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[REVIEW]

From Aquatic to Terrestrial Life: Evolution of the Mechanisms for Water Acquisition

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It is generally accepted that ancient fishes first experienced freshwater (FW), and then variably by lineage moved onto the land or re-entered the seas during evolution. As both land and sea are desiccating environments, animals must change their strategies for body fluid regulation from protecting against overhydration in FW to coping with dehydration in seawater (SW) or on land. The evolution of the mechanisms for acquisition of water surely must have accompanied these dramatic environmental changes. The major route for water acquisition is by oral drinking in terrestrial tetrapods (represented here by mammals) and in SW fishes (represented by teleosts as they are dehydrated in SW), but the regulation is contrasting between the two groups; mechanisms inducing thirst have developed in mammals, whereas inhibitory mechanisms are dominant in marine teleosts as observed in FW teleosts. Thus, the apparent difference was found not between hydrating and dehydrating habitat, but rather between terrestrial and aquatic habitats. This contrast is also reflected in regulatory hormones; dipsogenic hormones such as angiotensin II play pivotal roles in water homeostasis in mammals, whereas antidipsogenic hormones such as atrial natriuretic peptide are essential in teleosts. Imbibed water becomes body fluid only after absorption by the intestine, and there is a distinct difference in the mechanisms for water absorption between mammals and teleosts. Like regulation of drinking, we found that the inhibitory mechanisms are dominant for intestinal water absorption in teleosts. In the initial part of this short review, interesting differences in the body fluid regulation between mammals and teleosts are introduced, particularly with regard to water acquisition (drinking and intestinal absorption). Then an attempt was made to discuss the evolution of the mechanisms from the two perspectives; transitions from aquatic to terrestrial habitats and from hydrating (FW) to dehydrating (land and SW) habitats.

Key words: body fluid regulation, osmoregulation, drinking, intestinal absorption, ecological evolution

INTRODUCTION

Vertebrates appear to have evolved from chordates in the near-shore seawater (SW) or brackish water, where rivers flow into the ocean (Carroll, 1988). Thus, the earliest vertebrates likely had an excellent ability to swim against water currents (Romer, 1968). It is thought that primitive armored fishes once entered inland fresh waters (FWs) in the early Devonian period of the Paleozoic era and flourished there; from that environment, they next moved onto land or re-entered the sea (Colbert et al., 2001). The extant hagfishes are an exception to this scheme, as they seem not to have experienced FW as judged by their high plasma ion concentrations, which are equivalent to those in SW (and are characteristic of marine chordates), and the small numbers of glomeruli, which would be insufficient to filter the

large amount of water that would enter the body by osmosis from a FW environment (Colbert et al., 2001). Early bony fishes in FW may have suffered from excess water entry into the body. The first tetrapods, amphibians, evolved from lobe-finned fishes (lungfishes) that ventured onto land in the late Devonian period, and in this desiccating habitat, they had to combat dehydration. The situation for water regulation is the same in ray-finned fishes that moved into the seas in the Jurassic period of the Mesozoic era. Since extant ray-finned fishes, such as teleosts, have plasma osmolality much lower than SW, they must cope with osmotic loss of water and with ion entry across the gills, in contrast to the overhydration and hyponatremia that were experienced in FW during earlier evolutionary times. Therefore, teleosts regulate ions and water in opposite directions when they are in FW and SW, and migratory fishes such as salmonids and eels must reverse the regulation when they move between these environments. Accordingly, body fluid regulation mechanisms are highly diverse in teleosts because of their ecological evolution to various osmotic habitats (Takei et al., 2014). It appears that genome redundancy generated by an

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additional round of whole genome duplication in teleosts may have enhanced their adaptability to diverse environments, although the contribution of this duplication to species diversification appears limited (Santini et al., 2009).

