

Nasal-sinus Papillae of Hagfishes and Their Taxonomic Implications

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Hin-Kiu Mok (2001) Nasal-sinus papillae of hagfishes and their taxonomic implications. *Zoological Studies* 40(4): 355-364. Either a single medial papilla, two medial papillae placed anteroposteriorly, or a pair of bilaterally symmetric papillae mostly supported by cartilage occur in the inner dorsal surface of the nasal sinus near the apex in almost all members of the Myxiniinae, some species of *Eptatretus*, and *Paramyxine cheni*. A ventral median papilla on the floor of the nasal sinus also occurs in *Neomyxine biniplicata*, *Nemamyxine elongata*, and a few *Eptatretus* and *Paramyxine* species. The membrane on the nasal-sinus floor exhibits various degrees of tightness among hagfish genera. The gross morphology and distribution of these medial and bilateral papillae on the roof and folds and papillae on the floor of the nasal sinus in the family Myxiniidae are described and reported. The taxonomic implications of these structures in the nasal sinus are discussed.
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Key words: Myxiniidae, Papillae, Nasal sinus.

Hagfish have 4 pairs of external tentacles: two pairs of nasal tentacles surrounding the external rim of the nasal apex, a pair of oral tentacles next to the corners of the mouth, and a pair of labial tentacles posterior to the oral tentacles. The cartilage supporting the dorsal pair of nasal tentacles and the oral tentacles consists of the frontal branches of the anterior lingual cartilage, and the cartilage of the ventral pair of nasal tentacles consists of the anterior branches of the subnasal bar. Unlike these 3 pairs of tentacles, the labial tentacles are supported by their own cartilage which is not connected to any adjoining cartilage. Tentacles, papillae, or protrusions inside the nasal sinus (or nasal tube) have not been formally reported before. In this paper, I report on the occurrence of either a single medial papilla, two medial papillae placed anteroposteriorly, or a pair of symmetric tentacle-like papillae on the inner dorsal surface of the nasal sinus near the apex in some myxiniids. Although a small, short rod-shaped piece of cartilage was found beside the median cartilage connecting the 1st and 2nd nasal rings in Cole's illustration of the left-side view of the skull of a *Myxine* specimen, this cartilage was neither labeled nor mentioned in the text (Cole 1905). Actually that cartilage was the left nasal-sinus papilla described in this paper. A median small papilla on the floor of the nasal sinus occurs in some hagfishes. A longitudinal

fold of the membrane on the floor of the nasal sinus was observable in preserved specimens of some hagfishes. The morphologies of these structures in the nasal sinus are described, and the distribution of these structures in hagfishes and their taxonomic implications are reported and discussed.

MATERIALS AND METHODS

Twenty-four myxiniine species and 31 species of *Eptatretus* and *Paramyxine* were examined. The anterior section of the inner nasal sinus was examined under a stereomicroscope. Size, morphology, and presence or absence of supporting cartilage for the papilla were recorded. For species in which dissection was possible, the anteriorlateral section of the nasal sinus was cut open to provide a better saggital view of the papilla or fold in the nasal sinus. Scanning electron microscopy (SEM) was used to observe the nasal-sinus papillae of *Paramyxine cheni* and *Myxine formosana* (Mok and Kuo 2001). As cartilage of hagfish submerged in formalin for a long periods of time develops a red coloration, the supporting cartilage for the nasal-sinus papillae in some specimens could be seen without removing the skin. This is advantageous since dissection is usually not possible on many hagfish species known from only a

few specimens. A specimen of *M. formosana* and several specimens of *P. cheni* were cleared and stained to confirm the presence of the cartilage of the nasal-sinus papillae.

Cladistic methodology was adopted to analyze the number, position, and morphology of the nasal-sinus papillae and the fold. Autapomorphic characters in the morphology of these structures were viewed as supporting evidence for the validity of the species concerned, while synapomorphic characters were treated as important evidence supporting close phylogenetic relationships.

Materials examined

Eptatretus bischoffii USNM 260037, 208 mm; *E. burgeri* NSYSU uncat., 190 mm, 213 mm, 240 mm; *E. caribbeanus* UF 27892, 378 mm; USNM 218405, 356 mm; *E. carlhubbsi* BPBM 33933, 845 mm, 930 mm; *E. cirrhatous* AM I 35438001, 185 mm, 188 mm, NMV A6935, 340 mm; *E. chinensis* NSYSU 2867, 332 mm, 342 mm; *E. deani* CAS 56104, 370 mm, CAS 56105, 342 mm; *E. fritzi* SIO66-23, 385 mm, 412 mm; *E. hexatrema* SII 29421, 492 mm, SAM 13040, 467 mm; *E. indrambaryai* BMNH 1983.3.24: 1, 176 mm; *E. laurahubbsae* USNM 227441, 192 mm; *E. mccoonaugheyi* USNM 296320, 236 mm, 268 mm, 272 mm, 304 mm, 400 mm; *E. mccooskeri* USNM 344905, 280 mm; *E. mendozai* USNM 218400, 375 mm; USNM 268924, 364 mm, 390 mm; *E. minor* UF 27893, 1276 mm; USNM 218398, 340 mm; USNM 218399, 330 mm; *E. multidens* USNM 218402, 406 mm; *E. nani* USNM 272583, 432 mm, 550 mm; *E. okinoseanus* NSYSU uncat., 308 mm, 470 mm; *E. polytrema* USNM 272582, 388 mm; *E. profundus* SII 47212, 575 mm, SAM 33338, 630 mm; *E. sinus* USNM 296319, 300 mm, 315 mm, 360 mm; *E. stouti* NSYSU uncat., 234 mm, 360 mm, USNM 59834, 325 mm; *E. strahani* USNM 227442, 450 mm.

