanae* as a *Paramyxine*, and compared it with *P. atami*, but it is more closely related to *Q. nelsoni* and *Q. yangi*. Wisner (1999) changed the genus to *Quadratus*, because of the closely crowded, irregular pattern of the GA.

Quadratus yangi (Teng, 1958)

(Table 3; Figs. 10, 11b)

Paramyxine yangi Teng, 1958 (original description). The genus *Quadratus* was erected by Wisner (1999) to include 3 species formerly classified as *Paramyxine*. We hereby designate *Q. yangi* as the type species of the genus *Quadratus*.

Materials examined: NTUM #103528, 1, 260 mm TL, collected by H.-C. Yung, 21 Feb. 1958, at 100-150 m depth; SIO 00-32, 2, 192, 250 mm TL, collected by H.-K. Mok, 25 Sept. 1997, at 24°46.9'N, 121°54.1'E; 5 collections by L. Chen using otter trawl: SIO 76-255, 1, 224 m TL, off Ta-Chi, 15 Mar. 1972; SIO 76-256, 4, 165-273 mm TL, about 24°57' N, 121°53'E, at 31-46 m. depth, 26 May 1972; SIO 80-215, 2, 268, 272 mm TL, off Ta-Chi, NE coast of Taiwan, 18 Mar. 1977; SIO 80-299, 1, 197 mm TL, 24 May 1977, SIO 88-10, 2, 192, 243 mm TL, about 22°N, 120°E, SW coast of Taiwan, 16 Feb. 1978.

Diagnosis: Five pairs of gill pouches and apertures, GA crowded closely together in an irregular pattern; fused cusps 3/2, total cusps 32-40; trunk slime pores 39-47, total pores 68-79.

Description: Five GP, GA crowded together in an irregular pattern, length of 1st EBD about 3.5 times that of the last one; last GA confluent with the PCD; GA with pale rings, so close together that entire branchial area is white; 1-2 GP along DM, VA splitting at 4th or 5th GP. Fused cusps 3/2, AUC 5-8, PUC 6-9, total cusps 32-40. Slime pores: PBR 16-23 + TR 39-47 + TA 7-12, total pores 68-79. Body proportions for SIO specimens: PBR 29.2%-32.0%, BR 1.1%-1.7%, TR 53.2%-54.9%, TA 12.2%-15.6%, body width 3.6%-5.9%, depth w/VFF 6.9%-10.4%, depth w/oVFF 6.3%-10.0%, cloacal depth 6.3%-8.8%, tail depth 6.5%-10.0%. Body brownish-gray dorsally and lighter gray on lateral and ventral surface; eyespots absent; rostrum bluntly rounded; VFF vestigial to absent; CFF well developed. *Quadratus yangi* and *Q. nelsoni* both have 5 GP and 3/2 fused cusps, but *Q. yangi* has about 10 more trunk and total slime pores and the body depth is only about 2/3 that of *Q. nelsoni*. There is a small overlap in the trunk pore counts, but the frequency distribution charts of Kuo and Mok (1999) clearly show them to be 2 different species. Both species seem closely related to *Q. taiwanae*, but differ in having 5 rather than 6 GP. *Quadratus yangi* is a dwarf species maturing at less than 300 mm; one 293 mm female had eggs 19 mm long.

Distribution: *Quadratus yangi* has been collected in the coastal waters off NE and SW Taiwan and in the South China Sea, sometimes taken with *Q. taiwanae*, *Q. nelsoni*, and *E. burgeri*.

Remarks: *Quadratus yangi* is apparently one of the most widely collected of Taiwanese species, especially at shallower depths. Kuo and Mok (1999) collected 309 specimens for their study, and Mok and Chen (2001) reported 1,074 specimens taken from various depths and locations: 842 at 2 stations off NE Taiwan at 120-200 m, 103 at 190 m off SW Taiwan, and 27 at 547 m from the South China Sea.