Collectively, vertebrates have adapted to three major habitats in terms of body fluid regulation, namely, land, FW and SW. The truly and fully terrestrial vertebrates are the reptiles, birds, and mammals, although some species have secondarily returned to or adopted aquatic lifestyles. Members of another tetrapod group, the semi-aquatic amphibians, are prone to dehydration, and are thus an intriguing group with respect to body fluid regulation (Jørgensen, 1997). Concerning aquatic fishes, teleosts are the only group that is highly flourishing in both FW and SW. They account for more than half of the total vertebrates by species number, and they maintain plasma NaCl concentrations within a narrow range (ca. one third that of SW) regardless of environmental salinity (McCormick et al., 2013). Marine cartilaginous fishes and lobe-finned fishes (coelacanth) adopted unique body fluid regulation by accumulating urea and methylamines in the plasma to avoid osmotic water loss from body surfaces (Hazon et al., 1997). Overall, vertebrates have expanded their habitats during evolution and have developed independent mechanisms for body fluid regulation according to the habitat.

Using data obtained from species in three major habitats of different water and ion availability, this review aimed to build an original story of the evolution of body fluid regulation during the ecological evolution from aquatic to terrestrial life. Emphasis was also laid on the evolution of teleost osmoregulation during the transition from FW to SW, although the changes in regulatory mechanisms are not so profound compared with those seen in the transition to land. By comparisons among the three major habitats, I hope to reveal promising clues for adaptation to various osmotic environments. Unique body fluid regulation in species other than mammals and teleosts have been reviewed elsewhere and some have been discussed in view of their evolution (Hazon et al., 1997; Jørgensen, 1997; Bentley, 2002), and thus excluded from this review.

DIFFERENCES IN BODY FLUID REGULATION

Body fluid content is divided into extracellular and (intra) cellular compartments, with the extracellular fluids further distributed among vascular (plasma and lymph), interstitial, cerebrospinal and other spaces (Fitzsimons, 1979). Extracellular dehydration (hypovolemia) occurs when animals lose extracellular fluids by sweating, bleeding, etc., and cellular dehydration (shrinkage) occurs when extracellular fluid osmolality increases (Fig. 1). When terrestrial animals (represented in this discussion by mammals) are not allowed to drink water, their blood volume decreases and plasma

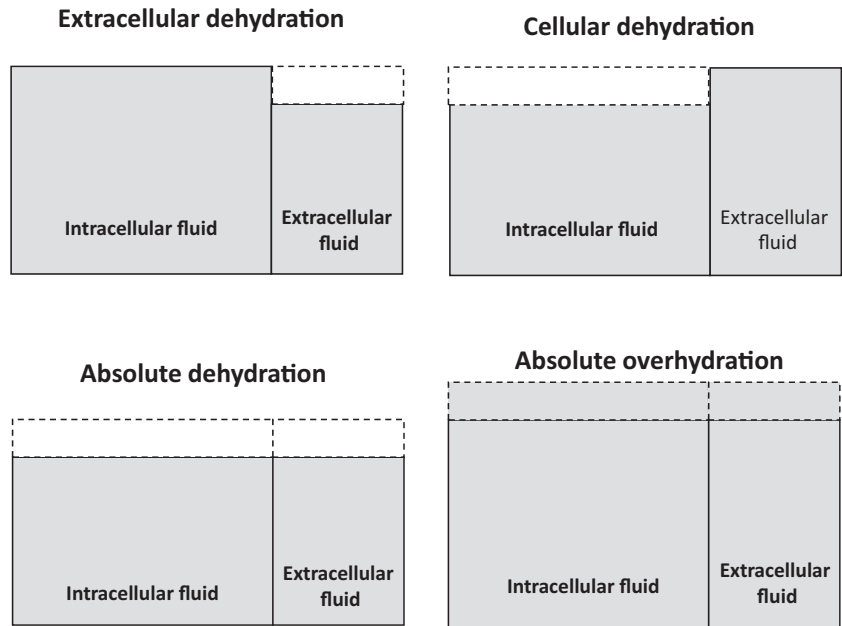


Fig. 1. Body fluid compartments and the change in the each compartment after disturbance of body fluid balance. The intracellular compartment is twice as large as the extracellular compartment. The extracellular fluids consist of blood plasma and intercellular (tissue) fluid, and the volume of the latter is four folds larger than that of the former. For details, see text.

osmolality increases, resulting in dehydration of both extracellular and cellular compartment (absolute dehydration). Similarly, absolute dehydration occurs in marine fishes (teleosts hereafter) when they cannot drink surrounding SW (Takei et al., 1998). By contrast, drinking is not the route for water acquisition in FW teleosts, and they are susceptible to overhydration of both compartments due to the osmotic influx of water and the concentration-driven efflux of ions (Fig. 1).

