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Hagfishes of Taiwan (I): A Taxonomic Revision with Description of Four New *Paramyxine* Species

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Chien-Hsien Kuo, Kao-Fong Huang and Hin-Kiu Mok (1994) Hagfishes of Taiwan (I): A taxonomic revision with description of four new *Paramyxine* species. *Zoological Studies* **33**(2): 126-139. Hagfishes from the northeast, east and southwest coasts of Taiwan were subjected to morphological analysis. Nine species (*Eptatretus okinoseanus, E. burgeri, Paramyxine nelsoni, P. yangi, P. cheni, P. sheni, P. taiwanae, P. fernholmi* and *P. wisneri*) were identified. Among them, *Paramyxine nelsoni, P. sheni, P. fernholmi* and *P. wisneri* are new species; *Eptatretus okinoseanus* is a new record. Descriptions and diagnostic characteristics are given for all hagfish species reported in Taiwan waters.

Key words: Taxonomy, *Eptatretus, Paramyxine*, Taiwan.

Shen and Tao (1975) revised the taxonomy of hagfishs from Taiwan. They provided new data on *Eptatretus burgeri* (Griard) and *Paramyxine yangi* (Teng), as well as describing two new species, *Paramyxine cheni* and *P. taiwanae*. Despite their increasing economic value as food and ornament no further work on Taiwanese hagfishes has appeared since then. During a survey cruise in 1988 off the southwest coast of Taiwan 240 hagfish specimens were collected. Subsequently, northeast and east coast specimens were obtained. These have provided additional information on hagfish taxonomy. The present paper reports on the hagfishes of Taiwan and gives detailed descriptions of four new species of *Paramyxine*.

MATERIALS AND METHODS

From February, 1988 to May, 1991 hagfishes were collected by shrimp traps from the coastal waters off the northeast, southwest and east coasts of Taiwan (Fig. 1). Terminology, count and measurement method follow those of Dean (1904), Shen and Tao (1975), Fernholm and Hubbs (1981), as well as McMillan and Wisner (1984). Specimens preserved in 10% formalin were deposited in the fish collection at the Institute of Marine Biology, National Sun Yat-sen University (NSYSU). They were straightened to approximate their life form to ensure accurate measurements. All counts (Fig. 2) were taken from the left side. Only those taxonomic characteristics which were deemed useful by previous researchers (Shen and Tao 1975, Fernholm and Hubbs 1981, McMillan and Wisner 1984) were recorded. They included: total length, head length, preocular length, prebranchial length, branchial length, trunk length, tail length, tail depth, body width, gill aperture and pouche counts, slime pores, fused unicuspid teeth, dental formula, and coloration (e.g., occurrence of eye spots and whitish mid-dorsal stripe) were recorded. No specimen of *Paramyxine cheni* was captured during this study. The holotype and two paratypes of *P. cheni* from the Department of Zoology, National Taiwan University (NTU) were examined.

RESULTS

Key to myxinid genera discussed herein

1a. All efferent ducts approximately equal in length ..... *Eptatretus*

1b. Anterior efferent ducts notably longer than the most posterior one ..... *Paramyxine*

Eptatretus Cloquet, 1819

Gill apertures ranged from 5 to 15, but most species with 5 to 7 apertures, the posteriormost one on the left side usually confluent with the external pharyngocutaneous duct (PCD) opening; branchial apertures well separated; branchial pouch efferent ducts equal in length. With very few exceptions, the majority of branchial apertures corresponded with slime pores (below and about midway between the adjacent gill apertures), often one less than gill aperture counts; fused unicuspid teeth on the outer and inner teeth row varied (3/3, 3/2 or 2/2). About 24 species are known.

Distribution: South Africa, Western Pacific, New Zealand, Pacific coasts of North and South America, Caribbean Sea (Norman 1957).

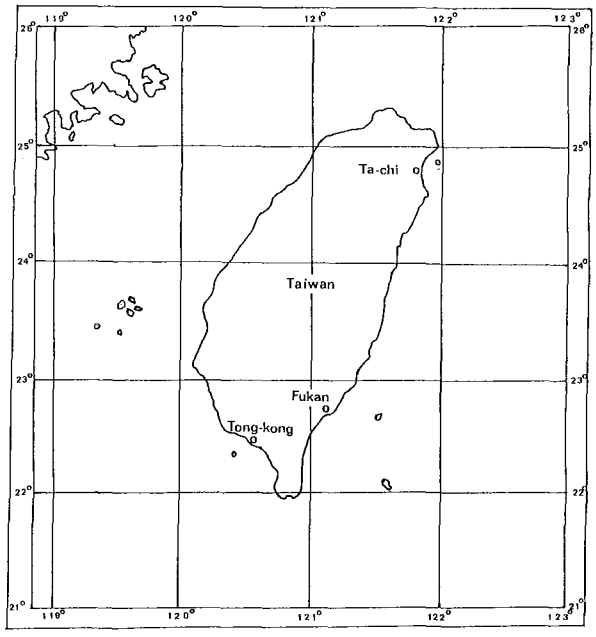

Fig. 1. Sampling site locations, Taiwan.

Key to species of *Eptatretus* from Taiwan waters

1a. Whitish mid-dorsal stripe absent; gill apertures 8; slime pores 13 + (7-8) + (54-56) + 13, total 88-89; dental formula: (9-10) + 3/2 + (9-10), total cuspids 48-50 .... *E. okinoseanus*

1b. Whitish mid-dorsal stripe present; gill apertures 6;slime pores (18-21) + 5 + (46-51) + (11-12), total 82-88; dental formula: (6-8) + 3/2 + (7-9), total cuspids 36-42 .... *E. burgeri*

Eptatretus okinoseanus (Dean, 1904)

(Tables 1-8)

Homea okinoseana Dean, 1904: 8-14 (Bay of Tokyo).
Eptatretus okinoseanus: Masuda et al., 1984: 1, Pl. 1.

Materials examined: NSYSU 2855, 1 specimen, eastern coast of Taiwan, 345 mm, depth 300 meters, 16 Aug. 1988; NSYSU 2856, 1 specimen, southwestern coast of Taiwan, 550 mm, depth 1020 meters, 9 Feb. 1988.

Diagnosis: Eight pairs of gill pouches and gill apertures, the latter arranged in a straight line, loosely spaced (Figs. 3A,B).

Description: Counts are listed in Tables 1-7 and proportions in Table 8. Color of live and preserved specimens dark purplish-brown; no light colored patches over the ocular area and no whitish mid-dorsal stripe, eye spots present, obscure gill apertures and slime pores without pale margin; ventral finfold present with whitish margin; eight pairs of gill apertures arranged in a straight line on each side and well-separated from one another; slime pores 13 + (7-8) + (54-56) + 13, total slime pores 88-89, 7-8 pairs of branchial slime pores; fused unicuspid teeth (FT): 3/2, dental formula: (9-10) + 3/2 + (9-10); average preocular length 5.99%, prebranchial length 19.94%, branchial length 6.97%, trunk length 52.32%, tail length 14.28% tail depth 8.74%, body depth 8.02% of total length.