Key to the 4 species of *Myxine* from the NW Pacific Ocean

1a. Fused cusps 2/2, less than 35 total cusps 2
1b. Fused cusps 3/2, more than 40 total cusps 3
2a. Total cusps 25-27; total slime pores 92-93 .. *M. paucidens*
2b. Total cusps 30-32; total slime pores 94-100 ..... *M. kuoi*
3a. Five gill pouches; VFF vestigial; total cusps 48-56 .... *M. formosana*
3b. Six gill pouches; VFF well developed; total cusps 42-46 ... . *M. garmani*

Fig. 10. *Quadratus yangi*, SIO 76-255, 224 mm TL.

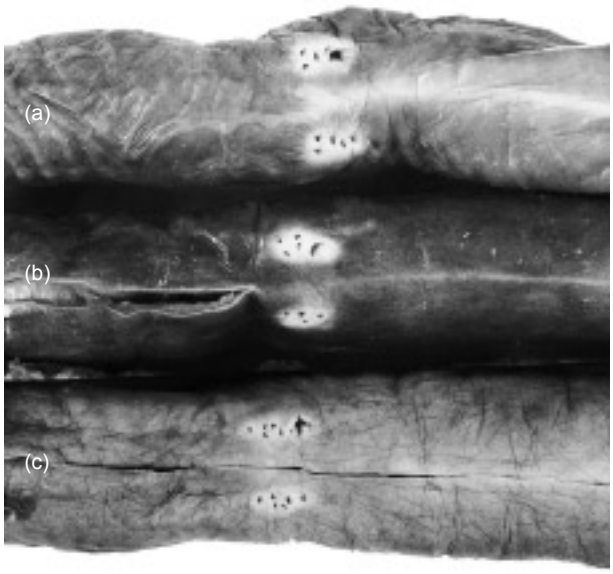

Fig. 11. Gill apertures of (a) *Quadratus nelsoni*, (b) *Q. yangi*, (c) *Q. taiwanae*.

Table 3. Cusps, slime pores and body proportions of NW Pacific Ocean *Quadratus*

	Q. nelsoni	*Q. yangi*	*Q. taiwanae*
Capture depth (m)	50-858	20-225	20-427
Maximum TL (mm)	234	296	334
Pairs gill pouches	5	5	6
Fused cusps	3/2	3/2	3/2
AUC	5-8	5-8	6-8
PUC	5-8	6-9	5-9
Total cusps	32-40	32-40	32-37
Slime pores:			
Prebranchial	13-20	16-23	16-20
Trunk	33-39	39-47	36-42
Caudal	6-10	7-12	6-9
Total pores	57-67	68-79	60-68
Body proportions in % of TL:			
Prebranchial length	30.5-32.6	29.2-32.0	28.1-35.0
Branchial length	1.1-2.8	1.1-1.7	1.3-2.7
Trunk length	49.5-52.6	53.2-54.9	51.8-56.0
Tail length	15. 0-18.0	12.2-15.6	12.1-14.6
Depth w/VFF	15.0-15.5	6.9-10.4	6.4-10.8
Depth w/oVFF	1 4.7-15.3	6.3-9.6	6.3-10.6
Tail depth	8.9-10.1	6.5-10.0	8.1-11.8

Myxine formosana Mok and Kuo, 2001
(Table 4)

Materials examined: SIO 01-191 [former NSYSU 3037, paratypes], 2, 282, 319 mm TL, collected by H.-K. Mok at 22°11.3'N, 120°13.7'E, at 843 m depth, SW Taiwan, 18 Dec. 1997.

Diagnosis: Five gill pouches; left GA confluent with PCD; light head; VFF low to vestigial; fused cusps 3/2, total cusps 48-56; total slime pores 80-96.