Paramyxine atami IZAS uncat., 499 mm; USNM 16442, 495 mm; *P. cheni* NSYSU uncat., 20 specimens, 148-462 mm; *P. fernholmi* NSYSU uncat., 226 mm, 252 mm, 308 mm; *P. nelsoni* NSYSU uncat., 190 mm, 201 mm, 231 mm, 240 mm, 242 mm; *P. sheni* NSYSU uncat., 230 mm, 345 mm, 374 mm, 401 mm; *P. springeri* UF 34267, 460 mm, USNM 161513, 340 mm; USNM 188210, 505 mm; USNM 218394, 386 mm; USNM 218395, 382 mm; USNM 218396, 396 mm, 517 mm; USNM 218397, 490 mm; *P. taiwanae* NSYSU uncat., 225 mm, 248 mm, 260 mm; *P. yangi* NSYSU uncat., 168 mm, 197 mm, 206 mm, 249 mm; *P. wisneri* NSYSU uncat., 192 mm, 265 mm.

Myxine affinis SIO 78-41, 515 mm, USNM 39039, 386 mm, 558.9 mm; *M. australis* USNM 153595, 320 mm, USNM 103769, 316 mm, USNM 117329, 204 mm; *M. capensis* SII 34846, 395 mm, 416 mm; *M. circifrons* SIO 068-118, 206 mm, 210 mm, 262 mm, 270 mm; *M. dubueni* SIO 90-140, 523 mm; *M. dorsum* SIO 92-21, 482 mm; *M. fernholmi* SIO 90-139, 570 mm; *M. formosana*, NSYSU uncat., 115 mm, 345 mm, 380 mm, 374 mm, 459 mm, 548 mm, 565 mm; *M. garmani* NSYSU uncat., 268 mm; *M. glutinosa* AMNH 56015, 480 mm, NSYSU uncat., 302 mm, USNM 25244, 287 mm, USNM 25245, 413 mm; *M. hubbsi* SIO 68-60, 415 mm, 440 mm; *M. hubbsoides* SIO 90-142, 657 mm; *M. ios* SIO 80-52, 412 mm; *M. knappi* SIO 90-144, 504 mm; *M. limosa* ROM 18057, 380 mm, USNM 197132, 335 mm; *M. mccooskeri* SIO 92-117, 226 mm; *M. mcmillanae* USNM 308407, 273 mm; *M. pequenoi* SIO 90-146; *M. robinsi* SIO 90-149, 505 mm; *Myxine* sp. 1 NSYSU 3176, 187 mm, NSYSU 3177, 123 mm, 136 mm, 185 mm, 187 mm; *Nemamyxine* (*Nem.*) *elongata* NMNZ P.37198, 787 mm; *Nem. kreffti* MOVI 01253, 376 mm; *Neomyxine* (*Neo.*) *biniplicata* NMNZ P.24388, 318 mm, 354 mm; *Notomyxine* (*Not.*) *tridentiger* BMNH 1869.5.3.21, 474 mm, SIO 78-45, 470 mm.

Institutional abbreviations are: AMNH, American Museum of Natural History; BHM, British Museum (Natural History); CAS, California Academy of Sciences; IZAS, Institute of Zoology, Academia Sinica; MOVI, Museu Oceanografico do Vale do Itajai, Universidade do Vale do Itajai; NMNZ, National Museum of New Zealand; NMV, National Museum of Victoria; NSYSU, National Sun Yat-sen University; ROM, Royal Ontario Museum; SAM, South African Museum; SII, JLB Smith Institute of Ichthyology; SIO, Scripps Institution of Oceanography; UF, University of Florida; USNM, National Museum of Natural History.

RESULTS

Papilla (papillae) on the roof of the nasal sinus

Fourteen of the 24 myxine species examined (including *M. affinis*, *M. australis*, *M. circifrons*, *M. debueni*, *M. dorsum*, *M. glutinosa*, *M. hubbsi*, *M. hubbsoides*, *M. knappi*, *M. ios*, *M. limosa*, *M. mcmillanae*, *M. pequenoi*, and *Myxine* sp. 1 from southwestern Taiwan) have a single nasal-sinus papilla located on the midline of the inner dorsal surface of the nasal sinus close to the nasal sinus apex (Figs. 1A, 2; Table 1). Fernholm (1991) used the

term “snout” for this part of the nasal sinus. *Nem. krefftii* also has a medial nasal-sinus papilla, but it is located at the mid point of the nasal sinus (Fig. 2M). The papilla in these species is much smaller than the above-mentioned oral and nasal tentacles (Fig. 1A-C), and its supporting cartilage, when present, is a ventral extension of the medial cartilage connecting the anteriormost nasal ring and the 2nd nasal ring (Fig. 2F, 2I). No supporting cartilage for the nasal-sinus papilla of *Nem. krefftii* was found. *M. robinsi* and *M. capensis* have 2 medial papillae aligned anteroposteriorly along the medial cartilage (Figs. 1B, 2K, 2L). The pieces of cartilage supporting these 2 papillae are also ventral extensions of this medial cartilage. In the remaining 6 myxine species (*Neomyxine biniplicata*, *Notomyxine tridentiger*, *M. fernholmi*, *M. garmani*, *M. mccoskeri*, and *M. formosana* from southwestern Taiwan) and all species of *Eptatretus* and *Paramyxine* with nasal papillae (i.e., *E. carlhubbsi*, *E. cirrhatus*, *E. hexatrema*, *E. laurahubbsae*, *E. mccoskeri*, *E. mendozai*, *E. minor*, *E. multiden*, *E. strahani*, and *P. cheni*) the papillae are tentacle-like and paired (Figs. 1C, 2-4; Table 1). These papillae are symmetrically placed on both sides of the medial cartilage of the anteriormost nasal ring close to the nasal sinus apex. *Nemamyxine elongata* and the other 13 *Eptatretus* and 8 *Paramyxine* species (*E. bischoffii*, *E. burgeri*, *E. caribbeanus*, *E. chinensis*, *E. deani*, *E. fritzi*, *E. indrambaryai*, *E. mcconnaugheyi*, *E. nani*, *E. okinoseanus*, *E. polytrema*, *E. profundus*, *E. sinus*, *E. stouti*, *P. atami*, *P. fernholmi*, *P. nelsoni*, *P. sheni*, *P. springeri*, *P. taiwanae*, *P. yangi*, and *P. wisneri*; Table 1) examined lacked papilla. No hagfish possesses both medial and bilateral papillae.