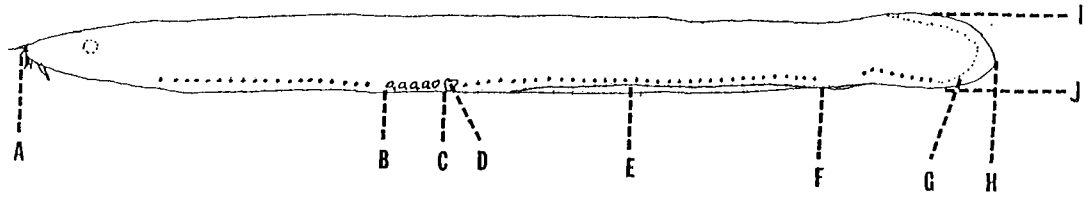

Fig. 2. Outline of a *Paramyxine* hagfish showing regions and features used in measuring and counting: A-H, total length (TL); A-B, prebranchial length; B-C, branchial length, including all gill apertures; D, external opening of pharyngocutaneous duct (PCD) and the last branchial aperture; E, ventral finfold; C-F, trunk length; F, origin of cloaca; G, caudal finfold; F-H, tail length; I-J, tail depth. The linear series of dots represents the prebranchial, branchial, trunk, and tail slime pores.

Table 1. Prebranchial slime pores in nine myxinid species

	Prebranchial slime pores														
Species	13	14	15	16	17	18	19	20	21	22	23	24	25	26	N
Eptatretus okinoseanus	2														2
E. burgeri						3	3		2						7
Paramyxine nelsoni							1								1
P. yangi				1			1	5	8	1	1				17
P. cheni														4	4
P. sheni	1	9	30	33	27	1									101
P. taiwanae				3	10	12	5								30
P. fernholmi				1	2	7	30	35	10	2	1				88
P. wisneri			1	1	10	25	17	5							59

Table 2. Branchial slime pores in nine myxinid species

	Branchial slime pores										
Species	0/0	1/1	1/0	2/1	2/2	4/4	5/4	5/5	7/7	8/8	N
Eptatretus okinoseanus									1	1	2
E. burgeri								10			10
Paramyxine nelsoni	1										1
P. yangi	17										17
P. cheni	4										4
P. sheni	82	10	7	1	1						101
P. taiwanae	30										30
P. fernholmi	88										88
P. wisneri	57		2								59

Table 3. Trunk slime pores in nine myxinid species

	Trunk slime pores																						
Species	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	N
Eptatretus okinoseanus																				1		1	2
E. burgeri												1	1	6	8	1	2						19
Paramyxine nelsoni	1																						1
P. yangi								5	4	6	1		1										17
P. cheni											2	1	1										4
P. sheni					1		14	11	23	23	22	7											101
P. taiwanae		1	4	7	3	10	3	2															30
P. fernholmi				6	11	28	17	13	8	5													88
P. wisneri		1	1	2	4	14	18	10	7	1													59

Eptatretus burgeri (Girard, 1854)
(Tables 1-7)

Bdellostoma burgeri Girard, 1854: 199. (coast of Japan)
Homea burgeri Dean, 1904: 2-8.
Heptatretus burgeri: Regan, 1912: 543-556.
Eptatretus burgeri: Matsubara, 1955: 91; Chu et al., 1963: 3-4; Uchida, 1965: 46; Tominaka, 1969: 52-53; Chen and Yu, 1986: 44-47; Shen and Tao, 1975: 65-79; Masuda et al., 1984: 1, pl.1.

Material examined: NSYSU 2854, 22 specimens, 290-450 mm,

Table 4. Tail slime pores in nine myxinid species

	Tail slime pores											
Species	5	6	7	8	9	10	11	12	13	14	15	N
Eptatretus okinoseanus									2			2
E. burgeri							6	16				22
Paramyxine nelsoni				1								1
P. yangi				5	7	3	2					17
P. cheni			1	3								4
P. sheni				1	16	51	29	4				101
P. taiwanae		1	14	6	9							30
P. fernholmi		1	2	30	43	11	1					88
P. wisneri		1	1	31	17	7	1					59

Table 5. Total slime pores in nine myxinid species

	Total slime pores																											
Species	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	N
Eptatretus okinoseanus																													1	1	2
E. burgeri																							1		2	4	10	4	1		22
Paramyxine nelsoni			1																												1
P. yangi							1						5	5	4	1			1												17
P. cheni																			4												4
P. sheni					1	1	7	3	15	18	24	15	14	1	2																101
P. taiwanae	1	3	2	1	7	6	4	4	2																						30
P. fernholmi					2	1	8	14	9	13	16	16	7																		88
P. wisneri				3	2	4	7	10	13	10	4	3	2																		59

Table 6. Total unicusps in the outer/inner rows in nine myxinid species from Taiwan

	Total unicusps in the outer/inner rows																				
Species	9/8	9/9	9/10	10/9	10/10	10/11	11/9	11/10	11/11	12/10	12/11	12/12	12/13	13/11	13/12	13/13	14/12	14/13	14/14	15/13	N
Eptatretus okinoseanus												1		1							2
E. burgeri		1		17				2	2												22
Paramyxine nelsoni							1														1
P. yangi		1	1	3	7	1		3	1												17
P. cheni													1			2		1			4
P. sheni															27	10	2	57	4	1	101
P. taiwanae	2	6		12	5	2	2														30
P. fernholmi								1	11	4	47	9		6	10						88
P. wisneri					7		1	11	27	2	10			1							59

Ta-chi (northeastern coast of Taiwan), depth 20-50 meters. 5 Aug. 1988.

Diagnosis: Six pairs of gill pouches and gill apertures in a rarely variable linear arrangement (Fig. 3C); branchial slime pores 4-6; last left gill aperture closely adjacent to but separate from the PCD; eye spots prominent.

Description: Counts are listed in Tables 1-7.

Table 7. Counts of *Eptatretus okinoseanus*, *E. burgeri*, *Paramyxine nelsoni*, *P. sheni*, *P. fernholmi* and *P. wisneri*.