An obvious difference between aquatic and terrestrial habitats is the ease of access to water. Thus, mammals have developed mechanisms for elicitation of thirst to mobilize them to seek water, and for antidiuresis to decrease urinary water loss. For instance, various hormones such as angiotensin II (Ang II) and vasopressin act in concert to increase the gain and decrease the loss of water. On the other hand, teleosts are exposed to direct influences of environmental water, and water is gained or lost via respiratory epithelia of the gills according to the osmotic gradient between plasma and environmental water. In this way, SW is a dehydrating environment as is the land. As discussed in detail below, however, marine fish have not developed mechanisms to increase directly the gain of water, but have developed active mechanisms to extrude ions. On the other hand, FW teleosts have developed mechanisms to increase both the gain of ions and the loss of water.

Based on water regulation, therefore, the three habitats can be classified into a hydrating FW habitat, and dehydrating terrestrial and marine habitats (Fig. 2). In dealing with these different habitats, mammals and marine teleosts acquire water by oral drinking, while FW teleosts scarcely drink water but obtain water osmotically via the gills. As the

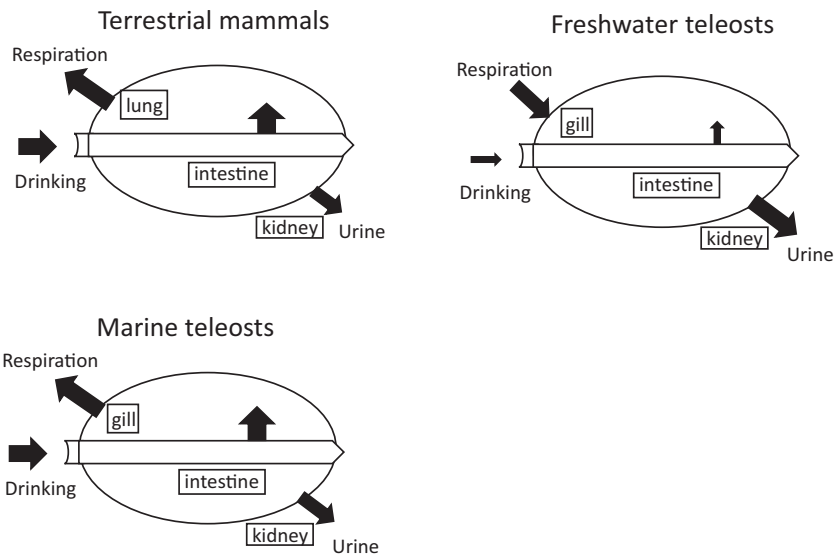


Fig. 2. Differences in the route, direction and relative amount of water budget among mammals, marine teleosts and freshwater teleosts. Major regulatory sites are mouth (drinking), gill, intestine and kidney (urine). The relative amount is shown by the size of arrows. For details, see text.

lumen of digestive tracts is continuous with the external environment, ingested water becomes body fluid only after it is absorbed by the intestine (Fig. 2). Water absorption is maximally enhanced in the intestines of mammals and marine teleosts, but is rather suppressed in the intestine of FW teleosts. Recently, we reported that metabolic water is a major source of acquired water in desert and marine mammals as their oral drinking is negligible (Takei et al., 2012). However, no study has been conducted on the contribution of metabolic water to water homeostasis in marine teleosts.