The size of the papillae is much smaller than the other types of tentacles mentioned above and is small in most species. The papillae of some species are relatively longer (i.e., *M. fernholmi*) or larger (i.e., *M. hubbsi* and *M. mccoskeri*), whereas those of *M. pequenoi*, *E. hexatrema*, *E. cirrhatus*, *E. mccoskeri*, *E. mendozai*, *E. minor*, and *M. pequenoi* are smaller, especially that of *E. mccoskeri* (Fig. 2). The length of the nasal-sinus papilla in a 570-mm TL specimen of *M. fernholmi* in which the nasal tentacles were about 4.5 mm in length was 1.5 mm. The height of the nasal-sinus papilla in a 225-mm TL *M. mccoskeri* in which the nasal papillae were about 3 mm in length was 0.8 mm. Sizes of the 2 medial papillae in *M. robinsi* are about equal (Fig. 2K), while those of *M. capensis* differ, with the anterior one being smaller (Fig. 2L). Myxine nasal-sinus papillae are either conical (e.g., *E. laurahubbsae* and *M. fernholmi*; Fig. 2C), or triangular and laterally compressed (e.g., *M.*

mccoskeri; Fig. 2D). Some exceptions were noted in *M. mccoskeri*, *M. dorsum*, *M. ios*, *E. mccoskeri*, and *E. cirrhatus* (Fig. 2B, 2D, 2E, 2H). The base of the papillae in *M. mccoskeri* is bulky, while the top portion becomes much more compressed and tapered (Fig. 2D). The median papilla in *M. dorsum* is bulky

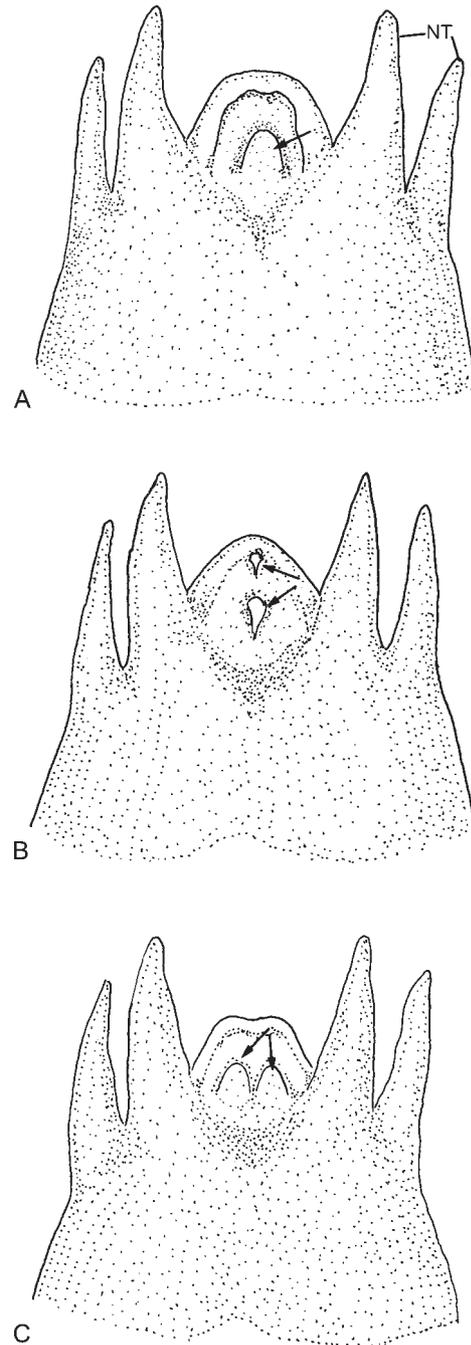


Fig. 1. Drawings of the ventral view of the apex of the nasal sinus (or the snout) showing the nasal-sinus papilla (papillae). A, *Myxine circifrons*; B, *M. capensis*; C, *Paramyxine cheni*. An arrow indicates the nasal-sinus papilla. NT: nasal tentacle.

and flat on its ventral surface (Fig. 2E), whereas the medial papilla in *M. ios* is pyramid shaped (Fig. 2H). The paired papillae of *E. mccoskeri* have a wide rounded base, and they are very low giving the appearance of a rounded lump of skin (Fig. 2B). The skin overlying these papillae in *E. cirrhatus* is much paler than the surrounding skin.

Most hagfish dorsal nasal-sinus papillae (e.g., those of *Neo. biniplicata*, *M. fernholmi*, *M. garmani*, *M. hubbsi*, and *M. formosana*) are anteriorly directed with the posteroventral section of the papilla con-

nected to the roof of the nasal sinus, leaving the anterior part free from the sinus roof (Fig. 2, drawings on the right; Fig. 3). The papillae in others (e.g., *M. mccoskeri*), particularly those of small size (e.g., *M. capensis*, *E. glutinosa*, *E. hexatrema*, *E. cirrhatus*, and *E. mccoskeri*) are vertical (Fig. 2).