Description: Gill pouches 5 (rarely 4), 1st GP at tip of DM; VA without branching from heart to end of dental muscle; GA with pale narrow margins; left GA confluent with PCD. Data from 2 SIO specimens: fused cusps 3/2, AUC 10-11, PUC 9-10, total cusps 48,50. Slime pores: PBR 24, 26 + TR 49, 46 + TA 14,13, total pores 87, 85. Body proportions: PBR 30.4%, 31.8%, TR 55.0%, 52.7%, TA 15.6%, 14.2%, body width 3.5%, 4.1%, body depth w/VFF 5.6%, 5.7%, depth w/oVFF 5.3%, 5.3%, cloacal depth 5.0%, 4.6%, tail depth 4.4%, 3.9%. Body dark grayish-black to purplish-brown with lighter head; no eyespots; rostrum slightly pointed; barbels small and close together; body extremely slender, tapering to narrow tail, about equal to or only slightly deeper than body depth at cloaca. Ventral finfold poorly developed to absent, only 1-2 mm at mid body, tapering to a line at cloacal origin, with faintly expressed or no pale margins; CFF vestigial or absent. *Myxine formosana,* with 5 GP, is easily distinguished from the other 3 Asian species of 6-gilled *Myxine*, *M. kuoi*, *M. paucidens,* and *M. garmani*. Also, *M. formosana* has 3/2 rather than the 2/2 fused cusps of *M. kuoi* and *M. paucidens*, and 48-56 total cusps rather than 26 in *M. paucidens* and 42-46 in *M. garmani*. The branchial arrangement of 1 GP at the end of DM and no bifurcation of the VA is the same as that found in all other *Myxine* spp. known from this region. The number of GP is very constant; only 1 specimen of the 291 in the original study had 4 rather than 5 GP. A few other species of *Myxine* have been described with a 3/2 fused cusps pattern and white head, only one of which, *M. garmani* Jordan and Snyder, 1901, has been collected from the NW Pacific Ocean.

Distribution: *Myxine formosana* has been reported only from SW Taiwan where specimens were collected in shrimp traps at 583-1500 m. This was the species "*Myxine* sp. 2" of the distribution survey by Mok and Chen (2001) taken from 22°15'34''N, 120°06'56''E at 753 m and from 22°11'20"N, 120°13'42"E at 843 m.

Remarks: The original description of *M. formosana* shows unusually wide ranges of body proportions (PBR 27%-42%, TR 46%-67%, TA 13%-24%) and slime pores: PBR 27-42 + TR 46-67+ TA

13-24, total 80-117 for the 271 "non-type" specimens; these unusually wide ranges indicate the possibility of another species of *Myxine* in this large collection of 320 specimens. We did not use 768 mm for the maximum TL in table 4 from the "non-paratypes" of Mok and Kuo (2001), since it was not a paratype, and was about twice the total length of any of the paratypes (possibly a word processing error or a different species).

Myxine garmani Jordan and Snyder, 1901
(Table 4; Fig. 12)

Myxine australis Dean 1904: 15-16, 23 (synonymy; Japanese records; near mouth of Tokyo Bay); *Myxine tridentiger* Garman 1899: 345 (description); *Myxine cirrhata* Garman 1899: 407 (listed as taken by the Challenger in Japan Seas at 345 fath [631 m]; description).

Materials examined: SIO 90-133, 8, 510-610 mm TL, collected 19 Apr. 1973 from Misaki Marine Biological Station, Sagami Bay, E coast of Honshu, Japan, at 500 m depth.

Diagnosis: Six gill pouches; VFF well developed; fused cusps 3/2, total cusps 42-46; total slime pores 95-101; anterior part of head lighter color than body.

Description: Gill pouches 6, GA on left side confluent with PCD; 1 GP at tip of DM; VA without bifurcation. Fused cusps 3/2, unicusps 8-9 each row, total cusps 42-46. Slime pores: PBR 27-29 + TR 52-61 + TA 12-13, total pores 95-101. Body proportions: PBR 27.9%-29.1%, TR 56.8%-59.52%, TA 11.7%-15.0%, body width 2.6%-4.2% depth w/VFF 5.3%-6.9%, depth w/oVFF 4.7%-6.2%, depth at cloaca 4.1%-5.2%, tail depth 4.1%-5.6%. Original description gave body color as "dark purplish-brown to plum", but after 30 years in preservative the SIO specimens are dark brown, slightly lighter ventrally, anterior portion of head slightly lighter than body; with no pale margins on GA, VFF, or CFF. Body depth only slightly greater than its width, tapering to thin pointed tail. Rostrum somewhat pointed; 1st 2 pairs of barbels small and nearly the same length, 3rd pair about 3 times that of 1st. Ventral finfold prominent at origin, becoming less deep toward cloaca; ventral outline nearly straight from PCD to end of tail; CFF developed only around tip of tail and dorsally to a vertical from origin of cloaca. *Myxine garmani* is easily distinguished from *M. paucidens* and from *M. kuoi by* having 3/2 rather than 2/2 fused cusps. Although the light "head" and non-branching of the ventral aorta are common to both *M. garmani* from Japan, and *M. formosana* from Taiwan, the former has 6 GP and the latter has 5 GP.