Terrestrial and marine environments pose similar challenges to water budget, but present quite different demands in terms of ion (Na^+ and Cl^-) regulation. Terrestrial mammals, particularly granivores and herbivores, can scarcely obtain Na^+ and Cl^- from food and thus retain them in the body; however, marine teleosts have devised a machinery (the gill ionocytes) to excrete excess NaCl that enters the body (Fig. 2). Ionocytes can excrete NaCl against a concentration gradient using energy-consuming, ATP-driven transport processes (Marshall and Grosell, 2005). Concerning divalent ions (Mg^{2+} , Ca^{2+} and SO_4^{2-}), mammals retain them at the kidney, but marine teleosts excrete them actively. Accordingly, mammals have several NaCl -retaining hormones such as Ang II and aldosterone, but ion-extruding hormones such as atrial natriuretic peptide and cortisol are more important in marine teleosts (Takei et al., 2007). FW teleosts excrete water as dilute urine by the kidney and take up Na^+ and Cl^- via ionocytes in the gills (Fig. 2), and prolactin is the primary established hormone for FW adaptation (Takei and Loretz, 2005). Ion absorption is maximized in the intestine of mammals and FW teleosts as they live in ion-deficient environment. Ions are absorbed actively also in the marine teleost intestine, but to drive the absorption of water. The mechanisms of teleost osmoregulation have been reviewed extensively elsewhere (Marshall and Grosell, 2005; McCormick et al., 2013). As mentioned above, there-

fore, another important difference between mammals and teleosts is that water and ions are regulated in the same direction in mammals but in the opposite direction in teleosts, although the regulation of each parameter is reversed when teleosts are in FW and SW.

DIFFERENCES IN REGULATION OF DRINKING

Reflex swallowing vs. thirst-motivated drinking

One of the major differences in regulation of drinking between terrestrial and aquatic animals appears to be the presence or absence of a 'thirst' sensation (Takei, 2002). Mammals must feel thirsty to be motivated to seek water and to start a series of drinking behaviors that include searching for water, taking it into the mouth, and swallowing. Meanwhile, as water is always present in the mouth of fishes, they can freely drink water by reflex swallowing without the sensation of thirst.

This idea originated from the fact that after removal of forebrain and midbrain, the eel responded to Ang II by drinking (Takei et al., 1979). Later, the site of action of Ang II was suggested to be the area postrema (AP), a circumventricular structure located in the caudal end of hindbrain (Mukuda et al., 2005). The circumventricular organs are highly vascularized tissues lacking a functional blood-brain barrier (BBB). Thus, they serve as a window for the brain to receive chemical information, such as hormones from blood. In fact, electric lesioning of the AP impaired Ang II-induced drinking (Nobata and Takei, 2011). These data strongly suggest that Ang II acts on the AP to induce reflex swallowing, and not thirst-motivated drinking behavior (Fig. 3A). In mammals, Ang II acts on the sensory circumventricular organs in the forebrain, the subfornical organ (SFO) and/or organum vasculosum of the lamina terminalis (OVLT) to induce thirst (McKinley et al., 2003), and the lesioning of these areas abolished drinking behavior. Thus the cerebral mechanisms subserving drinking differ between terrestrial mammals and aquatic teleosts (Fig. 3A). Recently, however, we identified an OVLT-like structure without BBB in the eel forebrain (Mukuda et al., 2013). Thus, it is possible that teleosts also feel thirsty when Ang II acts there (Fig. 3A), but nevertheless they can drink by induced swallowing through the AP if the OVLT-like structure in the forebrain is removed. The cerebral mechanisms for regulation of drinking in fishes have been reviewed extensively (Takei and Balment, 2009; Nobata et al., 2013).

Inhibitory vs. stimulatory mechanisms

The mechanisms that regulate drinking have been an active target of research in mammals. Drinking is principally induced by three stimuli, cellular dehydration (increased plasma osmolality), extracellular dehydration (decreased blood volume), and increased plasma Ang II concentration (Fitzsimons, 1979, 1998; Takei, 2000) (Fig. 3B). Although all three stimuli induce vigorous drinking in mammals, cellular