Except for *E. carlhubbsi*, *E. cirrhatus*, *E. mccoskeri*, *M. dorsum*, *M. mccoskeri*, and possibly *E. minor* as well, the paired papillae are each supported by cartilage that is not connected to adjoining cartilage (Fig. 4). No cartilage was found inside the

Table 1. Distribution of the characters and character states of papillae on the roof of the nasal sinus in hagfish with information on the area of occurrence of the species and the number of fused cusps on the anterior (afc) and posterior sets of cusps (pfc)

Species	Character states				Area of occurrence								afc/pfc
	A1	A2	B	C ¹	SCS	WP	OC	CP	EP	CGM	AO	IO	
<i>Eptatretus cirrhatus</i>			+				+						3/3
<i>E. carlhubbsi</i>			+					+					2/3
<i>E. hexatrema</i>			+									+	3/2
<i>E. laurahubbsae</i>			+						+				2/2
<i>E. mccoskeri</i>			+						+				3/3
<i>E. mendozai</i>			+							+			3/3
<i>E. minor</i>			+							+			3/3
<i>E. multidentis</i>			+							+			3/3
<i>E. strahani</i>			+		+								3/3
<i>Paramyxine cheni</i>			+			+							3/3
<i>Nemamyxine krefftii</i>	+										+		3/2
<i>Neomyxine biniplicata</i>			+					+					2/2
<i>Notomyxine tridentiger</i>			+								+		3/2
<i>Myxine affinis</i>	+										+		2/2
<i>M. australis</i>	+										+		2/2
<i>M. capensis</i>		+										+	2/2
<i>M. circifrons</i>	+								+				3/2
<i>M. debueni</i>	+								+				3/2
<i>M. dorsum</i>	+								+				2/2
<i>M. fernholmi</i>			+						+		+		3/2
<i>M. formosana</i>			+				+						3/2
<i>M. garmani</i>			+			+							3/2
<i>M. glutinosa</i>	+										+		2/2
<i>M. hubbsi</i>	+								+				2/2
<i>M. hubbsoides</i>	+								+				2/2
<i>M. ios</i>	+										+		2/2
<i>M. knappi</i>	+										+		2/2
<i>M. limosa</i>	+										+		2/2
<i>M. mccoskeri</i>			+								+		3/2
<i>M. mcmillanae</i>	+									+			2/2
<i>M. pequenoii</i>	+								+				2/2
<i>M. robinsi</i>		+								+			3/2
<i>Myxine</i> sp. 1	+					+							2/2

A1, single medial papilla; A2, 2 medial papillae; B, 2 symmetrical papillae; C, no papilla.

Area of occurrence: AO, Atlantic Ocean; CGM; Caribbean Sea and Gulf of Mexico; CP, central Pacific (around Hawaii); EP: eastern Pacific Ocean; IO, Indian Ocean (off South Africa); OC: Oceania (around Australia and New Zealand); SCS, South China Sea; WP, western Pacific Ocean.

¹Character state C (no papilla) occurs in 13 *Eptatretus* species (*E. bischoffii*, *E. burgeri*, *E. caribbeanus*, *E. chinensis*, *E. deani*, *E. fritzi*, *E. mcconnaugheyi*, *E. nani*, *E. okinoseanus*, *E. polytrema*, *E. profundus*, *E. sinus*, and *E. stouti*), 8 *Paramyxine* species (*P. atami*, *P. fernholmi*, *P. nelsoni*, *P. sheni*, *P. springeri*, *P. taiwanae*, *P. yangi*, and *P. wisneri*), *Nemamyxine elongata*, and *Notomyxine tridentiger*.

