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Morphological Studies of Gill and Mitochondria-rich Cells in the Stenohaline Cyprinid Teleosts, *Cyprinus carpio* and *Carassius auratus*, Adapted to Various Hypotonic Environments

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Tsung-Han Lee, Pung-Pung Hwang and Shin-Huey Feng (1996) Morphological studies of gill and mitochondria-rich cells in the stenohaline cyprinid teleosts, *Cyprinus carpio* and *Carassius auratus*, adapted to various hypotonic environments. *Zoological Studies* **35**(4): 272-278. The structure of the gills and the epithelial mitochondria-rich (MR) cells of the carp, *Cyprinus carpio*, and goldfish, *Carassius auratus*, adapted to various hypotonic media was studied by scanning electron microscopy. The gills consist of arches, rakers, filaments, lamellae, and the septum. The epithelium of the filament could be identified as having an afferent region, interlamellar region, and efferent region. According to the morphology of the apical surfaces, branchial MR cells which are responsible for ionoregulation were found to exhibit different types. With apical membranes larger than 2 μm in maximum dimensions, type A MR cells displayed broad and shallow apical surfaces. Type B MR cells measuring 1 to 2 μm were small and had deep openings. Distribution and densities of MR cells differed in the cyprinid teleosts acclimated to various hypotonic media. In 5‰ salt water, type A MR cells were found to decrease significantly in size and number. In deionized water, proliferation of MR cells was found in lamellae. The results revealed different morphologies of MR cells in stenohaline freshwater teleosts which suggests a possible correlation between morphology and function of MR cells.

Key words: Carp, Goldfish, Gill, Mitochondria-rich cell, Hypotonic environments.

Euryhaline teleosts are able to adapt to both seawater and fresh water while stenohaline teleosts live exclusively in seawater or fresh water. Both euryhaline and stenohaline teleostean fish maintain a constant internal osmotic pressure by excretion or absorption of external ions through the gill surfaces against the concentration gradient between the body fluid and the environment (Evans 1993). The epithelium of the gill is composed of 4 kinds of epithelial cells: pavement cells, mucous cells, mitochondria-rich (MR) cells (originally called "chloride cells"), and undifferentiated cells (Laurent 1984). Foskett and Scheffey (1982) demonstrated that MR cells are sites of active chloride secretion and exhibit the highest ionic permeability in the branchial epithelium of seawater teleosts. The correlation between active ionic absorption and morphology, and the number of MR cells was also found in some freshwater teleosts (see review by Perry and Laurent 1993). Thus, in the gill epithelium of teleosts, MR cells are likely sites of ion transport.

The ultrastructures of MR cells in euryhaline teleosts adapted to fresh water and seawater differ in their apical surfaces (Hossler et al. 1985, Pisam et al. 1987, Franklin 1990, King and Hossler 1991, Brown 1992, Kültz et al. 1995), tubular systems (Sardet et al. 1979, Wendelaar Bonga and van der

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Meij 1989, Cioni et al. 1991), intercellular junctions (Hwang and Hirano 1985, Hwang 1987 1988a, b 1990, Cioni et al. 1991), and other organelles (Wendelaar Bonga and van der Meij 1989, Cioni et al. 1991). These ultrastructurally different MR cells, namely, freshwater- and seawater-type MR cells, have been suggested to perform ion absorption and secretion in fresh water and seawater, respectively (Sardet et al. 1979, Foskett et al. 1981, Hwang and Hirano 1985, Karnaky 1986, Hwang 1987 1988a, b 1990, Pisam and Rambourg 1991). Moreover, in hypotonic environments, gills of teleosts are responsible for active absoption of ambient ions, for acid-base balance and for gas exchange (see review by Perry and Laurent 1993). Tiny changes in the ionic composition of hypotonic media can induce dramatic modifications in the functions of the gills and alter the morphology of MR cell apical surfaces (Laurent et al. 1985, Perry and Laurent 1989, Perry et al. 1992a, b). In our previous papers, the euryhaline tilapia, *Oreochromis mossambicus*, was found to have branchial MR cells with distinctive ultrastructures of the apical surfaces (Lee et al. 1995). Within 24 h, the abundance of different types of MR cells changed in response to external hypotonic media containing various concentrations of diverse ions (Lee et al. 1996b). Morphological alterations of MR cells were induced by changing the concentrations of specific ions, i.e., Na^+, Cl^-, or Ca^{2+}. Correlations were also found between Ca^{2+} uptake and MR cell morphology (Lee et al. unpublished data). Based on the results mentioned above, we propose that various types of MR cells play major roles in transport of different ions. Hence we may expect that the abundance and morphologies (or types) of MR cells should change with external environments to regulate diverse ions.