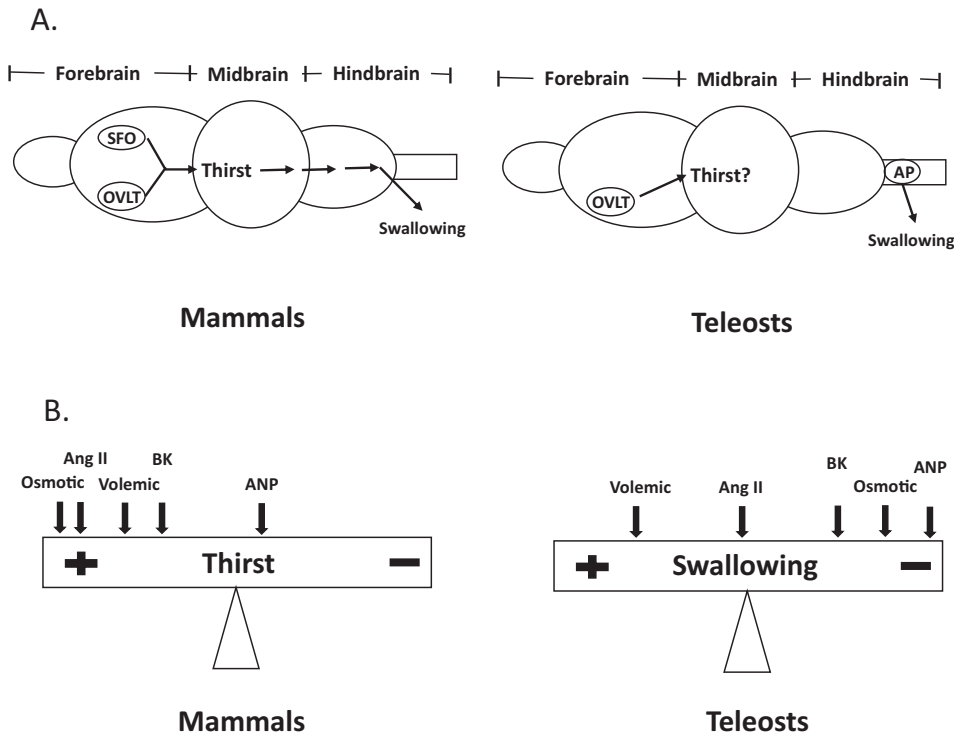


Fig. 3. Differences in regulatory mechanisms of drinking in mammals and teleosts. **(A)** The site of action of circulating hormones that influence drinking such as angiotensin II (Ang II) in the brain and the route that leads to drinking. In mammals, Ang II acts on the subfornical organ (SFO) and/or organum vasculosus of the lamina terminalis (OVLT) in the forebrain to induce thirst, which motivates a series of drinking behavior ended with swallowing. In teleosts, Ang II acts on the area postrema (AP) in the hindbrain to induce reflex swallowing, but the presence of OVLT-like structure is suggested recently (Mukuda et al., 2013). **(B)** Relative potency and efficacy of regulatory stimulus for drinking in mammals (Thirst) and teleosts (Swallowing). Obvious difference is the dominance of stimulatory mechanisms (+) in mammals and inhibitory mechanisms (-) in teleosts. ANP, atrial natriuretic peptide; BK, bradykinin.

dehydration is the most potent stimulus for thirst, as the most copious drinking occurs after osmotic stimulus even though blood volume increases and plasma Ang II decreases simultaneously. In eels, however, osmotic stimulus inhibited drinking profoundly although plasma Ang II unexpectedly increased simultaneously (Takei et al., 1988) (Fig. 3B). Furthermore, Ang II induced only small and transient drinking in eels, which is followed by prolonged inhibition of drinking. Thus, overall, the amount of water intake was decreased for 15 min after Ang II injection. In teleosts, therefore, only extracellular dehydration is a reliable but weak stimulus for drinking (Takei, 2002).

The dominance of stimulatory mechanisms in mammals and inhibitory mechanisms in teleosts is also supported by the relative potency of regulatory hormones (Fig. 3B). In mammals, hormones that stimulate drinking are much more potent and efficacious than in teleosts. For instance, 100-fold higher doses are required for Ang II to elicit drinking in teleosts and the induced water intake is much smaller than that in mammals (Takei, 2002). In contrast, atrial natriuretic peptide (ANP) injected into the circulation of SW eels almost stopped drinking at low physiological doses that do not change arterial pressure, but ANP is only a weak antidipsogenic hormone in mammals even at much higher hypotensive doses (Takei and Hirose, 2002). Furthermore,

many dipsogenic hormones have been identified in mammals, while most hormones that modulate drinking are antidipsogenic in eels (Takei, 2002; Kozaka et al., 2003). For instance, bradykinin is known as a dipsogenic hormone in mammals, but it is a potent antidipsogenic hormone in eels (Takei et al., 2001) (Fig. 3B). Thus, since antidipsogenic mechanisms are dominant in teleosts, dipsogenic mechanisms have developed in mammals, probably during the transition from aquatic to terrestrial life.