Species	*E. okinoseanus*	*E. burgeri*	*P. nelsoni*	*P. sheni*	*P. fernholmi*	*P. wisneri*
Number	2	22	1	101	88	59
No. of GA	8	6	4	6	6	6
No. of GP	8	6	4	6	6	6
Dental formula	9-10 + 3/2 + 9-10	6-8 + 3/2 + 7-9	8 + 3/2 + 7	9-12 + 3/3 + 9-11	8-10 + 3/2 + 8-10	7-10 + 3/2 + 7-9
Slime pores	13 + 7-8 + 54-56 + 13	18-21 + 5 + 46-51 + 11-12	19 + 0 + 35 + 8	13-18 + 0-2 + 39-46 + 8-12	16-23 + 0 + 38-44 + 6-11	15-20 + 0-1 + 36-44 + 6-11
Eye spots	present	present	absent	present	absent	present

GA: gill aperture; GP: gill pouch.

Table 8. Morphological characteristics in percentages of total length in four myxinid species

Species	*E. okinoseanus*	*Paramyxine nelsoni*	*P. sheni*	*P. fernholmi*
Number	2	1	101	88
Total length	345mm 550mm	190mm	205-436mm	167-357mm
Preocular length	6.35% 5.46%	*	5.44%	*
Prebranchial length	21.87% 19.00%	34.05%	25.95%	30.71%
Branchial length	8.70% 5.24%	1.26%	3.75%	2.66%
Trunk length	56.45% 48.18%	48.79%	56.24%	52.00%
Tail length	15.48% 13.09%	13.16%	15.27%	13.67%
Tail depth	9.03% 7.45%	8.26%	10.24%	9.04%
Body depth	10.00% 6.05%	8.95%	9.04%	10.40%
Body width	6.35% 6.07%	6.53%	6.61%	8.99%

Body brownish-grey dorsally and light grey ventrally in live and preserved specimens; prominent whitish mid-dorsal stripe and eye spots present, with well defined margins; gill apertures with narrow pale margins; the efferent duct of the last gill pouch on the left side not confluent with but closely adjacent to the PCD; the most posterior left gill aperture and the external opening of PCD surrounded by a pale ring; slime pores (18-21) + 5 + (46-51) + (11-12) (mean 21 + 5 + 49 + 12 and mean total slime pores 87), 5 pairs of branchial slime pores (Fig. 3C); fused unicuspid teeth 3/2 (both outer and inner rows), dental formula (6-8) + 3/2 + (7-9); average prebranchial length 26.72%, branchial length 6.43%, trunk length 53.87%, tail length 15.03% and tail depth 6.13% of total length.

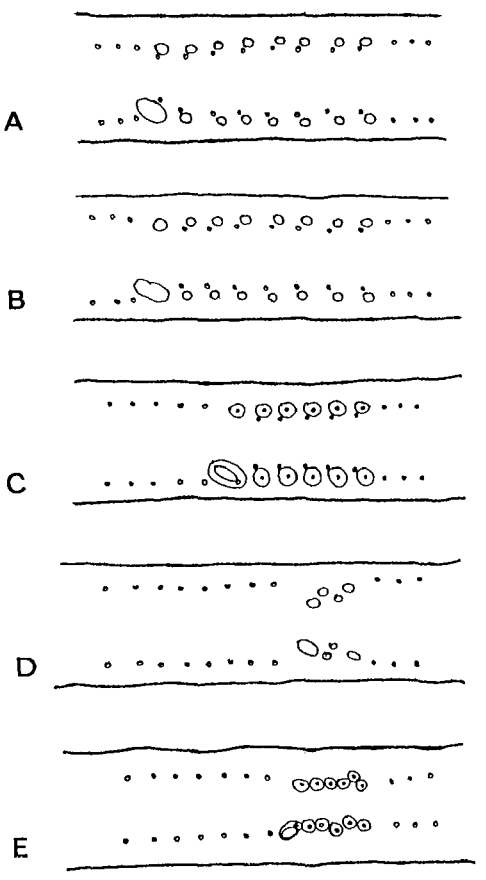

Fig. 3. Arrangement of gill apertures and slime pores in (A,B) *Eptatretus okinoseanus*, (C) *E. burgeri* (D) *Paramyxine nelsoni* (E) *P. fernholmi*. Head to the right. Smaller circles represent slime pores.

Paramyxine Dean, 1904.

Gill apertures 4 to 6 (5 of 8 species with 6 gill apertures); branchial apertures closely spaced; anterior branchial duct longer than posterior ones; the most posterior gill aperture on the left side larger, confluent with the PCD; no slime pores in the branchial region, (except for 20% of the *Paramyxine sheni* specimens examined); most species (5 of 8) with 3/2 fused unicuspid teeth. Eight species have been described.

Distribution: Western Pacific (Japan and Taiwan).

Key to species of *Paramyxine* from Taiwan waters

1a. Gill apertures 4 ..... *P. nelsoni*
1b. Gill apertures 5-6 2
2a. Gill apertures 5 3
2b. Gill apertures 6 4
3a. Dental formula: 7 + 3/2 + 7; gill apertures crowded together and all gill apertures contained in a pale area on each side of ventral surface; slime pores (16-23) + 0 + (42-47) + (8-11), total pores 66-78 ..... *P. yangi*
3b. Dental formula: 10 + 3/3 + 10; gill apertures arranged regular straight line, white rings absent; slime pores 26 + 0 + (45-47) + (7-8), total pores 78 ..... *P. cheni*
4a. Fused unicuspid teeth 3/3; gill apertures arranged in straight line, each gill aperture surrounded by a white ring ..... *P. sheni*
4b. Fused unicuspid teeth 3/2 5
5a. Each gill aperture not surrounded by a pale ring or all apertures surrounded by a single whitish area on both sides of ventral surface, irregularly crowded together; dental formula (8-9) + 3/2 + (8-10), total cuspids 38-42 ..... *P. taiwanae*
5b. Each gill aperture surrounded by a white ring, closely spaced; gill apertures in 1 or 2 rows; dental formula (7-10) + 3/2 + (7-9), total cuspids 42-50 6
6a. Gill apertures in 1 or 2 irregular rows; external opening of PCD not confluent with the left most posterior gill aperture; branchial length 2.66% in TL; entire ventral surface white ..... *P. fernholmi*
6b. Gill apertures in a straight line; external opening of PCD confluent with the left most posterior gill aperture; branchial length 4.58% in TL; only ventral finfold white ..... *P. wisneri*

Paramyxine nelsoni, n. sp.
(Tables 1-8)

Holotype: NSYSU 2857; 190 mm; southwestern coast of Taiwan; depth 50-200 meters; 5 June, 1988. Only one specimen known.

Diagnosis: Four pairs of gill pouches and gill apertures, crowded together (Fig. 3D).