Distribution: Known only from Hyalonema Grounds, Sagami Bay, E coast of Honshu, Japan, from about 500 m depth.

Remarks: *Myxine garmani* attains a total length of well over 600 mm, possibly the largest known *Myxine*, although Mok and Kuo (2001: 295) reported 1 *M. formosana*, 768 mm TL (NSYSU 3040) "non-paratype" taken in deep water, 1000-1500 m, off the SW coast of Taiwan, collected with 120 other specimens whose size range was only 102-370 mm TL.

Table 4. Cusps, slime pores, and body proportions of NW Pacific Ocean *Myxine*

	M. formosana	*M. garmani*	*M. kuoi*	*M. paucidens*
Capture depth (m)	583-1500	500-800	595	631
Maximum length (mm)	380	610	410	305
Gill pouches	5	6	6	6
Fused cusps	3/2	3/2	2/2	2/2
AUC	10-12	8-9	5-6	4-4
PUC	9-12	8-9	6-7	5-5
Total cusps	48-56	42-46	30-32	26
Slime pores:				
Prebranchial	23-30	27-29	24-30	25-26
Trunk	44-55	52-61	57-68	57-58
Tail pores	12-16	12-13	11-13	9-10
Total pores	87-85	95-101	95-100	92-93
Body proportions in % of TL				
Prebr. Length	27-42	27.9-29.1	25.9-28.7	27.2
Trunk length	46-67	56.8-59.5	56.9-63.2	54.3
Tail length	13-24	11.7-15.0	11.0-16.0	18.5
Depth w/VFF	5.6- 5.7	5.3-6.9	4.4-6.3	7.6
Depth w/oVFF	5.3- 5.4	4.7-6.2	4.4-5.3	4.9
Tail depth	3.9-4.4	4.1-5.6	3.1-6.6	4.4

Fig. 12. *Myxine garmani*, UMMZ 190387, 592 mm TL.

Myxine kuoi Mok, 2002
(Table 4)

No specimens were available to us; all data here and in table 4 are from the original description of 6 specimens: NSYSU 3176, 187 mm holotype, collected from SW Taiwan, 22°29'35''N, 120°03' 34''E at 595 m, 25 Nov. 1997, R/V Ocean Researcher III, cruise 380; NSYSU 3177, 4 specimens, 123-187 mm collected with the holotype; NSYSU 3178, 1, 410 mm female, found by H.-K. Mok, 15 Feb. 1997, in the Tung Kong fish market, taken by commercial fishermen off Tung Kong, SW Taiwan, about 22°28'N, 120°27'E.

Diagnosis: Six pairs of gill pouches, fused cusps 2/2, 5-6 cusps in anterior rows, 6-7 in posterior rows, total cusps 30-32; total slime pores 94-100; 1 GP at end of DM; VA not branched, VFF well developed in juveniles, but vestigial in mature specimens.

Description: Gill pouches 6; fused cusps 2/2, 5(5-6) cusps in the anterior rows, 7(6-7) in posterior rows, total cusps 32(30-32). Slime pores: PBR 24-30 + TR 57-68 + TA 11-13, total pores 94-100. Body proportions: PBR 25.9%-28.7%, TR 56.9%-63.2%, TA 11.0%-16.2%, body depth in branchial region 3.9%-4.6%, depth w/VFF 4.4%-6.3%, depth w/oVFF 4.4%5.3%, depth at cloaca 4.1%4.7% tail depth 3.1%6.6%. Mok (2002) described the body as slender, its color "brownish," upper 1/3 of body and abdomen behind gill apertures light brown, lower 2/3 dark brown, base of VFF light brown with pale margin, caudal finfold "not obvious." He stated that the VFF was "well developed in young and vestigial in mature specimens," a condition we have seen in *M. circifrons*, and also noted by Wongratana (1983) for *E. indrambarayai*. *Myxine kuoi* is distinguished from *M. formosana* and *M. garmani* by having 2/2 fused cusps rather than 3/2. *Myxine kuoi* is similar to *M. paucidens* in having 2/2 fused cusps and 6 GP, but has about 4-6 more cusps and 3-8 more total pores than the latter. It is easily recognized by the low count of cloacal slime pores (0-1 rather than the usual 3-4), and by the unusual color of the body, darker dorsally and lighter ventrally.