DIFFERENCES IN INTESTINAL ABSORPTION

For terrestrial animals, most of water ingested orally is absorbed by the intestine, so the gain of body fluid from intestinal absorption almost equals the oral intake (Kato and Romero, 2011). FW teleosts drink little, and thus the intestine plays a minor role in the gain of water. However, the intestine is a major site for water acquisition from imbibed SW in marine teleosts (Takei and Loretz, 2010). Ingested SW is processed during the passage through the digestive tracts and more than 80% of water is eventually absorbed by the intestine. This is in sharp contrast to mammals, where SW drinking causes severe diarrhea and resultant dehydration. In teleosts, the first step of processing is desalination of ingested SW by the esophagus, which is achieved by various transporters/channels for NaCl uptake (Takei and Loretz, 2010). In addition, osmotic water loss is minor in the esophagus of marine teleosts probably due to the scarcity of water channels (aquaporins, AQP) on either apical or basolateral side of epithelial cells. The luminal fluid is further diluted to isotonicity in the anterior intestine, and thereafter water is absorbed in parallel with Na⁺ and Cl⁻ in the distal regions (Takei and Loretz, 2010). SW contains substantial amounts of divalent ions such as Mg²⁺ and Ca²⁺. These ions are hardly absorbed from the intestinal lumen and thus their presence increases the luminal fluid osmolality after NaCl-coupled water absorption. Additionally, teleost intestine secretes a large amount of HCO₃⁻ into the lumen, which precipitates these ions largely as magnesian calcite (Mg/CaCO₃) (Grossell et al., 2005; Wilson et al., 2009). The precipitation decreases luminal fluid osmolality and facilitates further water absorption. Such processing of SW in the digestive tract is a unique and important underlying process that permits marine teleost intestine to absorb more than 80% of water from ingested SW.

Absorptive mechanisms

Mammalian intestinal epithelia have two predominant types of cells, absorptive villus cells and secretory crypt cells (Giebel, 2005). However, the teleost intestine seems to lack secretory type cells. This idea originated from the observation that the teleost intestine does not have the crypt-like structures that characterize mammalian intestine (Loretz, 1987). In mammals, fluid secretion is thought to purge from the intestinal lumen harmful bacteria that produce toxins such as bacterial heat-stable enterotoxin (STa) that binds to a guanylyl cyclase-coupled receptor C (GC-C, guanylin receptor) with extremely high affinity, and induces acute bowel movement and Cl^- and water secretion into the lumen. However, STa does not bind eel GC-C with high affinity (Yuge et al., 2006), and thus secretory diarrhea may not occur in the eel after the bacterial infection to the intestine. In the intestine of killifish, *Fundulus heteroclitus*, however, immunohistochemical data suggest the possible presence of a small number of secretory-type enterocytes (Marshall et al., 2002).

There are differences in the mechanism of NaCl and water absorption between the intestines of mammals and marine teleosts. In mammals, NaCl in the luminal fluid is absorbed into the enterocytes via concerted action of $\text{Cl}^-/\text{HCO}_3^-$ exchanger (SLC26A6) and Na^+/H^+ exchanger (NHE3 or SLC9A3) on the apical membrane (Kato and Romero, 2011), but it is mostly via $\text{Na}^+/\text{K}^+/\text{2Cl}^-$ co-transporter (NKCC2 or SLC12A1) in the marine teleost intestine (Ando, 1980; Musch et al., 1982; Takei and Loretz, 2011). In parallel with the ion absorption, water moves through a water channel (AQP1) into the cell. As the NKCC2 transports four ions (osmolytes) into the cell at a time, water absorption may be more efficient in marine teleosts than in mammals. Little is known about the relevant transporters for NaCl absorption in the intestine of FW teleosts, but mechanisms similar to those of mammals may be at work.