Freshwater stenohaline-teleost MR cells which were thought to be of no function in early work (Munshi 1964, Jozuka 1967) were found in gills in later studies (Kikuchi 1977, Hwang 1988a, b, Pisam et al. 1990). Different densities and types of MR cells in freshwater stenohaline medaka, *Oryzias latipes*, adapted to various hypotonic media were also reported (Lee et al. 1996a). Most cyprinid fish are stenohaline and inhabit freshwater environments (Nelson 1994). In the present study, the morphology of the gill and mitochondria-rich cells in 2 species of cyprinid fish, the carp, *Cyprinus carpio*, and goldfish, *Carassius auratus*, adapted to various hypotonic media were examined and compared with other teleosts to provide support for the hypothesis stated above.

MATERIALS AND METHODS

Both male and female carp, *Cyprinus carpio*, and goldfish, *Carassius auratus*, were obtained from laboratory stock. The wet weights of the carp and goldfish were 3.73 ± 1.60 and 12.41 ± 2.43 g, respectively. The fish, in groups of 5 individuals each, were randomly assigned to 1 of 3 different hypotonic media: local tap water (LFW; $[Ca^{2+}]$ = 0.16 mM, $[Mg^{2+}]$ = 0.12 mM, $[Na^+]$ = 0.26 mM, $[K^+]$ = 0.17 mM); deionized water (DW; $[Ca^{2+}]$ below detection level, $[Mg^{2+}]$ below detection level, $[Na^+]$ = 0.023 mM, $[K^+]$ = 0.173 mM); or 5‰ salt water (SW; $[Ca^{2+}]$ = 0.30 mM, $[Mg^{2+}]$ = 0.31 mM, $[Na^+]$ = 27.93 mM, $[K^+]$ = 0.34 mM). All fish were kept in aerated environments at 25 °C under a photoperiod of 12L:12D and acclimated for 2 weeks. Dissolved oxygen concentrations in each environment were about 95% of saturation. LFW and SW were continuously circulated through fabric-floss filters and DW was partially replaced at least 3 times per week. The pH levels of the media were maintained between 6.1 and 6.9. The fish were fed a daily diet of commercial pellets.

The morphologies of the gill and mitochondria-rich (MR) cells of fish adapted to different hypotonic media were examined by SEM. Excised gills were fixed at 4 °C in a fixative consisting of 5% glutaraldehyde and 4% paraformaldehyde in 0.2 M phosphate buffer (pH 7.2) for 12 h. These were rinsed for 1 h with 3 changes of 0.1 M phosphate buffer (pH 7.2) at 4 °C, then post-fixed with 1% osmium tetroxide in 0.2 M phosphate buffer (pH 7.2) for 1 h. After fixation, the gills were rinsed in the buffer described above, and dehydrated in ascending concentrations of acetone from 50% to absolute. Samples were then critical point dried using liquid CO_2 in a Hitachi HCP-2 critical point drier, mounted on aluminum stubs with silver paint, and sputter coated for 3 min with a gold-palladium complex in an Eiko 1B-2 vacuum evaporator. The coated specimens were examined with a Hitachi S-2500 scanning electron microscope at an accelerating voltage of 15 kV.

The methods for determination of the density and size of filamental MR cells were similar to those described in Lee et al. (1996b). Areas on the filamental afferent side were chosen at random for cell counting at 1 500× magnification. One area (70 × 40 μm^2) was counted on each of 5 gill filaments from each fish. An average of measurements in these 5 areas was obtained. Five fish of each group (LFW, SW and DW) were examined.

The numbers of MR cells in fish gills among the 3 water conditions were analyzed by one-way ANOVA (Minitab 1993). The number of MR cells appearing in each lamella was counted directly on the screen. The measured size of MR cells was recorded as the greatest linear diameter (the maximum dimension) of the apical surface. At least 10 MR cells were measured for each fish of the various groups.

RESULTS

The gill structure of carp and goldfish is similar to that of other teleosts consisting of arches, rakers, filaments, and lamellae (Fig. 1A, B). However, an obvious "septum" was found just beneath the arch, which expands to join the neighboring filaments (Fig. 1A, B). Filamental surfaces could be identified as being an afferent, interlamellar, or efferent region (Fig. 1C) based on the distribution of the arteriole system. Trapezoidal lamellae branched bilaterally from the central axis of the filaments (Fig. 1C). Most MR cells were found in the filamental epithelium, especially in the afferent and interlamellar regions (Fig. 1D). There were none or only a few MR cells seen in the lamellae (Fig. 1D).