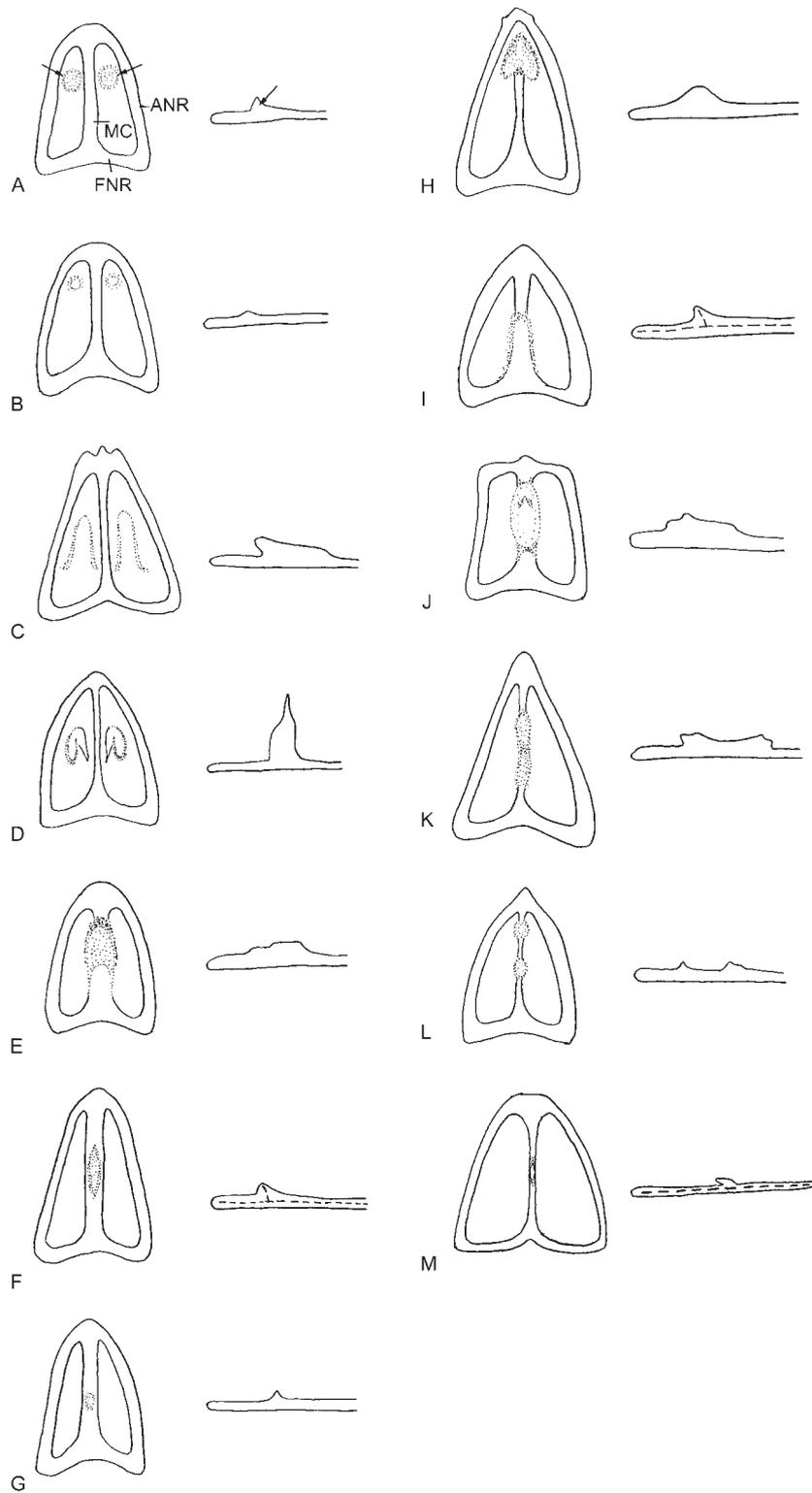


Fig. 2. Ventral view of the first 2 nasal rings and the connecting medial cartilage, the position and morphology of the nasal-sinus papilla (or papillae) (left drawings), and the sagittal view of the nasal-sinus papilla (right drawings). A, *Eptatretus hexatrema*; B, *E. mccoskeri*; C, *Myxine fernholmi*; D, *M. mccoskeri*; E, *M. dorsum*; F, *M. glutinosa*; G, *M. limosa*; H, *M. ios*; I, *M. hubbsoides*; J, *M. hubbsi*; K, *M. robinsi*; L, *M. capensis*; M, *Nemamyxine krefftii*. MC: medial cartilage connecting the anteriormost nasal ring (ANR) and the ring immediately following (FNR). Arrows indicate the nasal-sinus papillae. A dotted line represents the medial cartilage and its ventral extension into the papilla.

papillae of *E. carlhubbsi*, *E. cirrhatus*, *E. mccoskeri*, *M. dorsum*, or *M. mccoskeri*. The absence of supporting cartilage in the papillae of *E. carlhubbsi*, *E. minor*, and *M. mccoskeri* remains to be confirmed by histological means when additional specimens of this species become available.

Fold and papilla on the floor of the nasal sinus

The nasal rings are semicircular with the ventral sides not fused medially. The space between these sides of the rings are joined by a membrane. In the majority of eptatretines, this membrane is not tightly stretched by the sides of the rings. Consequently longitudinal fold(s) along the ventral midline of the membrane occurs in fresh specimens (Fig. 5A), whereas

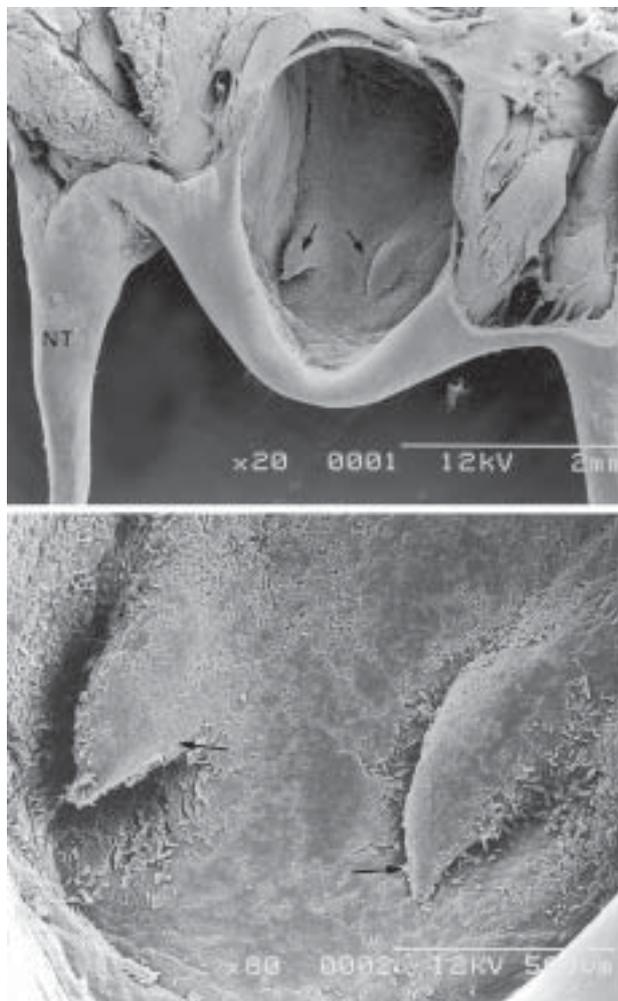


Fig. 3. SEM pictures of *Myxine formosana* nasal-sinus papillae in 2 magnifications. Scale: bar = 2 mm, top picture; bar = 500 μ m, bottom picture. Arrow indicates 1 of the 2 nasal-sinus papillae. NT: nasal tentacle.

a medial longitudinal fold on the floor of the nasal sinus was observable in preserved specimens of *Eptatretus* and *Paramyxine* (Fig. 5C). The fold is usually low but obvious. However, height and thickness vary to a certain degree among species. The front end of the fold does not reach the edge of the nasal sinus. The anterodorsal edge is slightly anterior to the anterior base. In a few species, including *E. bischoffii*, *E. deani*, *E. fritzi*, *E. burgeri*, *E. hexatrema*, *E. okinoseanus*, *P. nelsoni*, *P. wisneri*, and *P. yangi*, the fold is much less obvious but there is a small papilla near the front (Fig. 5A). In *E. fritzi*, this papilla is particularly close to the apex of the nasal sinus.