Description: Counts are listed in Tables 1-7 and proportions in Table 8. Color of live and preserved specimens grey-brownish; no light colored patches over the ocular area and no whitish mid-dorsal stripe or eye spots; four pairs of gill apertures, crowded together (Fig. 3D), each surrounded by a pale ring; the most posterior left gill apertures larger, confluent with PCD; ventral finfold with a pale margin and originating near the body midpoint; slime pores 19 + 0 + 35 + 8, total slime pores 62, branchial slime pores absent; fused unicuspid teeth 3/2 (both outer and inner rows); dental formula: 8 + 3/2 + 7; prebranchial length 34.05%, branchial length 1.26%, trunk length 48.79%, tail length 13.16% and tail depth 8.26%, body depth 8.95% of total length (Table 7,8).

Etymology: Named after Dr. Gareth J. Nelson of the Ichthyology and Herpetology Department, American Museum of Natural History for his contribution to the promotion of phylogenetic systematics.

Paramyxine yangi Teng, 1958
(Tables 1-6)

Paramyxine yangi Teng 1958: 3-6 (Taiwan); Strahan and Honma 1961: 340; Shen and Tao 1975: 69-71.

Materials examined: NSYSU 2862, 17 specimens, 190-240 mm, northeastern coast of Taiwan, depth 20-50 meters, 5 Aug. 1988.

Diagnosis: Five pairs of gill pouches and gill apertures, the latter irregularly crowded together (variation in arrangement of gill apertures shown in Fig. 4).

Description: Counts are listed in Tables 1-6. Color of preserved specimens brownish-grey dorsally and grey laterally, no whitish mid-dorsal stripe; ventral finfold absent or vestigial; eye spots absent; five pairs of gill apertures crowded together and all gill apertures contained in a pale area on each side of ventral surface; most posterior left gill aperture confluent with PCD; slime pores (16-23) + 0 + (42-47) + (8-11) (mean 20.47 + 43.41 + 9.12); total slime pores 66-78 (mean 72.99), branchial slime pores absent; fused unicuspid teeth 3/2, dental formula: (6-8) + 3/2 + (7-9) (mean 7.12 + 3/2 + 7.88). They inhabit shallow water between 20-50 meters. The largest egg found in 293 mm TL female was 19 mm.

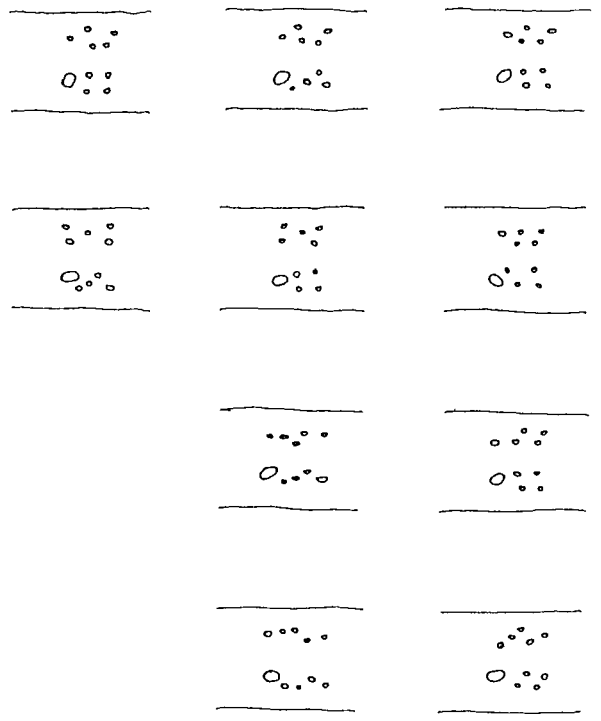

Fig. 4. Variation in arrangement of gill apertures in *Paramyxine yangi*. Head to right.

Paramyxine cheni Shen and Tao, 1975
(Tables 1-6)

Paramyxine cheni Shen and Tao, 1975: 71-73 (Tong-Kong), (20° 25.0'N 120° 26.3'E, off the southwestern coast of Taiwan).

Materials examined: No specimen was collected in this study. NTUM 02723 (holotype, a female, 377 mm, southwestern coast of Taiwan); NTUM 02724 (2 paratypes, 226 mm, 357 mm, southwestern coast of Taiwan).

Diagnosis: Five pairs of gill pouches and gill apertures, closely spaced in a straight line; branchial slime pores absent; fused unicuspid teeth 3/3; dental formula: 10 + 3/3 + 10 (Tables 1-6); no whitish mid-dorsal stripe.

Description: Counts are listed in Tables 1-6. Color light brown; five pairs of gill pouches and gill apertures, closely spaced in a straight line, white ring absent; the efferent duct of the last gill pouch, left side, is not confluent with that of the PCD; the anteriormost efferent duct of the gill pouch is 3.5 times longer than the length of the posteriormost one; slime pores 26 + 0 + (45-47) + (7-8); branchial slime pores absent; fused unicuspid teeth 3/3; dental formula: 10 + 3/3 + 10 (Tables 1-6); no whitish mid-dorsal stripe; prebranchial length 34.86% of total length, branchial length 2.78%, trunk length 48.8%, tail length 13.53% of total length.

Remarks: According to the original description, the dental formula was 10 + 3/2 + 11. Shen and Tao later noted an error in their original description of the holotype and paratypes; the fused teeth counts on the lower teeth row should be 3 instead of 2 (Shen and Tao, personal communication).

Paramyxine sheni n. sp.
(Fig.6, Tables 1-8)

Holotype: NSYSU 2585, 380 mm TL, southwestern coast of Taiwan; depth 450 meters, 30 Jan. 1989.

Paratypes: NSYSU 2865, 11 specimens, 320-436 mm; Southwestern coast of Taiwan; depth 400 meters, 9 Feb. 1988.

Additional study materials: NSYSU 2859, 30 specimens, 320-430 mm, southwestern coast of Taiwan, depth 350 meters, 9 Feb. 1988; NSYSU 2860, 59 specimens 205-390 mm, eastern coast of Taiwan, depth 300 meters, 16 Aug. 1988.

Diagnosis: Six pairs of gill pouches and gill apertures; gill apertures usually closely spaced in a straight line, but never crowded together (Fig. 5); fused unicuspid teeth 3/3; dental formula: 11 + 3/3 + 10; no whitish mid-dorsal stripe; eye spots

prominent.

Description: Counts and proportions are listed in Tables 1-9. Color of preserved specimens brownish; no whitish mid-dorsal stripe; eye spots prominent; six gill apertures and pouches, gill apertures arranged in a straight line, variation in arrangements of gill apertures shown in Fig. 5, each aperture with a pale ring; PCD confluent with the posteriormost left gill aperture, and much larger than all other apertures; tongue muscle blankets gill pouches 2-4; slime pores (13-18) + (0-2) + (39-46) + (8-12) (mean 14.83 + 0.25 + 44.58 + 10.33), total slime pores 64-74 (mean 69.92), 75% of the specimens lacked slime pores next to all branchial apertures; fused unicuspid teeth 3/3; dental formula: 11 + 3/3 + 10; average prebranchial length 25.95%, branchial length 3.75%, trunk length 56.24%, tail length 15.27%, tail depth 10.24% and body depth 9.04% of total length (Tables 1-8).