The surfaces of the gill filaments were covered with polygonal pavement cells. Apical membranes or crypts representing MR cells were located at the borders of adjacent pavement cells. In these cyprinid fish, 2 types of MR cells could be distinguished in the filaments depending on the size and the ultrastructural features of the apical surfaces (Table 1). Exceeding 2 μm in maximum dimension, the apical surfaces of type A MR cells were broad, shallow or even slightly raised above the adjacent pavement cells (arrowheads in Fig. 2A-D). The apical structures of type B MR cells, which were only 1 to 2 μm in maximum dimension (arrows in Fig. 2A, C), were narrow, deep or even recessed to form "pits". The majority of filamental MR cells were type A cells (Table 1, Fig. 2A-C).

The distribution and abundance of MR cells of carp and goldfish acclimated to various hypotonic media, i.e., LFW, SW, or DW, appeared to differ (Table 1). It is noteworthy that numerous MR cells proliferated on the lamellae of DW-adapted fish (Table 1, Figs. 1D, 2D). Moreover, in DW-adapted goldfish, the average maximum dimensions of filamental type A MR cells were significantly larger than those in LFW- and SW-adapted fish (Table 1, Fig. 2C). In SW-adapted fish, the size and number of filamental type A MR cells decreased significantly compared with those of LFW- and DW-adapted fish (Table 1, Fig. 2A-C). Unlike type A MR cells, the abundance and size of type B cells in gill filaments of both carp and goldfish were not influenced by changing environments (Table 1).

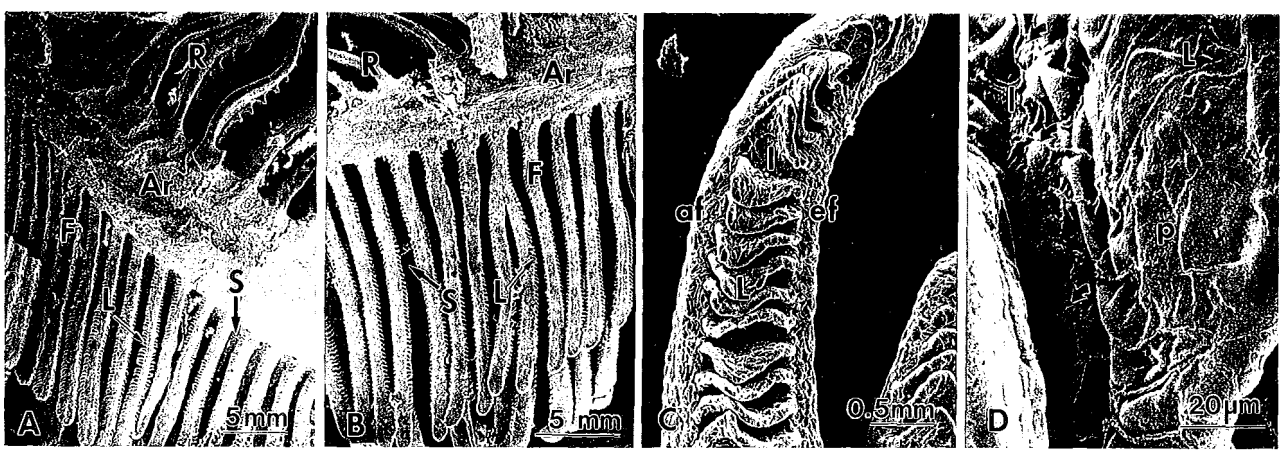

Fig. 1. SEM pictures of the gill structures of carp and goldfish. The gills of goldfish (A) and carp (B) consist of the arch (Ar), rakers (R), filaments (F), lamellae (L), and septum (S). Higher magnification of the gill filament of the goldfish. C: according to the distribution of the arteriole system, the filamental epithelium could be identified as being the afferent region (af) , the efferent region (ef), or the interlamellar region (I). Thin, platelet-like lamellae (L) branched bilaterally from the central axis of the filament. D: MR cells (arrows) were generally located in the filamental epithelium and rarely found in the lamellar (L) epithelium. I, interlamellar region of the filament; p, pavement cells.

DISCUSSION

The structures of carp and goldfish gills are similar (Fig. 1A-D). The "septum" located between the adjacent filaments and developed along the arch is long and obvious in both carp and goldfish. However, this structural feature was not observed in the cichlid fish, *Oreochromis mossambicus*, or the cyprinotid fish, *Oryzias latipes* (Lee et al. 1996a, b). Among the 3 types of teleostean gills mentioned by Hughes (1980), the "cypriniform" type exhibited the most prominent septum. The degree of development of the septum may influence the pattern of water flow, but more detailed studies are necessary to ascertain this.