Distribution: *Myxine kuoi* is only known from the SW coast of Taiwan, 22°29'35''N, 120°03' 34"E, at 595 m and off Tung Kong at about 22°28' N, 120°27'E.

Remarks: Apparently, this was "*Myxine* species #3" reported in the distribution survey of Mok and Chen (2001). Mok (2002) correlated the presence of a single nasal-sinus papilla with the 2/2 fused cusp pattern in *M. kuoi* and other species of *Myxine*.

Myxine paucidens Regan, 1913
(Table 4; Fig. 13)

Materials examined: TUM 1448, 1, 185 mm TL, from Hyalonema Ground, Honshu, Japan, at 630 meters depth (possibly collected by K. Aoki in 1904 to 1906).

Diagnosis: Six pairs of gill pouches, last GA not confluent with PCD; VFF well developed; fused cusps 2/2, AUC 4-4, PUC 5-5, total cusps 26; total slime pores 92-93.

Description: Six gill pouches; left GA usually anterior to PCD; 1 GP along end of DM; VA without bifurcation. Fused cusps 2/2, each anterior rows 4-4, posterior rows 5-5, total cusps 26. Slime pores: PBR 25 + TR 58 + TA 9, total pores 92. Body proportions of the 185 mm specimen: PBR 27.2%, TR 54.3%, TA 18.5%, body width 3.8%, depth w/VFF 7.6%, depth w/oVFF 4.9%, cloacal depth 4.4%, tail depth 4.4%. Body color light brown; rostrum slightly pointed; first 2 pairs of barbels about equal in length, third pair only slightly longer than the first two. Slime pores with pale margins, VFF well developed, with pale margin; CFF not well developed. Regan (1913) did not mention body color, sexual development, or presence of any eggs in the "type" specimens, 240 and 305 mm TL that were sent to the British Museum. His very short description of *M. paucidens* stated "6 branchial pouches. 6 teeth in the first series and 7 in the second, the 2 most anterior teeth in each series united. Pores 26 + 57 + 10. Length of head 3.6 in the total length. Japan. 2, 240 & 305 mm (types) (Challenger)." The TUM specimen was 190 mm long and its body color "warm brown" when measured by the senior

Fig. 13. *Myxine paucidens*, TUM 1448, 185 mm TL.

author in 1976, but had shrunk to 185 mm and faded to a very light brown color after another 26 years in alcohol. It is too small to determine the sex. Regan did not mention the space between the left GA and the PCD, but Fernholm (1998: 40) also found this fleshy separation in both specimens in the British Museum. This is analogous to, but far less than, the very large space separating the left GA and PCD in *Notomyxine tridentiger*, a genus and species known only from South America. This separation is unusual in species of the genus *Myxine*, but not uncommon in *Eptatretus*; Dean (1904) reported that he found this last left GA separate from PCD in about 10% of *E. burgeri*. Unless more study material of this species becomes available, we cannot be certain that the separation of the left GA from PCD in the 3 specimens of *M. paucidens* is a constant character so we have not used it in the diagnosis or in the key to the species. This species apparently has the lowest number of total cusps of any hagfish, at 26, which distinguishes it from the other species; *M. kuoi* has 30-32, *M. garmani* 42-46 and *M. formosana* 48-56 total cusps. Also, *M. paucidens* has 2/2 fused cusps, which distinguishes it from *M. formosana* and *M. garmani*, as well as about 5 fewer cusps and about 8 fewer slime pores than *M. kuoi*. The branchial configuration in *M. paucidens* is the same as that in the other NW Pacific species of *Myxine*, 1 GP at the end of the dental muscle and ventral aorta without bifurcation.

