Zoological Studies **38**(3): 307-313 (1999)

Zoological Studies

Descriptions of Two New Subfamilies and a New Genus of Hagfishes (Cyclostomata: Myxinidae)

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(Accepted May 10, 1999)

Robert L. Wisner (1999) Description of two new subfamilies and a new genus of hagfishes (Cyclostomata: Myxinidae). *Zoological Studies* **38**(3): 307-313. Two new subfamilies of myxinid fishes, Paramyxininae and Quadratinae, are designated, and a new genus, *Quadratus*, is described. Subfamilies Myxininae and Eptatretinae are redescribed. The four subfamilies are distinguished by the numbers of gill apertures, the placement of the first (anteriormost) gill aperture relative to the first gill pouch, the length of the first efferent branchial duct relative to the last, and the linearity or non-linearity of the patterns of gill apertures. The putative taxonomic position of *Paramyxine springeri* is discussed.

Key words: Myxinidae, Hagfishes, Subfamilies.

Hagfishes are primitive, cartilaginous, eel-like agnathous craniates that are entirely marine and benthic. They have three paired sets of sensory barbels, feed on bottom invertebrates and dead or moribund fishes, and are noted for the production of copious amounts of mucus (slime). Two sets of keratinous teeth (cusps) on each side of the mouth are attached to cartilaginous dental plates which in turn are attached to the anterior end of a sub-cylindrical complex of muscle and cartilage (the dental, lingual, or club-like muscle of various authors) which inverts and retracts the two medially opposing sets, providing a biting-cutting mechanism for feeding. Hagfishes are essentially blind, with rudimentary, light-sensitive vestigial “eyes” set in the flesh of the head and covered with integument, which in some species is often less pigmented than the surrounding tissue, resulting in whitish eyespots. Internal gill pouches (GP) are supplied with water entering the nasopharyngeal opening above the mouth and propelled by the pumping of a muscular velum in the pharynx. Water passes from the pharynx through the afferent branchial duct (ABD) to the GP, and exits through the efferent branchial duct (EBD) and out through one or more pairs of external openings or gill apertures (GA). Surplus water and detritus are discharged through the pharyngocutaneous duct (PCD), an enlarged opening confluent with or contiguous to the last (or only) GA on the left side (Fig. 1). As stated by Fernholm (1998), recent hagfishes are monophyletic with many common features: no vertebrae (only a notochord), no paired fins, body fluids nearly isosmotic with sea water, and a single orifice (nasopharyngeal aperture) conducting respiratory water to the pharynx and gill pouches. No attempt is made to discuss possible relationships of the family Myxinidae to any other taxa.

The hagfish family Myxinidae has recently doubled in numbers of described species, from about 30 in 1965 to at least 60 at present. Two subfamilies, Myxininae and Eptatretinae, erected by Nelson (1976), were based largely on data from Adam and Strahan (1963).

The subfamilies of Myxinidae are characterized primarily by patterns formed by the gill apertures, the lengths of the anteriormost (first) and posteriormost (last) efferent branchial ducts, the positions of the corresponding gill apertures relative to the nearest gill pouches, and the ratios of lengths of gill pouch units to gill aperture units (the distance between the outer margins of the row of internal gill pouches and of the row of external gill apertures).

The subfamily Myxininae is characterized by having a single GA on each side, the first EBD much longer than the last, and all efferent branchial ducts discharging through the PCD (Fig. 1) and through a

single GA on the right side. Subfamily Eptatretinae is characterized by having 5 through 14 GP, each one discharging to the exterior through its own EBD to its corresponding GA. All GA are in a straight line with the first GA opposite the second GP; all EBD are about equal in length (Fig. 2).

Dean (1904), when describing the new genus and species, *Paramyxine atami*, introduced as taxonomic characters the closely spaced gill aperture and the relative positions of the first and last GA and GP, and the diagnostic character of the first EBD being several times longer than the last (Fig. 3). Dean contrasted this condition with that found in genus *Eptatretus* in which all ducts are about equal in length (Fig. 2).