Earlier authors considered that the stenohaline freshwater teleosts could not adapt to a hypertonic environment, e.g., seawater, due to the lack of MR cells in the gill epithelium (Munshi 1964, Jozuka 1967). However, TEM observations revealed the presence of MR cells in gill epithelia of several species of stenohaline freshwater teleosts including carp and goldfish (Kikuchi 1977, Hwang 1988a, b, Pisam et al. 1990). Moreover, using an oxalate-

Table 1. Densities, relative percentages, and sizes of MR cells (MRC) in filamental and lamellar epithelium of the carp or goldfish adapted to various hypotonic media

Media	Densities of MRC* in filaments		Densities of lamellar MRC	Size of Type A MRC (μm)
	Type A (%)	Type B (%)		
Carp				
LFW	10.4 ± 1.6 (91.2)[a]	1.0 ± 0.1 (8.8)[a]	≤ 1	5.9 ± 0.3[a]
SW	4.6 ± 0.5 (73.0)[b]	1.6 ± 0.4 (27.0)[a]	≤ 1	3.4 ± 0.3[b]
DW	8.2 ± 0.8 (89.5)[a]	1.0 ± 0.2 (10.5)[a]	≥ 5	4.9 ± 0.3[a]
Goldfish				
LFW	9.2 ± 1.0 (84.0)[a]	1.7 ± 0.4 (16.0)[a]	≤ 1	4.2 ± 0.2[a]
SW	4.4 ± 0.4 (78.6)[b]	1.2 ± 0.4 (21.4)[a]	≤ 1	2.9 ± 0.1[b]
DW	10.3 ± 1.8 (88.0)[a]	1.4 ± 0.2 (12.0)[a]	≥ 5	5.1 ± 0.3[c]

*Densities expressed as the number of MRC per 70 × 40 μm^2 in the filamental epithelium. Values shown are mean ± SE.

Different superscrpit letters within a given species indicate significant differences of MRC number or size between various media at the $p \leq 0.05$ level. LFW, local tap water; SW, 5‰ salt water; DW, deionized water.

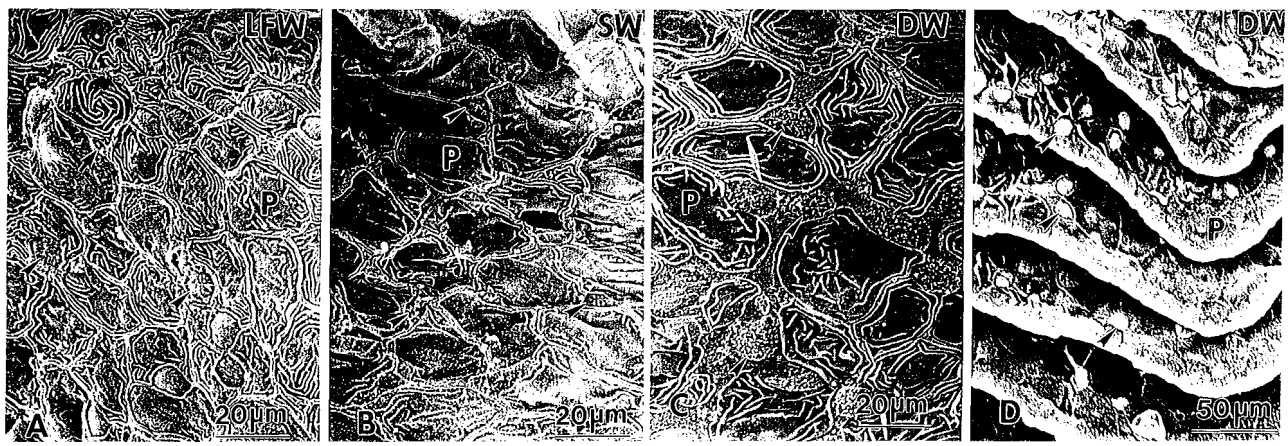

Fig. 2. The epithelium of the lamellae and the afferent region of the filaments of the goldfish adapted to local tap water (LFW; A), 5 ‰ salt water (SW; B), and deionized water (DW; C and D). Type A MR cells (arrowheads) decreased in both apical surface and number in SW-adapted fish. Type B MR cells (arrows) were scarce. Note the MR cells (arrowheads) proliferated in lamellae of the goldfish adapted to DW. P, pavement cells.

based method, Ishihara and Mugiya (1987) provided ultrastructural evidence of calcium uptake by MR cells in the gills of goldfish. Hence it is clear that MR cells are found in gill epithelium of stenohaline freshwater fish and could play a role in ambient ion absorption.