Hormonal regulation

In mammals, studies on hormonal regulation of water and NaCl absorption are rather scanty as most orally-ingested water is obligatorily absorbed by the intestine in parallel with Na^+ -coupled nutrient transport (Kato and Romero, 2010). On the other hand, several circulating hormones and transmitters/modulators secreted from the innervating neurons regulate water and NaCl absorption by the intestine of marine teleosts. These studies showed that most of these chemical messengers, including acetylcholine, serotonin, histamine, ANP and vasoactive intestinal peptide, are inhibitory, and that no stimulatory regulators have been identified yet (Ando et al., 2003). Acetylcholine and serotonin seem to be released from the nerve terminals or from enterochromaffin cells of the intestine, since electrical field stimulation mimics the inhibitory effects of these neurotransmitters, which is blocked by the specific antagonists (Mori and Ando, 1991). Despite not being stimulatory when given alone, adrenaline, noradrenaline, dopamine, clonidine (α_2 -adrenoceptor agonist), somatostatin, and neuropeptide Y diminishes the inhibitory effect of acetylcholine and serotonin, with somatostatin being the most potent in this regard (Ando et al., 2003). It appears that chemical messengers that act on the Gs-coupled receptors and increase intracellular

cAMP (or cGMP) inhibit water/NaCl absorption, but those that act on the Gi-coupled receptors and decrease intracellular cAMP restore the absorption.

All of these regulators act from the serosal side of intestinal epithelia. Guanylin is the only intestinal hormone that is secreted into the lumen and acts from the mucosal side. Guanylin was first discovered in mammals as an endogenous ligand for STa receptor (Currie et al., 1992). In the eel intestine, guanylin is produced in the goblet (mucus) cells (Yuge et al., 2003), and acts in a luminocrine fashion (Takei and Yuge, 2007). Guanylin is also a potent inhibitory hormone for NaCl/water absorption across the SW eel intestine (Yuge and Takei, 2007).

EVOLUTIONARY PERSPECTIVES

As discussed above, homeostatic body fluid regulation maintains extracellular and cellular volume and osmolality within narrow ranges appropriate for survival. Thus, the gain and loss of both water and ions, particularly monovalent Na^+ and Cl^- , need to be regulated strictly between the body and environment. When looking back on the evolutionary history of vertebrates, the divergence of bony fishes into two lineages, the ray-finned fishes and lobe-finned fishes, seems to have occurred in a FW habitat. Then, a group of lobe-finned fishes ventured to expand their habitat onto the land. As a consequence of this excursion, retention of water in the body should have become of primary importance during this transition, and profound adjustment must have occurred in the body fluid regulation scheme. Meanwhile, some ray-finned fish groups later re-entered the oceans, where teleosts have occupied this ecological niche and have now become the most successful and diversified group of all vertebrates. The clue to their success is rather straightforward; acquisition of the ability to extrude excess Na^+ and Cl^- from the body and maintain these ions in plasma much lower than SW. Therefore, the mechanisms of body fluid regulation in teleosts have undergone adaptive evolution during the transition from FW to SW.

Based on such evolutionary history, it is apparent that vertebrates experienced two major events in terms of body fluid regulation during their evolution, transitions from FW to the land and to the ocean. Therefore, it is important to discuss the evolution of body fluid regulation from the two aspects; aquatic vs. terrestrial habitat, and hydrating (FW) vs. dehydrating (land and SW) habitat.