Distribution: Known only from the type locality, Hyalonema Ground, Misaki at about 630 m, and from nearby Sagami Bay at about 1,000 m, on the E coast of Honshu I., Japan.

Remarks: Regan sent the small specimen of *M. paucidens* to the Tokyo Museum and 2 larger "syntypes," 240, 305 mm TL to the British Museum in 1879 (BMNH 1879: 5.14.444 and BMNH 912:11.28.6). These were collected by the HMS Challenger in 1879 from Sagami Bay at 545 to 550 fms [ca. 1000 m]. We obtained notes on these from Fernholm (1998), and have combined his data with those of the TUM 1448 specimen. It closely resembles the "types" described by Regan (1913); cusp counts are exactly the same and slime pore counts agree closely. We are not aware of any other specimens of *M. paucidens* deposited in museums.

DISCUSSION

We follow Dean (1904), Bigelow and Schroeder (1952), Teng (1958), Shen and Tao (1975), Kuo et al. (1994) and Huang et al. (1994) in considering *Paramyxine* as a genus distinct from *Eptatretus*, and agree with Wisner (1999) and Mok et al. (2001) that *Quadratus* is separate from *Paramyxine*. The genera *Eptatretus* and *Myxine* are both found in the NW Pacific Ocean, but with fewer species than are found off the coasts of North and South America. Species of *Eptatretus* and *Paramyxine* are numerous in this region, especially in Taiwan. The genera *Neomyxine*, *Notomxine*, and *Nemamyxine* have only been found in the southern hemisphere off South America, Australia and New Zealand. Dean (1904) remarked that it was significant that there were several forms of myxinids in the same locality [Japan]. He believed it to be evidence that hagfishes are an ancient group, which has passed through a period of evolution, with *Paramyxine* a transitional form between *Eptatretus* and *Myxine*. At that time he found in the vicinity of Misaki [Marine Biological Station, Sagami Bay, Honshu] "three distinct genera living side by side represented by at least four species." Since then, 2 new species of *Paramyxine* have been found in Japan and 12 species in 4 genera have been described from Taiwan. Only 4 species of *Myxine* have been reported from the NW Pacific, in contrast to about 19 species known from North and South America (Wisner and McMillan 1995). Species of *Myxine* are generally found in water over 400 m deep and are less apt to be collected by trawling or by commercial fishing, but more species may be discovered in this region with increased trapping efforts by research vessels. These geographic imbalances of genera and species do not appear to be artifacts of sampling. Many collections have been made in the northern part of the Atlantic Ocean and along the coasts of North and South America with the collection of only 1 species each of *Quadratus* and *Paramyxine*, *Q. ancon* Mok, Saavedra-Diaz and Acero, 2001 from Colombia, South America and *P. springeri* Bigelow and Schroeder, 1952.

Paramyxine atami has long been the subject of controversy in the literature. Apparently no other *Paramyxine* with 3/3 fused cusps had been reported from Japan for several years after the original description of *P. atami*, and some authors asserted that Dean's type specimen was not "typical". Strahan (1962) presented data from specimens from Suruga Bay of *P. atami* with 3 "fused teeth in inner row", and Fernholm (1998) collected 19 specimens with 3/3 fused cusps from