Bigelow and Schroeder (1952) described *Paramyxine springeri* from the Gulf of Mexico, basing the generic name on the stated to be more closely spaced gill apertures than normally found in species having numerous apertures, but which is common in *Paramyxine*. Internal characters were not mentioned. Fernholm and Hubbs (1981) placed the species *springeri* in the genus *Eptatretus*, stating that the gill apertures were not unduly closely spaced. These authors also did not mention internal characters. Fernholm (1998) acknowledged Dean's 1904 statement regarding the relative positions of the GA and GP, but did not investigate the relationship. Rather, he stated that the genus *Paramyxine* is problematical, and its distinction from *Eptatretus* cannot be upheld.

Intrigued by the apparent lack of interest in Dean's principal character of differing lengths of the first and last EBD, and having adequate material at hand, I began the investigation that led to this study and formed the basis of the two new subfamilies, Paramyxininae and Quadratinae, and the new genus *Quadratus*.

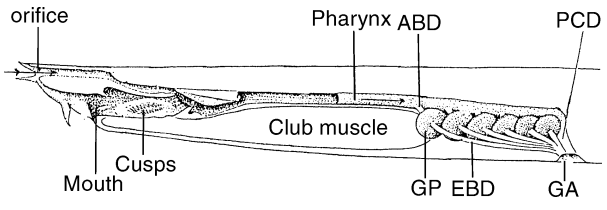

Fig. 1. Anterior part of a hagfish (*Myxine glutinosa*) showing path of water from intake at orifice, through pharynx, afferent branchial duct (ABD), gill pouch (GP), efferent branchial duct (EBD), to discharge via the gill aperture (GA) and pharyngocutaneous duct (PCD). (Modified from Johansen and Strahan 1963).

MATERIALS AND METHODS

Methods and abbreviations follow those of McMillan and Wisner (1984) and Wisner and McMillan (1988). In order to examine the internal organs, the gill pouch unit and EBD, an incision was made along the ventral surface from the oral cavity to the liver, posterior to the PCD, exposing the club-like dental muscle, gill pouches, and the efferent branchial ducts (EBDs).

Species and number of each examined are: 50 specimens each of *Myxine affinis*, *M. australis*, *M. hubbsi*, *M. circifrons*, and *M. limosa*; 50 specimens each of *Eptatretus stoutii*, *E. deani*, *E. fritzi*, and *E. sinus*; 16 of *E. mcconnaugheyi*; 10 each *E. bischoffii* and *E. polytrema*; 7 of *E. burgeri*; 3 of *E. cirrhatus*; 1 each of *E. strahani*, *E. okinoseanus*, and *E.* sp.; 1 each of two new species of *Paramyxine*; 20 of *Paramyxine cheni*; 2 of *P. sheni*; 1 each of *P. atami* and *P. springeri*; and 1 each of two species of the genus *Paramyxine* (putative).

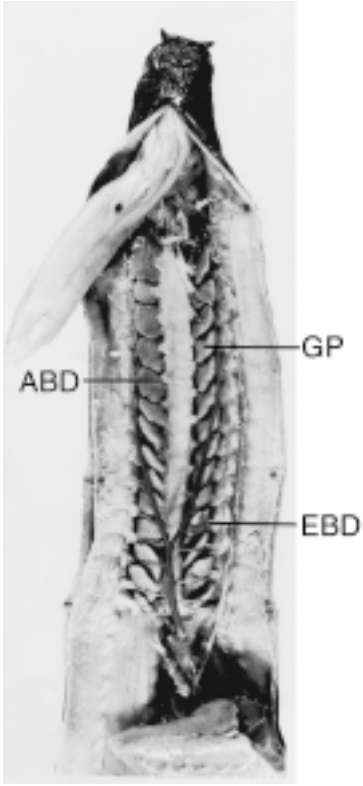

Fig. 2. Branchial region of a 14-gilled hagfish, *Eptatretus polytrema* Girard, 1855 (SIO66-676, 422 mm TL) showing the anterior few GP flattened and slightly displaced by pressure of the overlying dental muscle (pinned aside). Note the very short, and all of about equal length, efferent branchial ducts (EBD)—a diagnostic character of the subfamily Eptatretinae.

RESULTS

No significant variation from the pattern of GA shown in figure 4 was found in 249 specimens of the genus *Eptatretus* Cloquet (1819; Fig. 4A) despite the great range in numbers of gill pouches and apertures (5-14) within this genus. Similarly, no variation was observed among 250 specimens of the genus *Myxine* L. (1758; Fig. 4D).