Aquatic vs. terrestrial habitat

The prototetrapods that moved onto the land were faced with two major challenges: gravity (or the loss of the natural buoyancy provided by the watery habitat) and desiccation. Concerning the gravity issue, they have developed circulatory systems with a powerful heart to pump out the blood throughout the body against gravitational force, resulting in high arterial pressures in mammals and birds. We found that hormones that increase blood pressure and cardiac performance, including Ang II, vasopressin/vasotocin, and endothelin, play critical roles in the circulatory system of these tetrapods (Takei et al., 2007). On the other hand, vasodepressor hormones such as natriuretic peptides, adrenomedullins, and vasoactive intestinal peptides are dominant and play important roles in cardiovascular regula-

tion of fishes. Concerning the desiccation issue, mechanisms that induce thirst and antidiuresis have been strongly developed in mammals to increase the gain and decrease the loss of water as exemplified by potently dipsogenic Ang II and antidiuretic vasopressin. In teleost fishes, however, Ang II is an antidipsogenic hormone at high doses, and vasotocin has no effect on the kidney at low doses and pressure diuresis occurs at high doses (Takei and Loretz, 2005). In contrast to Ang II, ANP is a profound antidipsogenic hormone in teleost fish and its potency and efficacy were 2–3 orders of magnitude higher than those in mammals. This is also true for the effect on the intestine; ANP is a potent inhibitor for water and ion absorption in teleosts but the effect is negligible in mammals. On the renal effect, however, ANP is weakly natriuretic and antidiuretic in SW eels, suggesting that the common action of ANP in mammals and teleosts is to decrease NaCl from the body but not water (Takei and Hirose, 2002).

Incorporating all of the observations and experimental results available to date, the hormonal regulation of fluid balance can be distinguished between terrestrial mammals and aquatic teleosts, with water regulation further being distinguished between FW and SW teleosts. For instance, Ang II did not increase water intake, and ANP decreased water intake and intestinal water absorption in both FW and SW eels, although SW eels must increase these fluxes to cope with dehydration. Possible interpretation of the dominant inhibitory mechanisms in teleosts is as follows. As water is always in the mouth of teleosts, it enters the intestine only by swallowing. Therefore, they are faced with constant threat of excessive drinking in both FW and SW. Overdrinking in SW teleosts results in excessive increases in plasma osmolality as SW contains much higher concentration of NaCl than plasma. This situation is completely different from that in terrestrial animals, which must search for water motivated by thirst before drinking. This is an important difference between aquatic teleosts and terrestrial mammals, but not between teleosts in FW and SW.

Hydrating vs. dehydrating habitat

Both mammals and marine teleosts live in the dehydrating environments, so water acquisition and retention is essential for their survival. By contrast, FW fishes must protect against hypervolemia by reduction in drinking and production of copious dilute urine (Takei, 2000). There is a distinct difference in the need for water between FW teleosts and terrestrial/marine animals. However, the regulatory mechanisms for water acquisition in the latter groups are clearly different between mammals and SW teleosts, as discussed above. More important difference may be in ion regulation; mammals need to ingest NaCl from the environment but marine teleosts must limit and reduce NaCl accumulation to maintain ion balance. Therefore, a possible interpretation for the dominance of inhibitory mechanisms for drinking and intestinal absorption in marine teleosts is to limit excess ion uptake from the environment. As described above, in order to obtain water from SW, more NaCl must be absorbed than water in view of the relative NaCl concentration between teleost plasma and SW. Thus, plasma NaCl concentration certainly increases after drinking SW. This result coincides well with the inhibitory effect of osmotic

stimulus on drinking in teleost fishes (Takei, 2002). It seems therefore that the primary goal of body fluid regulation in teleosts may not be to maintain plasma volume but, instead, to maintain plasma osmolality within a narrow range. This is also true in mammals and other terrestrial species (Takei, 2000).

Finally, in closing, what are the consequences of mammals drinking SW? As AQP_s are abundant in the digestive tract, in most mammals imbibed SW is diluted by osmotic efflux of water into the lumen, which decreased plasma volume. Water is absorbed together with Na⁺ and Cl⁻ after dilution, but because SW contains high concentrations of divalent ions that are scarcely absorbed by the intestine, most of imbibed volume will be eliminated as diarrhea. Moreover, the mammalian kidney is not capable of concentrating urine above SW as is gill ionocytes of teleosts, which further facilitate the loss of water as urine. By contrast, as discussed herein, the intestine of SW teleosts can absorb more than 80% of imbibed SW, and the excess NaCl that enters the body is adequately excreted by gill ionocytes. Despite the presence of machinery for water acquisition in marine teleosts, it is interesting to note that inhibitory mechanisms are dominant at both drinking and intestinal absorption.

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