Etymology: Named after Professor Shih-Chieh Shen of the Department of Zoology, National Taiwan University for his contribution to the knowledge of the fish fauna of Taiwan.

Remarks: The occurrence of 1 to 2 pairs of branchial slime pores corresponding to the second and third gill apertures in 10 to 25% of the specimens is of great interest. Occurrence of slime pores in the anterior section of the branchial region but not throughout the branchial region is rare, a condition noted only in *Eptatretus springeri*. No slime pores are found in the branchial region in the other *Paramyxine* species. *Paramyxine sheni* resembles the holotype of *Paramyxine atami* in having 3/3 fused unicuspid teeth. All *Paramyxine atami* specimens described by other ichthyologists have 3/2 fused unicuspid teeth. *Paramyxine sheni* and the holotype of *Paramyxine atami* are dissimilar in numbers of slime pores 14.83 + 0.25 + 44.58 + 10.33 vs. 19(20) + 0(?) + 58(59) + 5-6

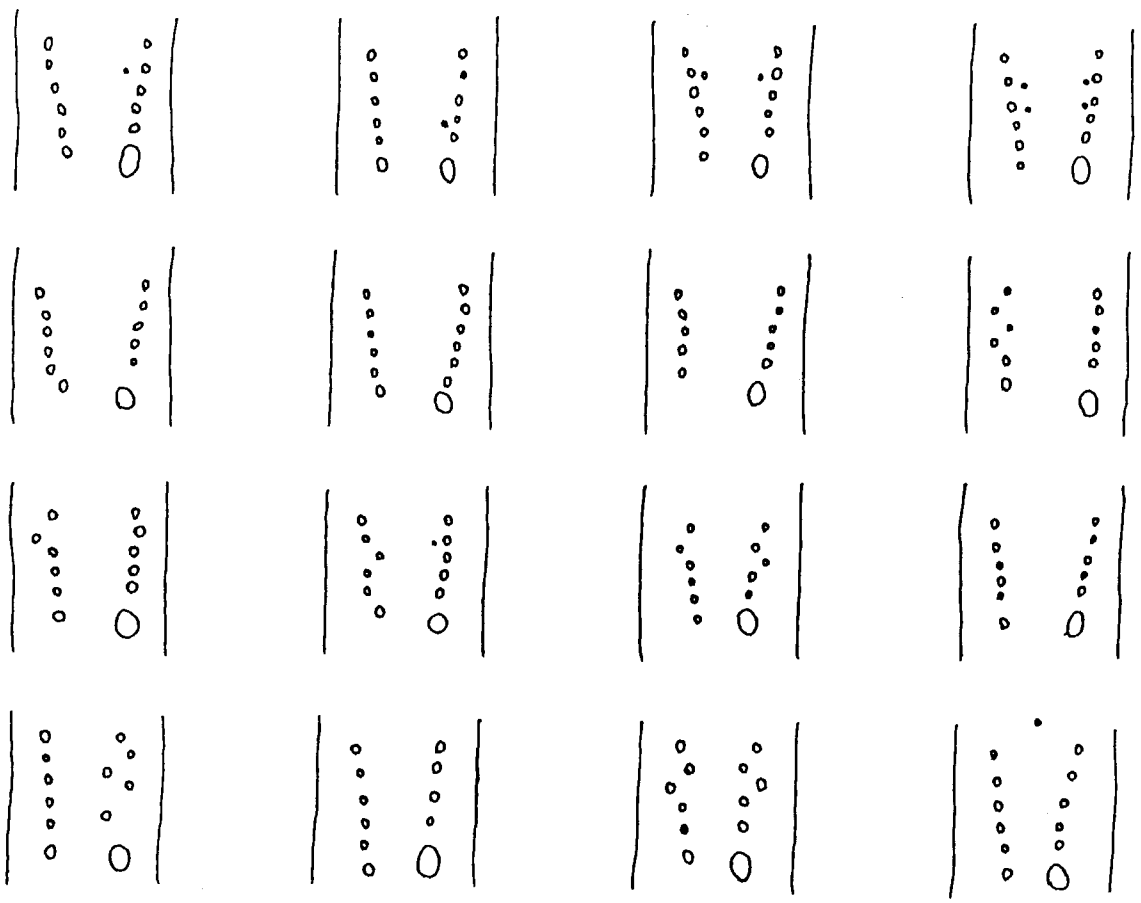

Fig. 5. Variation in arrangement of gill apertures in *Paramyxine sheni*. Smaller circles represent slime pores.

(Dean 1904), and the prebranchial and trunk slime pore counts are notably different. We therefore distinguish the group of hagfishes with fused unicuspid teeth 3/3 from Taiwan waters and the holotype of *P. atami* as not conspecific and name the former group *Paramyxine sheni*. Meanwhile *P. atami*, as characterized by the morphology of the holotype, remains valid. The genetic affinity of the species *Paramyxine sheni* is evident from mtDNA restriction patterns (Huang 1989).

Ecology: *P. sheni* inhabits depths of 200 to 800 meters. The reproductive season in Taiwan is from January to March. In February, 12.5% of the specimens collected from the southwest region carried eggs. The largest eggs was 38.8 mm. The smallest female with eggs, most in round or slightly ovoid stages, was 355 mm TL. Evaluating from their stomach content, *P. sheni* eats shrimp, crab, mollusk and fish.

***Paramyxine taiwanae* Shen and Tao, 1975**
(Tables 1-6)

Paramyxine taiwanae Shen and Tao 1975: 73-76; Ta-Chi, (northeastern coast of Taiwan, 24° 56.5'N. 121° 53.0'E)

Materials: NSYSU 2861, four specimens, 190-230 mm, northeastern coast of Taiwan, depth 20-50 meters, 5 Aug. 1988.

Diagnosis: Six pairs of gill pouches and gill apertures, crowded together in various arrangements (Fig. 6).

Description: Counts are listed in Tables 1-6 and proportions in Table 9. Color of preserved specimens brownish grey dorsally and laterally, whitish ventrally; no whitish mid-dorsal stripe or eye spots; each gill aperture not surrounded by a pale rings or all apertures surrounded by a single whitish area on both sides of ventral surface; six pairs of gill pouches, gill apertures crowded together and arranged irregularly; the efferent duct of the most anterior gill pouch more than 3 times the length of the most posterior one; ventral finfold absent; slime pores (16-19) + 0 + (36-42) + (6-9) (mean 17.25 + 0 + 39.5 + 7.5), total slime pores 62-67 (mean 64.50), branchial slime pores absent; fused unicuspid teeth 3/2; dental formula: (6-8) + 3/2 + (6-7); head length 25-35%, branchial length 1-3%; trunk length 42-56%, tail length 11-14%; body depth 5-9% of total length.