The less speciose genera of subfamily Myxininae, *Notomyxine* Nani and Gneri (1951), *Neomyxine* Richardson (1953), and *Nemamyxine* Richardson (1958), with only one or two species and specimens each, display the same positions of GP relative to the single GA- PCD. The lack of morphological variation in the positions of the first GP and GA in the species of the four subfamilies, regardless of great differences in numbers of GP emphasizes the consistent differences and appears to warrant subfamilial status.

The genus *Paramyxine* (as previously understood), though notably less speciose than genera *Eptatretus* and *Myxine*, included two distinct groups of specimens. In one group, the GA are arranged in a linear pattern (Fig. 5), as described by Dean (1904, pl. 1, figs. 3,4), or nearly linear pattern (as determined by subsequent investigators), with one or two GA slightly above or below a straight line through the series. Also, the first GA lies opposite the penultimate GP or the space between it and the ultimate GP (Fig. 4B). I designate this group as subfamily Paramyxininae.

In the second group, the GA arrangement is decidedly non-linear and forms patterns of nearly square, rectangular, or rhomboidal shapes (Fig. 6). Also, the first EBD is very much longer than the last (Fig. 7a,b), and the first GA is about on or slightly before a vertical from the posterior margin of the last GP, a position more posterior than that found in the Paramyxininae (Fig. 4B,C). I designate this group as subfamily Quadratinae with the genus *Quadratus* (from the Latin meaning square). The type specimen is *Quadratus taiwanae* (Shen and Tao, 1975), a female, 288 mm TL (SIO-215), from Taiwan Strait.

In summary, the new subfamilies Paramyxininae and Quadratinae have each 4 to 7 GP discharging through its own EBD and GA as in the Eptatretinae, but differ in having the first EBD much longer than the last, the first GA about opposite the penultimate GP, and all GA usually smaller and more closely spaced than those in the Eptatretinae. Also, all Eptatretinae have slime pores just below and behind each GA; slime pores are rarely found in the branchial region of the Paramyxinae and never in the Quadratinae. The two subfamilies differ from each other mainly in the arrangement of GA in a pattern which is a straight or nearly straight line in Paramyxininae and which forms a closely grouped, rec-

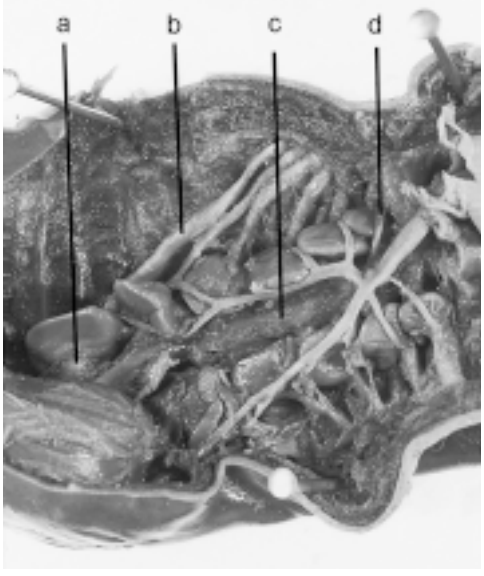

Fig. 3. EBDs on the left side in *Paramyxine atami*. Note the much longer first EBD as compared with that of *E. polytrema* (Fig. 2); ABD (a), first EBD (b), last EBD (c), and pharynx to PCD (d).