The membrane between the ventral sides of the nasal rings in *P. cheni*, *Myxine*, *Nemamyxine*, *Neomyxine*, and *Notomyxine* is so tight that the above-mentioned fold is absent. In *Neo. biniplicata*, a small conical, medial papilla is found near the apex, whereas in *Nem. elongata*, a very short, low and thin triangular papilla is on and parallel to the middle line of the nasal-sinus floor at the level through the base of the dorsal nasal tentacles (Fig. 5C). For *P. cheni*, all *Myxine* species examined, and *Nem. krefftii*, no papilla was seen. The above-mentioned papilla on the floor of nasal sinus has no supporting cartilage.

Differences in the tightness of the membrane between most eptatretines and myxinines (*Myxine*, *Nemamyxine*, and *Neomyxine*) indicate that lateral expansion of the nasal sinus between these 2 groups may differ. Expansion, which may be related to the influx of water through the nasal sinus of the hagfish, is expected to be higher for the former

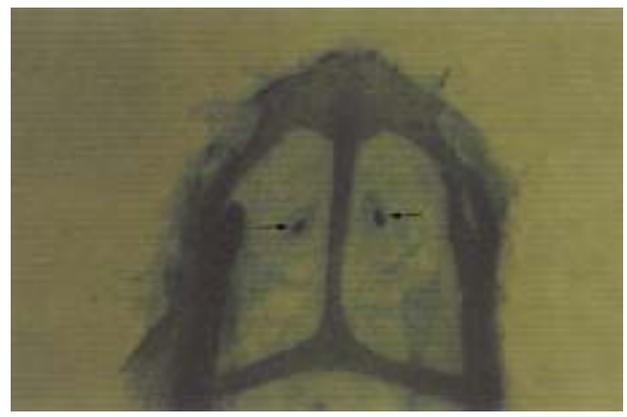


Fig. 4. Ventral view of the anterior portion of a cleared and stained nasal tube of *Myxine formosana* showing the paired nasal-sinus papillae (indicated by arrows) and their symmetric position relative to the medial cartilage connecting the first 2 nasal rings. Scale bar = 1 mm.

group. Functional adaptation leading to such structural differentiation deserves further studies.

DISCUSSION

Nasal-sinus papillae of the 20 *Paramyxine cheni* specimens examined (range of total length: 148–462 mm) showed no obvious morphological variation. Unfortunately very few specimens of most *Myxine* species examined for nasal-sinus papillae or papillae are available making complete description of the morphological variation of the papilla impossible. However, specimens of the species with more than 1 specimen available to this study had no obvious intraspecific morphological differences in their dorsal nasal-sinus papillae. Morphological consistency in this material supports the taxonomic value of this structure for species discrimination or even for phylogenetic inferences.

As the positions of the bilateral papillae and medial papilla (papillae) on the roof of the nasal sinus differ and both are supported by different cartilage structures, these 2 types of papillae are not treated as homologous structures. The bilateral, dorsal papillae are found in both myxinines and eptatretines; this distribution pattern suggests that the common ancestor of hagfishes could have had these papillae. On the other hand, restriction of the medial papilla (or papillae) to only some *Myxine* species suggests that this is an apomorphic character. Consequently, those *Myxine* species possessing this character should have a closer phylogenetic relationship. The paired nasal-sinus papillae in *P. cheni* and myxinines have well developed rod-shaped supporting cartilage, whereas those in eptatretines tend to lack supporting cartilage; the latter condition may be an apomorphic character state. However, detailed histological examinations of the papillae of the latter group remain to be done before such phylogenetic interpretation becomes more favorable.

Distributions of the character states of the fold on the floor of the nasal sinus in myxinids (absent in myxinines and *P. cheni*, but present in most eptatretines) suggest that the common ancestor of hagfishes might not have possessed such a fold. The presence of the fold represents an apomorphic character state for myxinids. As a consequence, *P. cheni* may be the plesiomorphic sister group for the rest of the eptatretines. A small, medial papilla on the floor of the nasal sinus appears sporadically among hagfishes indicating that it may have been derived more than once in the Myxininae and Eptatretinae.

Concepts of the taxonomy of Atlantic Ocean

Myxine species diverge as a consequence of the difficulties in employing slime pore counts, cusp counts, and body proportions in species diagnosis