Ecology: *P. taiwanae* inhabits depths of 20-50 meters. In February, 12.2% of the specimens from the southwest region carried eggs. The largest egg (20.6 mm) was found in a 295 mm TL female with 10 eggs.

Table 9. Characteristics of *Paramyxine* species with 6 gill aperture pairs

Character	*P. sheni*	*P. atami*		*P. taiwanae*	*P. fernholmi*	*P. wisneri*
		Holotype[1]	Non-holotypes[2]			
Total length (mm)	205-436	550	500	169-334	167-357	140-388
Measurements:						
Preocular length	5.44%					
Prebranchial length	25.95%	26.00%	27.00%	30.72%	30.72%	27.97%
Branchial length	3.75%	2.50%	2.40%	2.66%	2.66%	4.58%
Trunk length	56.24%			52.00%	52.00%	49.37%
Tail length	15.27%			14.62%	13.67%	13.64%
Tail depth	10.24%			9.04%	9.04%	10.47%
Counts:						
Cusps on						
fused unicuspid	3/3	3/3	3/2	3/2	3/2	3/2
outer	9-12	10		6-8	8-10	7-10
inner	9-11	9-10		5-9	8-10	7-9
Slime pores:						
(left side)						
Prebranchial	13-19	19-20	16	16-19	16-23	15-20
Branchial	0-3	0	0	0	0	0-1
Trunk	40-47	58-59	47	36-42	38-44	36-44
Tail	8-12	5-6	10	6-9	6-11	6-11

[1]taken from Dean, 1904; [2]taken from Bigelow and Schroeder, 1952.

Paramyxine fernholmi, n. sp.
(Tables 1-9)

Holotype: NSYSU 2864, total length 280 mm, southwestern coast of Taiwan, 8 Feb. 1988.
Paratypes: NSYSU 2863, 2 specimens, 280,295 mm, Tongkong, eastern coast of Taiwan, depth 300 meters. Feb. 1991.

Diagnosis: Six pairs of gill pouches and apertures, gill apertures usually crowded in a slightly curved line; the most posterior left gill aperture not confluent with the external opening of the PCD; eye spots present but not obvious.

Description: Morphological data are listed in Tables 1-9. Color of preserved specimens greyish-brown, no white-colored patches over ocular area and no whitish mid-dorsal stripe; six gill apertures arranged in one or more irregular rows (Fig. 3E), pale rings around each, adjacent rings may meet; afferent duct of the last left gill aperture not confluent with the PCD; tongue muscle blankets gill pouches 2-4; slime pores (16-23) + 0 + (38-44) + (5-11), total slime pores 64-71; fused unicuspid teeth 3/2; dental formula (8-10) + 3/2 + (8-10), total 42-50; average prebranchial length 30.72%, branchial length 2.66%, trunk length 52.00%, tail length 13.67%, tail depth 9.04% and body depth 10.40% of total body length (Tables 7,9).

Etymology: Named after Dr. Bo Fernholm of the Swedish Museum of Natural History, for his contribution to hagfish biology.

Remarks: The *Paramyxine atami* Dean holotype has 6 gill pouches and 3/3 fused unicuspid teeth. All specimens identified as *Paramyxine atami* by other ichthyologists (Matsubara 1937, Okada et al. 1948, Bigelow and Schroeder 1952, Strahan and Honma 1961) have 3/2 fused unicuspid teeth. The *Paramyxine atami* holotype also differed from the present specimens in slime pores numbers. Holotype: (19-20) + 0 + (58-59) + (5-6) (total 82). Specimens examined by Bigelow and Schroeder (1952) had 73 slime pores (16 + 0 + 47 + 10). Strahan and Honma (1961) analysed the specimens from eastern and western Japan; the slime pore counts were 16.6 + 0 + 45.5 + 9 (eastern Japan) and 18.8 + 0 + 45 + 10.9 (western Japan). The holotype is obviously different from other specimens in number of fused unicuspid teeth, and in slime pore counts (58-59 vs. 45). We therefore propose that the holotype described by Dean and the specimens identified as *P. atami* by other ichthyologists represent two different species and that the latter group of specimens should be given a new species name. During the present study, we have collected 6-gilled *Paramyxine* specimens with fused unicuspid teeth 3/3 and 3/2. The specimens with 3/2 fused unicuspid teeth agree with the materials used by Matsubara (1937) and Okada et al. (1948). We designate these specimens *Paramyxine fernholmi*. The specimens with fused teeth 3/3 are described as another new species, *Paramyxine sheni* (see above).

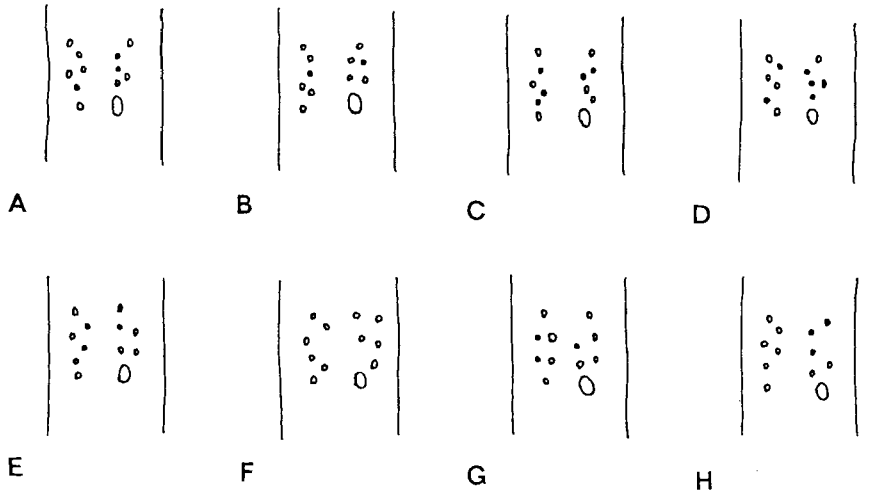

Fig. 6. Variation in arrangement of gill apertures in *Paramyxine taiwanae*. A-D, taken from Shen and Tao (1975); E-H, taken from this study.

Bigelow and Schroeder (1952) described *Paramyxine springeri* from the Gulf of Mexico, having six gill pouches and 3/2 fused unicuspid teeth. Strahan and Honma (1961) applied the same species name to the specimens in which 3-6 pairs of branchial slime pores are present. Fernholm and Hubbs (1981), however, substituted this species name with *Eptatretus springeri*. Presence of branchial slime pores in this species indicates that possibly it is not closely related to other *Paramyxine* species in which branchial slime pores were most likely to be absent (see below). We therefore agree with Fernholm and Hubbs (1981) in placing this species in the genus *Eptatretus*.