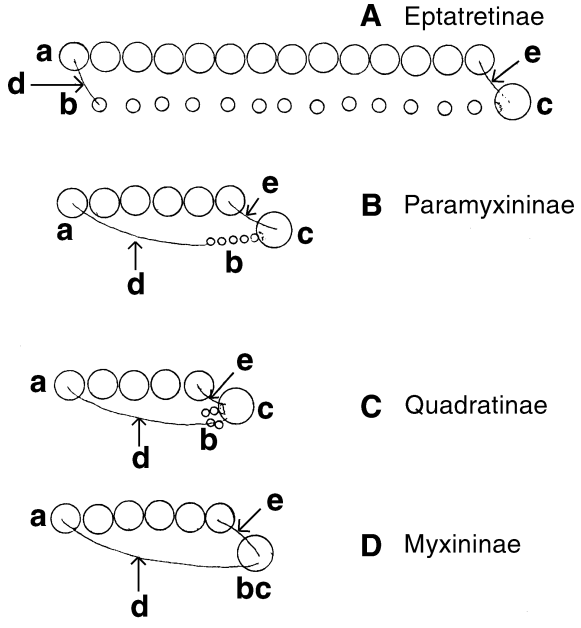

Fig. 4. Stylized sketches (left sides) of four subfamilies of Myxinidae showing relationships of first GP (a) and GA (b), PCD (c), and first (d) and last EBD (e).

tangular, or rhomboidal pattern in the Quadratinae (Fig. 6).

Key to identification of subfamilies of family Myxinidae

1a. All gill pouches discharge water via a single pair of gill apertures (Fig. 1); anteriormost efferent branchial duct much longer than posteriormost; all gill apertures posterior to a vertical from last gill pouch ..... Subfamily Myxininae (Fig. 4D)

1b. Each of 4 to 14 gill pouches discharges water via its own efferent branchial duct and gill aperture 2

2a. First gill aperture opposite the second gill pouch; last gill aperture slightly posterior to a vertical from the last gill pouch; all efferent branchial ducts about equal in length; ratio of length of gill pouch unit to that of gill aperture unit about 1 to 1 ..... Subfamily Eptatretinae (Fig. 4A)

2b. First efferent branchial duct much longer than the last; four to six (rarely seven) gill apertures, the series linear or non-linear 3

3a. Gill apertures linear, or nearly linear; the first gill aperture lies opposite either the penultimate or ultimate gill pouch, or the space between; ratio of length of gill pouch unit to that of gill aperture unit about 3.5 (2.4-4.0) to 1 ..... Subfamily Paramyxininae (Fig. 4B)

3b. Gill apertures definitely non-linear, closely clustered in patterns resembling square, rectangular, or rhomboidal shapes; first gill aperture lies slightly before, opposite, or slightly behind a vertical from posterior margin of last gill pouch; ratio of length of gill pouch to that of gill aperture unit 5.5 (3.8-6.5) to 1 ..... Subfamily Quadratinae (Fig. 4C)

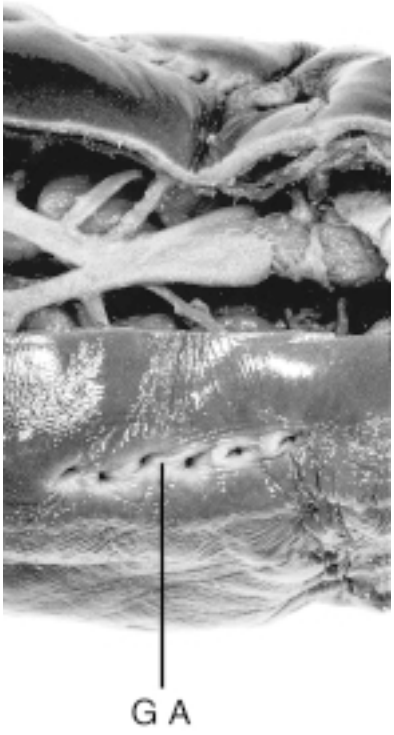

Fig. 5. Linear pattern of GA (left side) of *Paramyxine atami* (TUM 9696), subfamily Paramyxininae.

DISCUSSION

The hagfish literature contains no studies similar to this; prior studies have been based on other characters. On such criteria, Nelson (1976) recognized two subfamilies within the Myxinidae: the Myxininae and Eptatretinae. In the subfamily Myxininae he placed genera *Myxine*, *Notomyxine*, *Neomyxine*, and *Nemamyxine*. He placed genera *Eptatretus* and *Paramyxine* in the Eptatretinae on the basis that, in each, the GP opens separately to the exterior via its own efferent branchial duct, but he made no comparison of relative positions of the first and last EBD. Also, he did not distinguish between the linear and non-linear groups of the genus *Paramyxine* (as formerly understood), and he did not compare relative positions of the first and last GA and GP (subfamilies Paramyxininae and Quadratinae herein).