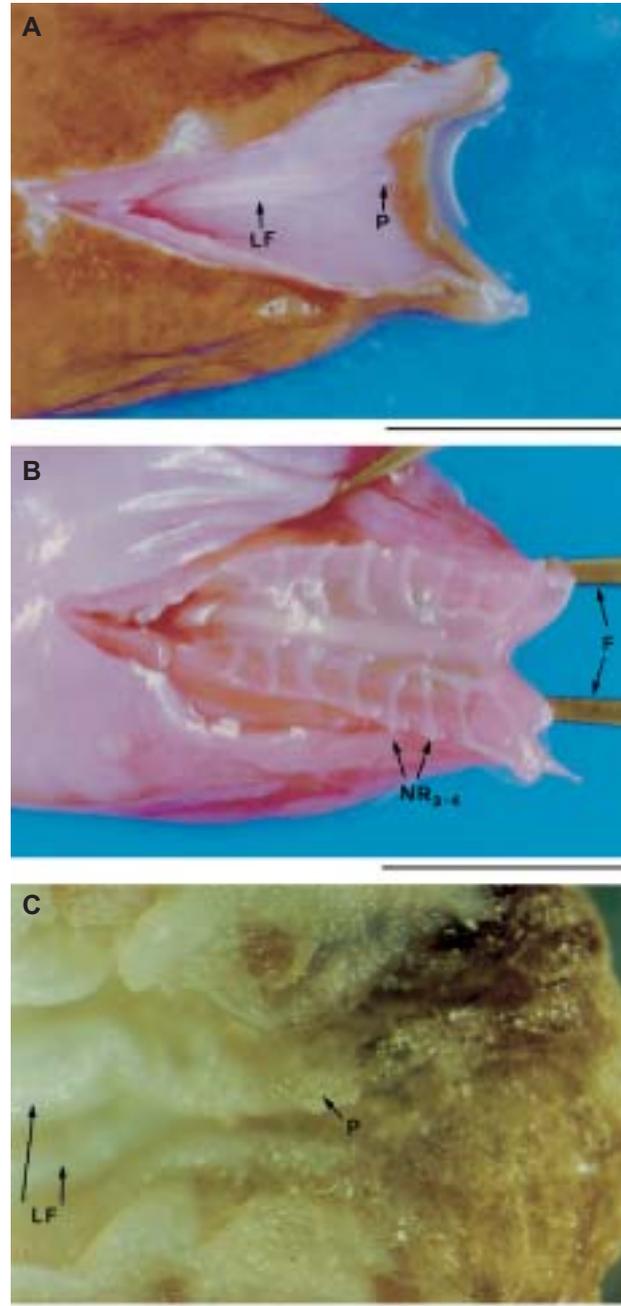


Fig. 5. Dorsal view of the nasal-sinus floor showing the conditions of the membrane connecting the nasal rings and the medial papilla. The roof of the nasal sinus was cut open along the midline. A, a fresh 500-mm TL specimen of *Eptatretus burgeri*; B, a fresh 600-mm TL specimen of *Myxine formosana*; C, a preserved 173-mm TL specimen of *Paramyxine nelsoni*. F: forcep; LF: longitudinal fold; P: papilla; NR: nasal ring. Opening of the nasal sinus to the right. Scale: bars in A and B = 10 mm; bar in C = 1 mm.

and identification (Fernholm 1981). Holly (1933) recognized 5 Atlantic species (*M. glutinosa*, *M. limosa*, *M. australis*, *M. atlantica*, and *M. capensis*) of which 2 species were of uncertain status. Adam and Strahan (1963), in contrast, recognized only 1 species (*M. glutinosa*) in this region. Fernholm (1981) described an additional species, *M. ios*, from the Atlantic and accepted *M. glutinosa* and *M. capensis* as valid species. He later (1998) recognized *M. australis*, *M. limosa*, and *M. affinis* as well. All of these judgements were based on the conventional meristic and morphometric characters mentioned above. Morphological variations exhibited by the dorsal-medial nasal-sinus papillae of *M. capensis*, *M. ios*, *M. dorsum*, and *M. robinsi* suggest that these are all valid species. The dorsal nasal-sinus papilla in *M. limosa* is much smaller than that of *M. ios*, but is only slightly smaller than that of *M. glutinosa* (Fig. 2). On the basis of nasal-sinus papilla alone, no obvious morphological difference exists between *M. limosa* and *M. glutinosa*. All in all, the dorsal nasal-sinus papilla of several myxinid species, including *M. capensis*, *M. dorsum*, *M. fernholmi*, *M. hubbsi*, *M. mccoskeri*, *M. robinsi*, and *Nem. krefftii* has autapomorphic morphological characters that are useful for species identification and taxonomic verification.

Table 1 presents data on the geographical distribution of myxinid species with either a single medial papilla, two medial papillae, a pair of symmetric nasal-sinus papillae, or the absence of papilla on the roof the sinus. A single nasal-sinus papilla placed medially on the roof of the nasal sinus is notably

common for *Myxine* species including *M. affinis*, *M. australis*, *M. circifrons*, *M. debueni*, *M. dorsum*, *M. glutinosa*, *M. hubbsi*, *M. hubbsoides*, *M. ios*, *M. limosa*, *M. mcmillanae*, *M. pequenoii*, *M. capensis*, and *M. robinsi* (Table 1) in the New World (western coasts of North and South America), the Atlantic Ocean, and the Mediterranean Sea (Fig. 4). Among western Pacific myxinines only *Myxine* sp. 1 from southwestern Taiwan currently being described by this author has this character. These 15 *Myxine* species may have a closer relationship. The presence of a medial papilla on the nasal-sinus roof in *Nem. krefftii* is either a case of convergence or an indication for a close relation of this species to the 15 *Myxine* species just mentioned. The absence of both medial and paired papillae in the congener of *Nem. krefftii*, i.e., *Nem. elongata*, is a unique condition for all myxinines. Similarities in the number and position of the nasal-sinus papillae (i.e., having 2 dorsal medial papillae) between *M. capensis* from South Africa and *M. robinsi* from the Caribbean Sea deserve further attention for their possible close phylogenetic relationship. The remaining *Myxine* species (including *M. fernholmi*, *M. formosana*, *M. garmani*, and *M. mccoskeri*), *Neo. biniplicata*, and *Not. tridentiger* have the plesiomorphic character of having paired dorsal nasal-sinus papillae.

The eptatretines with nasal-sinus papillae on the roof of the nasal sinus (a plesiomorphic character state) occur in the Caribbean Sea, the western coast of Central America, Hawaii, the Indo-Pacific, Australia, New Zealand, and South Africa (Table 1;