Sagami and Suruga Bays. H.-K. Mok reported (pers. commun. July 2001) that he had examined the *P. atami* specimen mentioned by Bigelow and Schroeder (1952) and found it has the 3/3 fused cusps described by Dean (1904). These examples prove that the holotype of *P. atami* with 3/3 fused cusps was not an aberrant specimen. Fernholm (1998) explained the prevalence in the literature of 6-gilled *Paramyxine* specimens with 3/2 fused cusps that have been misidentified as *P. atami* saying they were a different species, more often collected because they were found in shallower waters than the 350-435 m where he collected specimens. Many *Paramyxine* specimens from the Sea of Japan with 3/2 fused cusps have been described as a variation of *P. atami* by authors who did not realize they were dealing with a separate species. Matsubara (1937) described specimens identified as *P. atami*, and provided figures showing 3/2 fused cusps, stressing the variation in the pattern of the cusps. Dean (1904) who had examined several hundred each of *E. burgeri* and *E. okinoseanus*, thought that the fusion of the 2 or 3 cusps at the median end of each row of cusps appeared to be constant for each species. Fernholm and Hubbs (1981) found the fused cusp patterns did not vary within species of *Eptatretus* and *Paramyxine*, and we have also found this to be true for *Myxine* (Wisner and McMillan, 1995). In over 600 specimens of *E. burgeri*, Dean (1904) found only 1 specimen with 7 pairs of GP and Lindberg and Legaza (1967) found 1 with only 5 pairs of GP. Thus, there may be slight variation in numbers and patterns of GP and GA, and often a wide range of slime pores in large collections. However, in nearly 2,000 hagfishes studied, we have found no variation in the numbers of fused cusps in any species. We agree with Kuo et al. (1994) and Fernholm (1998) that Dean's 1904 description is valid, and we shall retain the name *P. atami* only for those specimens with 3/3 fused cusps. All 6-gilled *Paramyxine* specimens with 3/2 fused cusps identified as *P. atami* should be treated as different species, and study materials of authors who failed to state the fused cusp pattern should be re-examined.

Fernholm (1998: 39) speculated that the "Taiwanese species with crowded GA [*Paramyxine* and *Quadratus*] may have evolved by speciation from the widespread species *E. burgeri*." He also stated "In contrast to the Japanese species, all Taiwanese *Paramyxine* are dwarfed forms". This is true of the 3 former *Paramyxine*, now *Q. nelsoni*, *Q. taiwanae*, and *Q. yangi*, and 2 other Taiwanese species, *P. fernholmi* and *P. wisneri*, which mature at less than 300 mm, but reach a maximum length of about 400 mm. The largest Taiwanese *Paramyxine* (reported by Mok and Chen 2001) are *P. sheni* (480 mm) and *P. cheni* (473 mm), maximum lengths being a little greater than that of the new species from Japan, *P. moki* (470 mm), but less than that of *P. walkeri* (518 mm) or *P. atami* (610 mm).

Fernholm (1998) proposed that the most likely primitive state of gill apertures is one in which each gill pouch has its own short direct opening to the exterior, and the tendency is for the GA to move into a gradually more-crowded posterior location, with the end result that all EBD discharge through a common posterior pair of apertures as in *Myxine*. An example of this is the collection SIO 94-140 of *P. walkeri*, where 3 aberrant specimens with 5-6 gill pouches had only 3-5 apertures on 1 or both sides. The joining of 2 or 3 efferent branchial ducts to discharge through only 1 GA or the PCD was also noted in *Q. nelsoni* (Kuo and Mok 1999). This transition toward fewer GP and GA is in agreement with Fernholm's theory, indicating that *Eptatretus* is the most primitive, *Paramyxine* and *Quadratus* are intermediate forms, and *Myxine* is the most advanced of the hagfish genera. Huang et al. (1994) stated that *E. burgeri* (6 GP) was more advanced than *E. okinoseanus* (8 GP), which was the most primitive of any of the 6 species studied. They also reported that *Q. taiwanae* (6 GP) was "the primitive sister species of the *P. yangi--P. nelsoni* group" (with 5 GP). In those cases the mitochondrial DNA analysis apparently supports the theory that species with the greatest number of GP are the most primitive.