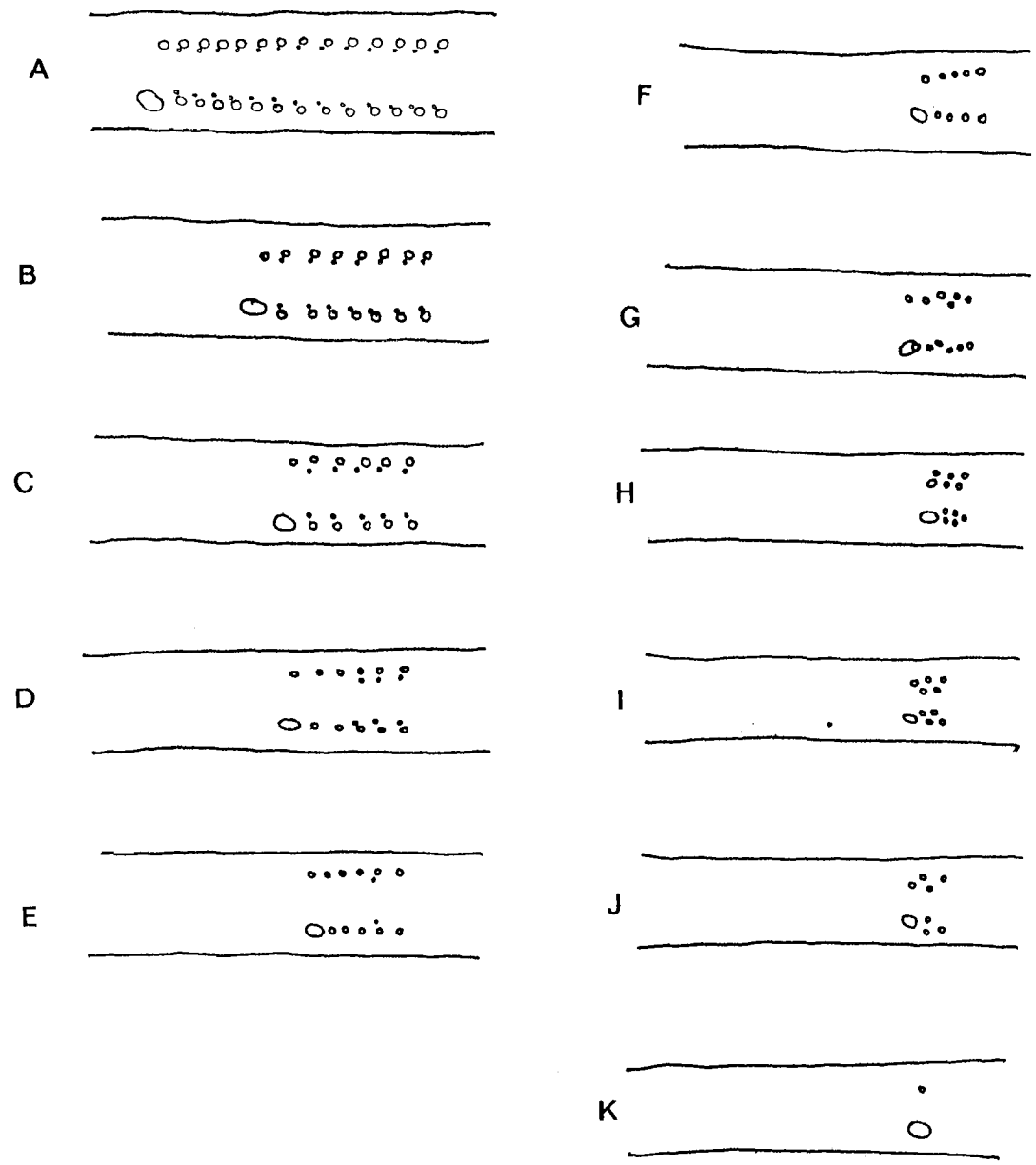

Fig. 7. Arrangement of the gill apertures and branchial slime pores changed in a sequence according to the branchial length, gill aperture and branchial slime pore count (Head to the right). (A) *Eptatretus stoutii* (Dean, 1904); (B) *E. okinoseana* (Dean, 1904); (C) *E. burgeri* (Shen and Tao, 1975); (D) *E. springeri* (Bigelow and Schroeder, 1952); (E) *Paramyxine sheni*; (F) *P. cheni* (Shen and Tao, 1975); (G) *P. fernholmi*; (H) *P. taiwanae* (Shen and Tao, 1975); (I) *P. yangi* (Teng, 1958); (J) *P. nelsoni*; (K) *Myxine paucidens* (Regan, 1912).

Strahan and Honma (1961) compared material of *Paramyxine atami* (now *Paramyxine fernholmi*) with *E. springeri* and indicated significant differences in slime pore counts. *E. springeri* also differed from the *P. atami* holotype in fused and unicuspid teeth numbers.

Ecology: *Paramyxine fernholmi* inhabits depths of 200 to 400 meters. In February, 12.2% of the specimens from the southwest region carried eggs. The largest egg, 28.3mm, occurred in a 357 mm TL female. The smallest female with egg was 275 mm TL.

***Paramyxine wisneri* n. sp.**
(Figs. 8-9, Tables 1-9)

Holotype: NSYSU 2868; 335 mm TL; coastal water of Fukan (Fig. 1); at about 200 meters depth; Feb. 1991.

Paratypes: NSYSU 2869; 3 specimens; 308 mm, 275 mm, 204 mm TL; taken with the holotype. NSYSU 2870; 2 specimens; 198 mm, 159 mm TL; 28 Sept. 1990.

Diagnosis: Branchial length 4.58% of total length; six pairs of gill pouches and gill apertures, gill apertures closely spaced in a straight line; external opening of the PCD confluent with the most posterior left gill aperture (51 of 59 specimens examined), and much larger than other apertures; the most anterior efferent ducts notably longer than the most posterior; fused unicuspid teeth: 3/2 (both outer and inner rows); eye spots present but not clear; ventral finfold prominent, with white margin.

Description: Counts are listed in Tables 1-7 and proportions in Table 9. Color of preserved specimens brownish, no whitish mid-dorsal stripe; ventral finfold prominent, with a pale margin, the pale originating near the body midpoint and ending at cloaca; six gill apertures arranged in a straight line, never crowded together (Fig. 9B), each gill aperture with a pale ring, adjacent rings may not meet; posteriormost left gill aperture confluent with PCD and larger than other gill apertures; the most anterior efferent duct notably longer than the most posterior (more than 3 times); slime pores (15-20) + (0-1) + (36-44) + (6-11), branchial slime pores rarely present (only 2 of 59 specimens); fused unicuspid teeth 3/2 (both outer and inner rows); dental formula (7-10) + 3/2 + (7-9); Tongue muscle covers gill pouches 2-4; average prebranchial length 27.97%, branchial length 4.58%, trunk length 49.37%, tail length 13.64%, and tail depth 10.47% of total body length.