Strahan (1962) questioned the distinction between the genera *Eptatretus* and *Paramyxine* on the basis of lengths of the first and last EBD. He repeated Dean's statement that in *E. cirrhatus* (Bloch and Schneider, 1801) the ducts of the most anterior gills are slightly longer than the most posterior one, and that in *E. burgeri* (Girard, 1855) they are "somewhat longer". Strahan reported that dissection of several specimens of *E. burgeri* indicated that this was not a reliable character since there may be considerable differences between the lengths of the most anterior and the most posterior ducts.

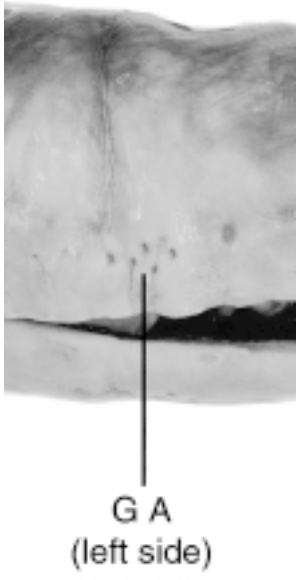

Fig. 6. Pattern of GA (left side) of *Quadratus yangi*, showing highly angular, nearly square layout.

In this study, examination of seven specimens of *E. burgeri* and three of *E. cirrhatus* revealed that variation in lengths of EBD in *E. cirrhatus* is very slight. However, considerable variation was found in lengths of the first and last EBD of *E. burgeri*, with the first usually the longest (possibly due to pressure from the overlying club-like dental muscle), and the remaining EBD slightly decreasing in length posteriorly. Regardless of the length of the first EBD, in all cases the first GA was opposite the second GP, or the space between it and the first—a pattern which is characteristic of the Eptatretinae (Fig. 4A), unlike that of the Paramyxininae (Fig. 4B), and very unlike that of the Quadratinae (Fig. 4C).

Strahan (1975), when describing *Eptatretus longipinnis*, asserted that the difference between the lengths of the first and last EBD in *Paramyxine* was not a valid distinguishing character. He reported that in *E. longipinnis* the anteriormost EBD was about twice the length of the others and stated (in seeming negation) that this was due to a dorsad displacement of the first few gills by the overlying muscle, rather than a caudad displacement of its EBD. He concluded, "On the above consideration I am of the opinion that *Paramyxine* must be regarded as a junior synonym of *Eptatretus*."

No specimen of *E. longipinnis* was available to this study; however, examination of 50 specimens each of *Eptatretus stoutii* (Lockington, 1878) and *E. deani* (Evermann and Goldsborough, 1907), and 8 specimens of 5 species of *Paramyxine* with linear GA patterns, showed that in *Eptatretus* the first GA is always opposite the second GP, or the interspace between the first and second GP, and that in *Paramyxine* (as herein restricted) the first GA is much more posterior and always opposite the penultimate GP or the interspace between it and the ultimate GP (Fig. 4B).

It may be expected that the overlying club-like muscle would exert a deforming and displacing force on any GP beneath it, and that the EBD would change length accordingly. Such displacement is common in species in which this muscle overlies gill pouches and it does not merit species distinction.

Fernholm and Hubbs (1981), dealing mostly with the length of the GA unit and spacing of the individual GA of *Paramyxine springeri* Bigelow and Schroeder (1952), did not mention lengths of the first and last EBD or the relationship of the first GA to the first GP. They placed this species in the genus *Eptatretus*, arguing that the original description of close spacing of GA was not sufficient to merit inclusion in *Paramyxine*, wherein the GA unit is usually notably shorter because of closer spacing of individual GA than in species of *Eptatretus* with similar numbers of GA. However, based on a ripe female (542 mm TL), the present study clearly indicates that the species *springeri* is referable to the genus *Paramyxine* (as originally described) because the first GA is opposite the interspace between the last and next to last GP (Fig. 8), and also because the first EBD is much longer than the last, a major char-