We feel that fused cusp patterns and slime pore counts are generally of more value than body proportions in the comparison of species, since they are more accurate and repeatable than measurements. Examples of counts as a distinguishing character are the low number of cusps in *M. paucidens*, the high number of prebranchial slime pores of *P. cheni*, and the low number of cloacal pores in *M. kuoi*. Body proportions within a genus are apt to be very similar, and there is also the problem of the differential stretching by different investigators, as well as shrinkage in old collections. Some of our study material had been measured in the years 1972-1976 and when recently measured again, specimens had shrunk several mm. Two specimens of *Q. nelsoni* that were 240 and 263 mm TL had shrunk in length to 235 and 253 mm, respectively, by Aug. 2001 when again measured by the

senior author. The large specimens of *M. garmani* had shrunk 10-14 mm in total length since first measured by us in 1976. This typical shrinkage in total length presents a problem, especially when comparing body proportions of new collections with data from the earlier literature or with specimens preserved for a long time. Two other factors affecting body measurements are when specimens are curled from being put into too small a container or before completely hardened in formalin in a straight form. Instead of using isopropyl alcohol, some museums use ethanol as the preservative, which causes even greater shrinkage. Apparently there is less change in the prebranchial and branchial regions of the body where the dental muscle and gill pouches help to maintain the body shape, producing different body proportions in the same species after long preservation. Although we do not consider body measurements as a very reliable and repeatable method for comparison of species, one exception to this is the distinction between *P. fernholmi* and *P. wisneri* based mainly on the branchial length. This was obtained by the study of specimens collected about the same time, preserved and measured by the same investigators using the same methods. Another character that is not infallible is that of the last left GA not being confluent with the PCD, especially when only a few specimens are available for study, as in *M. paucidens*. Dean (1904: 12) found that the last left GA was "in front of the PCD" in about 10% of specimens of *E. burgeri* in "upwards of 600" of the specimens he studied. Two other characters considered important by Dean (1904) are included in our descriptions: the number of gill pouches along the tip of the dental muscle and the position of branching of the ventral aorta. It is interesting that all of the Asian *Eptatretus* spp. have the same branchial configuration with complete bifurcation of the ventral aorta just anterior to the heart, while all the *Myxine* discussed here have only 1 GP at the end of the DM and no branching of the ventral aorta. Dean also felt that the character of the egg was important, but females with fully mature eggs are seldom available for comparison. In this same study he said that the number of slime pores was "variable" and found them difficult to count. We have found it useful to scrape off any slime first, and use a head lens and strong light to count the slime pores. Honma (1960: 803) found that in the case of *Paramyxine*, a study of variation showed that the arrangement and total number of slime glands are of the most reliable diagnostic characters. In Kuo and Mok (1999) the frequency distribution of slime pores from a large number of specimens of 2 very similar species, *Q. yangi* and *Q. nelsoni*, clearly shows that slime pore counts are important in differentiating between species. We agree with Fernholm (1998) in that it is useful to note depth distribution in addition to geographical distribution, but it is not always possible to get the depth of capture, especially when many collections were made by commercial fishermen rather than scientific expeditions.

Dean (1904) stated that it is very important to obtain many specimens for study to ensure that one has a good range of counts and measurements. In spite of this, he described *P. atami* from only 1 specimen; fortunately many more have been collected since then (Strahan 1962, Fernholm 1998). Kuo et al. (1994) described *Q. nelsoni* from only 1 specimen, but the 309 specimens reported by Kuo and Mok (1999) affirmed the validity of the species. Regan (1912) had only 3 specimens of *M. paucidens* in the original description of the species, but more specimens may be collected eventually by trapping in deep water. We were fortunate to have 1 of these for study, and 1 or 2 of the original paratypes from Taiwanese collections that were limited to 5 or fewer specimens. In 2 cases, no specimens were available to us, and we had to rely completely on the literature for their descriptions.

Huang et al. (1994) pointed out that the validity of classifications based on the usual methods of morphological and meristic features might be uncertain since the differences could be explained by intraspecific phenotype variation. The determination of mitochondrial DNA will surely prove a valuable method for identification of new species and for elucidating relationships among known species; it has already shown how some species of *Eptatretus* differ from *Paramyxine* and *Quadratus*. We agree with Fernholm (1998: 37) that among the most useful characters for systematic work in hagfishes are gill apertures and their position relative to the gill pouches, the pattern of fused cusps and number of cusps, numbers and patterns of slime pores, the relative position of the ventral aorta bifurcation and gill pouches, finfolds and body proportions. It is highly probable that the use of some newer characters such as nasal papillae, skeletal morphology, mitochondrial diversity and other genetic studies may play a larger part in hagfish taxonomy in the future.

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