Etymology: Named after Robert L. Wisner of the Scripps Institution of Oceanography, University of California, for his contribution to hagfish biology.

Remarks: Morphologically, *P. fernholmi* and *P. wisneri* are similar (Tables 1-9). They differ in (1) branchial length (2.66% in *P. fernholmi* and *4.58%* in *P. wisneri*), (2) arrangement of gill apertures (in an irregularly curved line in *P. fernholmi* and in a straight line in *P. wisneri*; Fig. 9); (3) PCD external opening of (not confluent with the posteriomost left gill aperture in *P. fernholmi* and confluent in *P. wisneri*); (4) ventral surface coloration (entire surface white in *P. fernholmi*); (5) finfold (only in *P. wisneri*). However, these two species are very different in their allozyme patterns (pers. data). Accordingly, we treat *P. wisneri* as a valid species.

DISCUSSION

Dean (1904) distinguished the genus *Paramyxine* from *Eptatretus* with branchial duct length. These ducts in *Eptatretus* are equal due to the well separated branchial apertures. Branchial apertures of *Paramyxine* species are clustered to various degrees and forms (Fig. 7). In *Paramyxine* a close placement of the apertures leads to a condition of elongated anterior ducts. In addition to this difference, *Eptatretus* and *Paramyxine* also differ in the number of slime pores in the branchial region. In *Eptatretus*, each branchial aperture is associated with a medial slime pore (Fig. 3). Dissimilarly, 50% or all of the branchial apertures in *Paramyxine* lack an accompanying slime pore. When slime pores are present, they are located medially to the branchial apertures (Fig. 3). In *Myxine*, there is a slime pore next to the common branchial aperture. Unlike the location of the branchial slime pores in the *Eptatretus* and *Paramyxine* species, this slime pore in *Myxine* is placed on the external side of the common branchial aperture. According to the distribution of these characteristics, we assume that the loss of slime pores in *Paramyxine* is apomorphic for myxinids. Consequently, *Paramyxine* is a monophyletic group. Since no slime pores were observed in lampreys (pers. obser.), the ancestral characteristic state of the relative position of the branchial aperture and its corresponding slime pore in hagfishes issue remains moot. If a medial position of the slime pores is treated as a synopomorphic character state, then *Eptatretus* and *Paramyxine* become sister groups. An alternative assumption is that an external placement represents a derived state which leads to a trichotomy of these three genera. A third assump-

Fig. 8. Left side-view of *Paramyxine wisneri*. 348 mm.

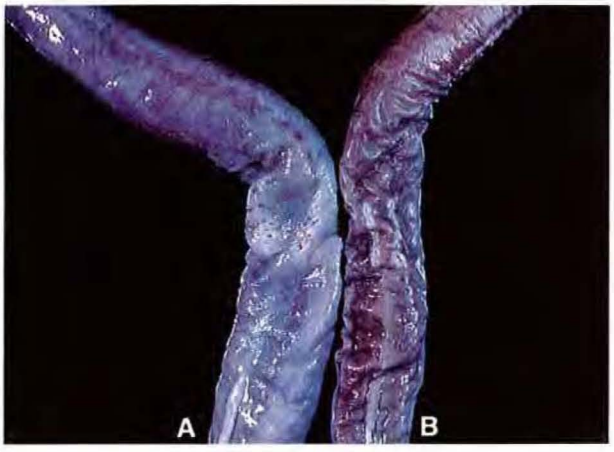

Fig. 9. Arrangement of gill apertures of *Paramyxine fernholmi* (A) and *P. wisneri* (B).

tion is that both characteristic states are derived, which would support a similar phylogenetic hypothesis to the consequences of our first assumption. At present, no criterion is known to prefer any of these assumptions.

The taxonomic value of different counts and proportions in *Paramyxine* and *Eptatretus* has been discussed by Dean (1904), Matsubara (1937), Strahan (1975), and Fernholm and Hubbs (1981). Dean (1904), Fernholm and Hubbs (1981) stressed the taxonomic importance of the relative position of gill apertures and various body region proportions relative to total length. Wisner and McMillan (1990) also suggested the importance of body proportions in hagfish taxonomy. Fernholm and Hubbs (1981) found fused cuspid patterns in the inner and outer teeth rows to be constant within the species *Eptatretus* and *Paramyxine* and therefore deemed it an important taxonomic characteristic. Gill aperture counts exhibit very low intra-specific variation in the *Paramyxine* species (Matsubara 1937, Strahan and Honma 1960 1961).

There are only four six-gilled *Paramyxine* species in Taiwan waters (Shen and Tao 1975): *P. sheni*, *P. taiwanae*, *P. fernholmi*, and *P. wisneri*. *P. sheni* differs from the other three species in the fused unicuspid teeth count (3/3 vs. 3/2) and can be distinguished from *P. wisneri* by its higher multicuspid teeth count 9-12/9-11 (7-10/7-9 in *P. wisneri*), and 3/3 cuspids (vs. 3/2 in *P. wisneri*); (outer row/inner row; Table 9). Among the latter three species, *P. taiwanae* is a shallow-water species and is separable from *P. wisneri* by the close placement of gill apertures and shorter branchial region (2.66% vs. 4.58%; Table 9). *P. fernholmi* and *P. wisneri* are distinguishable by morphology and allozyme patterns (see above).

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臺灣的盲鰻 (I)：分類與四個副盲鰻新種之描述

郭 建 賢　黃 國 峰　莫 顯 蕎

本文載述臺灣東北部，東部及西南部沿海九種盲鰻(紫黏盲鰻*Eptatretus okinoseanus*、蒲氏黏盲鰻*Eptatretus burgeri*、楊氏副盲鰻*Paramyxine yangi*、陳氏黏盲鰻*Paramyxine cheni*、紐氏副盲鰻*Paramyxine nelsoni*、沈氏副盲鰻*Paramyxine sheni*、台灣副盲鰻*Paramyxine taiwanae*、費氏副盲鰻*Paramyxine fernholmi*，及懷氏副盲鰻*Paramyxine wisneri*之形態。其中紫黏盲鰻爲台灣新記錄種，而沈氏副盲鰻、費氏副盲鰻、紐氏副盲鰻及懷氏副盲鰻爲新種。

關鍵詞：分類，黏盲鰻，副盲鰻，臺灣。