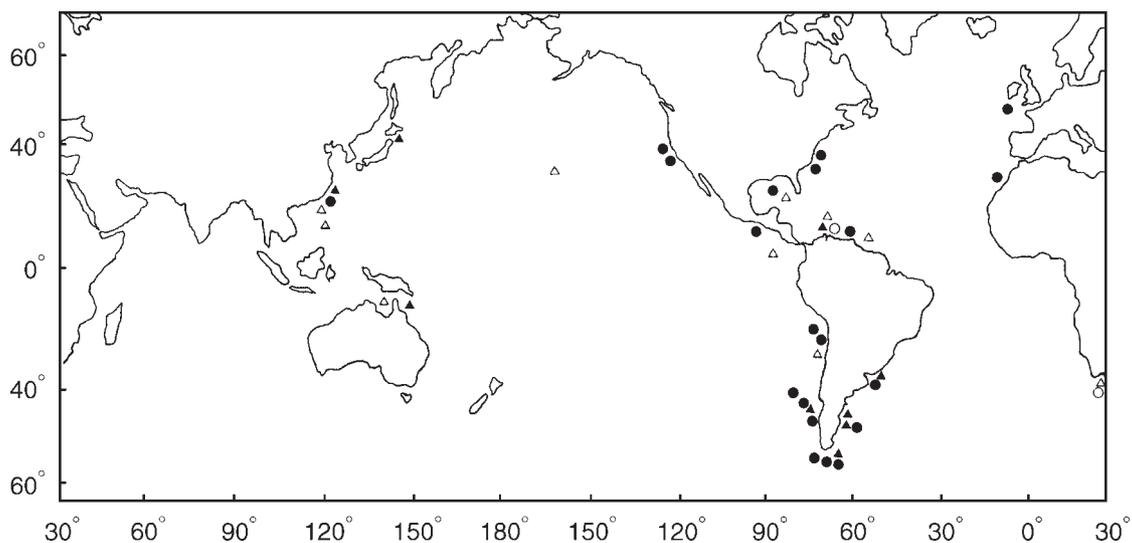


Fig. 6. Map showing the geographical distributions of the 3 characters of the nasal-sinus papillae in eptatretines and myxinines. ●: single medial nasal-sinus papilla in myxinines; ○: 2 medial nasal-sinus papillae in myxinines; ▲: symmetric paired nasal-sinus papillae in myxinines; △: symmetric paired nasal-sinus papillae in *Eptatretus* and *Paramyxine* species.

Fig. 5). Interestingly, none of the species in the eastern Pacific Ocean (along the western coast of the Americas), western Pacific Ocean (Taiwan and Japan) and Andaman Sea has nasal-sinus papillae (Table 1; Fig. 6). These papillae could have been lost several times within the Eptatretinae.

There seems to be a correlation between the character states of the dorsal nasal-sinus papillae count and the number of fused cusps in the multicusps. All myxinines have a 2-cusp multicusp on the posterior cusp set. Ten of the 12 myxine species with the 2-cusp multicusp on the anterior cusp set and with papilla have a single nasal-sinus papilla (83%, Table 1). In contrast, five of the 8 myxine species with the 3-cusp multicusp on the anterior cusp set possess a pair of papillae (63%, Table 1). As the majority of hagfishes have a 3/2-cusp multicusp condition for the anterior and posterior multicusps, this dental pattern might be the primitive state for myxinines. If this is true, the number of fused cusps on the anterior multicusp is reduced to 2 in some myxinines, whereas the number of fused cusps in the posterior multicusp is increased to 3 in some eptatretines. Different trends in these changes have taken place in the anterior multicusp versus the posterior multicusp—a hypothesis seems more complicated than if both multicusps have the same trend (i.e., either an increase or decrease in numbers of fused cusps for both multicusps). In other words, the hypotheses that the ancestor of hagfishes had either 2 or 3 fused cusps in both the anterior and posterior multicusps are also equivocal. Consequently, the apomorphic character state of having only 2 fused cusps on the anterior multicusp and the character of having a medial nasal-sinus papilla correlate in myxinines. In addition, all *Eptatretus* species (except for *E. hexatrema*) and *P. cheni* with nasal-sinus papillae (i.e., paired symmetric papillae) share the character state of having a 3-cusp multicusp on the posterior cusp set. Almost all *Eptatretus* species (except for *E. hexatrema*) and *Paramyxine* species with a 3-cusp and 2-cusp multicusps on the anterior and posterior cusp sets, respectively, do not possess nasal-sinus papillae (Table 1). This latter correlation increases the chance of the character state of having 2 fused cusps on the posterior multicusp being

apomorphic in eptatretines.

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REFERENCES

- Adam H, R Strahan. 1963. Systematics and geographical distribution of Myxinoids. In A Brodal, R Fange, eds. The biology of *Myxine*. Oslo: Universitetsforlaget, pp 1-8.
- Cole FJ. 1905. A monograph on the general morphology of the Myxinoid fishes based on a study of *Myxine*. Part I. The anatomy of the skeleton. Trans. Roy. Soc. Edinburgh **41**: 749-788.
- Fernholm B. 1981. A new species of hagfish of the genus *Myxine*, with notes on other eastern Atlantic myxinids. J. Fish Biol. **19**: 73-82.
- Fernholm B. 1991. *Eptatretus eos*: a new species of hagfish (Myxinidae) from the Tasman Sea. Jpn. J. Ichthyol. **38**: 115-117.
- Fernholm B. 1998. Hagfish systematics. In JM Jorgensen, JP Lombolt, RE Weber, H Malte, eds. The biology of hagfishes. London: Chapman and Hall, pp. 33-44.
- Holly M. 1933. Cyclostomata. Das Tierreich. **59**: 1-62.
- Mok HK, CH Kuo. 2001. *Myxine formosana*, a new species of hagfish (Myxiniformes, Myxinidae) from the southwest waters of Taiwan. Ichthyol. Res. **48**: 295-297.

盲鰻鼻管乳突及其分類之應用

莫顯喬

在盲鰻亞科絕大部份的種類中，黏盲鰻屬內部份種類和陳氏副盲鰻的鼻管前端背中線上有一至兩枝短細的乳突，或在該中線的兩側有一對短細的乳突，而在黏盲鰻屬及副盲鰻屬內的少數種數之鼻管腹面中線前端有一小乳突。鼻管腹部皮膜之鬆緊度有屬間變異的情況。本研究描述鼻管乳突的形態、鼻管腹部皮膜狀態及記錄其乳突形態在盲鰻科內的變異與分布情況，並應用此形態變異研討盲鰻的分類問題。

關鍵詞：盲鰻科，乳突，鼻管。

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