In contrast to hypertonic seawater, hypotonic media are characterized by an extremely variable ionic composition. Effects of these diverse conditions on MR cell morphology in both euryhaline and stenohaline fish had been noted. In response to ion-poor water, proliferation of MR cells and enlargement of MR cell apical surfaces were reported (Laurent et al. 1985, Avella et al. 1987, Pisam et al. 1995). Moreover, both the number and morphology of MR cells changed with varying levels of external Ca^{2+}, Na^{+}, and Cl^{-} (Laurent et al. 1985, Avella et al. 1987). Morphological alterations of MR cells were also found when acid-base disturbances were induced in freshwater teleosts (Goss et al. 1992, Perry and Goss 1994). Taken together with other physiological evidence, these phenotypic changes were suggested to be crucial in the mechanism of ionic (Perry et al. 1992a, b) or acid-base (Perry and Laurent 1993) regulation in fish gills. In tadpoles of the euryhaline frog, *Rana cancrivora*, 4 types of MR cells were found with each suggested to have its own physiological function in adaptation (Uchiyama and Yoshizawa 1992). Hence, subpopulations of MR cells with their own morphology and function may exist in the branchial epithelium of the teleosts to deal with diverse ionic changes in external environments. The present study has revealed that, in the carp and goldfish, there are 2 types (A and B) of MR cells, and the number and size of type A MR cells changed with hypotonic environments (Table 1). The results, similar to those observed in stenohaline medaka (Lee et al. 1996a) and euryhaline tilapia (Lee et al. 1996b), are consistent with the hypothesis outlined above. It is possible that branchial MR cells of the cyprinid fish, like those of the freshwater catfish, *Ictalurus nebulosus*, modify their morphology when involved in regulation of ion transport in various environments (Perry et al. 1992a, b).

It is noteworthy that lamellar MR cells as well as filamental MR cells appeared in large numbers in DW-adapted carp and goldfish (Table 1, Fig. 2D). Appearence of MR cells in lamellae also occurs in DW-adapted eel, *Anguilla anguilla*, rainbow trout, *Salmo gairdneri* (Laurent and Dunel 1980); and medaka, *O. latipes* (Lee et al. 1996a). Most MR cells found in lamellae of carp and goldfish protruded outwards and appeared rounded (Fig. 2D). Avella et al. (1987) reported that changes in the number of the "round" MR cells located in lamellae of the rainbow trout were related to modifications in the maximal transport rate of sodium. Obviously the MR cells appearing in lamellae of DW-adapted cyprinid teleosts are a response to some specific ion deficiency. Proliferation of lamellar MR cells makes it unnecessary to have more MR cells in filaments of carp and goldfish adapted to DW than to LFW (Table 1). It remains to be determined whether changes in the composition of ions can induce the proliferation of lamellar MR cells.

In summary, changes in the distribution and density of different types of MR cells in carp and goldfish acclimated to various hypotonic media strongly suggest that these stenohaline freshwater teleosts, like the other euryhaline species (Perry and Laurent 1993, Lee et al. 1996b), adaptively respond to changing levels of environmental ions. More studies are needed to precisely determine the exact environmental factors, such as particular ions, which induce the morphological changes in branchial MR cells when the fish adapt to various media.

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在不同低張環境中，鯉魚 (*Cyprinus carpio*) 和金魚 (*Carassius auratus*) 鰓表皮上 MR 細胞之形態變化

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本實驗以掃描式電子顯微鏡觀察鯉科魚類—金魚和鯉魚，鰓表皮上 MR 細胞 (mitochondria-rich cells) 在不同低張環境下的形態變化。鯉科魚類的鰓絲表皮可分爲出鰓動脈區、鰓薄板間區和入鰓動脈區；MR 細胞大多分佈於入鰓動脈區和鰓薄板間區。在鰓表皮上可觀察到兩種形態的 MR 細胞。A 型 MR 細胞口徑大於 2μm，開口大而淺；B 型 MR 細胞口徑約 1−2 μm，開口小而深。在不同低張環境中，A 型 MR 細胞的數量與口徑會有變化：在 5‰ 海水中，其數量與口徑都明顯地小於在自來水與去離子水中的細胞；而在去離子水中鰓薄板上的 MR 細胞會大量地增生。窄鹽性的鯉科魚類非但有 MR 細胞的存在，且其形態會隨著低張環境的離子組成不同而產生變化。這便隱喻著不同形態的 MR 細胞具有不同的功能，而在淡水魚離子調節的生理功能上扮演著舉足輕重的角色。

關鍵詞：鯉魚，金魚，鰓，MR 細胞，低張環境。

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