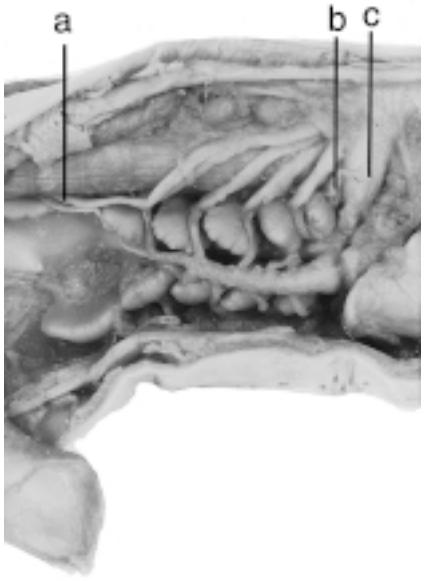

Fig. 7. Efferent branchial ducts on left side of *Quadratus yangi* (Teng, 1958); first EBD (a), last EBD (b), pharynx to PCD (c).

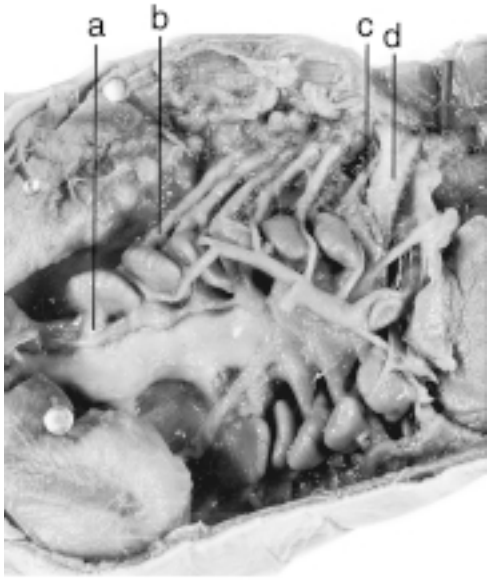

Fig. 8. EBD, left side, of *Paramyxine springeri*; first ABD (a); first EBD (b), last EBD (c); pharynx to PCD (d). Note similarity of the first to last EBD lengths to those of *P. atami* (Fig. 4).

acter of the genus *Paramyxine*.

In a comparison of *P. atami* with *P. springeri*, Strahan and Honma (1961) supported the validity of *P. springeri*. They reported that there are no branchial slime pores in *P. atami*, but from 3 to 6 pairs in *P. springeri* (3 specimens: 338, 555, and 590 mm TL). Branchial slime pores are uncommon in *Paramyxine*; none have been found in *Quadratus*. However, they occur in all species of *Eptatretus*, ordinarily just posterior to and slightly below each GA.

In addition, as shown in figure 4A,B, the position of the first GA relative to that of the first GP obviates any attempt at synonomy of *Paramyxine* with *Eptatretus*. Also any crowding together of the GA in *Eptatretus* must be regarded as chance as it occurs so infrequently as to be exceptional. However, noticeably close spacing of GA is normal in *Paramyxine,* and in *Quadratus* especially (Fig. 6), due to the close grouping of the GP.

Fortunately (perhaps fortuitously) only a slight impact on generic and species arrangements resulted from this study. The greatest changes involve the division of *Paramyxine* to add the genus *Quadratus* (see above), and the return of the species *springeri* to the genus *Paramyxine* as originally described, because the length of first EBD is about three times longer than the last, a diagnostic character of the genus, and the first GA is opposite to the space between the penultimate and ultimate gill pouches.

Acknowledgments: I thank Joseph S. Nelson and H.J. Walker for reviewing the manuscript. I especially thank Charmion B. McMillan for both review and final typing of the manuscript. Final copy and disc were prepared by Rose Yamasaki.

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盲鰻（圓口類：盲鰻科）兩新亞科及一新屬之描述

Robert L. Wisner[1]

本文主要決定副盲鰻亞科 (Paramyxininae) 與方盲鰻亞科 (Quadratinae) 兩個盲鰻新亞科及描述一個新屬，方盲鰻屬 (*Quadratus*) 。並重新描述盲鰻亞科與黏盲鰻亞科。這四個亞科是以鰓孔數目、第一對鰓孔相對於鰓囊的位置、第一對出鰓導管相對於最後一對的長度，以及鰓孔排列形式是直線型或非直線型來加以區別。另外也討論 *Paramyxine springeri* 的分類地位。

關鍵詞：盲鰻科，盲鰻，亞科。

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