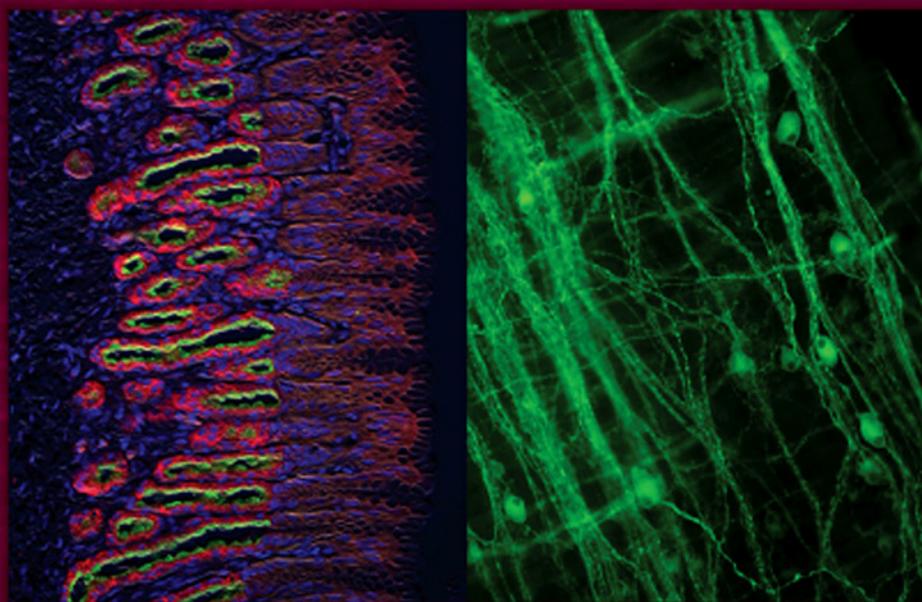


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The Multifunctional Gut of Fish



Martin Grosell, Anthony P. Farrell
and Colin J. Brauner

SERIES EDITORS: Anthony P. Farrell and Colin J. Brauner



THE MULTIFUNCTIONAL
GUT OF FISH

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THE GI TRACT IN AIR BREATHING

JAY A. NELSON

A. MICKEY DEHN

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1. INTRODUCTION

The difficulty in obtaining oxygen from many aquatic environments has led to the frequent evolution of air breathing among fishes. Among several groups of fish, elements of the gastrointestinal (GI) tract have been exploited to extract oxygen from the air and have become air-breathing organs (ABOs). Despite the perceived difficulties in balancing digestive and respiratory function, gut air breathing (GAB) in fishes has evolved multiple times and GAB fishes have become very successful. The modification of esophagus, stomach, or intestine into ABOs always involved increased

vascularization with capillaries embedded in the epithelium close enough to inspired air for significant O₂ diffusion to occur. The gut wall in ABOs has generally undergone substantial reduction, is separated from digestive portions of the GI tract with sphincters and is capable of producing surfactant. GAB fishes tend to be facultative air breathers that use air breathing to supplement aquatic respiration in hypoxic waters, but some hind-gut breathers also appear to be continuous, but not obligate, air breathers. Gut ABOs are generally used for oxygen uptake; CO₂ elimination occurs primarily via the gills and/or skin in tested species. Aerial ventilation in GAB fishes is driven primarily by the partial pressure of oxygen in the water (P_wO_2) and possibly by metabolic demand. Hypoxic water elicits a bradycardia from GAB fishes that is often, but not always, ameliorated following an air breath. Blood from GAB fish generally has a low hemoglobin-oxygen half-saturation pressure (P_{50}) with a very low erythrocytic (nucleotide tri-phosphate (NTP)). Gut air-breathing behavior in nature depends upon ecological as well as physiological factors. Evidence for the role of the gut of GAB fish in nitrogen excretion is limited.

Fish have followed an evolutionary path that requires the additional energy extraction from foodstuff molecules that exploitation of oxygen as a terminal electron acceptor allows. Thermodynamics dictates that the primary goal of fish existence is to obtain sufficient energy from food to offset randomization, grow and reproduce, but a close secondary goal is to position itself in an environment where oxygen can be exploited to transform this energy efficiently. Formation of ATP chemical bond energy from food anaerobically extracts about 8.1% of the energy from food that can be extracted aerobically (Gnaiger 1993). Adopting the conventions of Fry (1971), oxygen can then be considered a limiting factor for fish; i.e. exploitable niche space will be a complex function of oxygen availability, extraction ability and utilization rate. Some fish can survive extended periods in anoxic water (Nilsson 2001), but all fish are obligate aerobes and require at least some minimal amount of oxygen to complete their lifecycle. Because oxygen availability in water is very dependent upon environmental conditions (Diaz and Breitburg 2009), but always far less available than in air, the evolution of air breathing has occurred on the order of 50 times in the vertebrate lineage (Graham 1997).

Gas solubility in water obeys Henry's law:

$$[gas]_{H_2O} = P_{gas} * \alpha_{gas} * V_{H_2O}$$

which states that the concentration of a gas in water will be a simple product of the partial pressure of the gas (P) in air above that water, its unique solubility coefficient (α) and the volume of water (V) being considered. The solubility coefficient for oxygen in water is fairly low and variably dependent

upon water temperature and salinity. Oxygen solubility in pure liquid water is maximal at 0°C and falls to $\sim 1/2$ that value over the 40°C temperature range experienced by fish on earth (Withers 1992). Oxygen solubility in liquid water at a given temperature is also maximal in pure water and is reduced by up to 20% across the 40‰ salinity gradient that fish experience on earth (Withers 1992). Thus the prediction from the solubility coefficient and Henry's law is that warm, salty waters such as tropical oceans would have the least amount of oxygen to support fish life and thus foster the evolution of air breathing. However, biotic and climatic factors generally overwhelm the physical constraints of Henry's law in aquatic ecosystems so that tropical oceans turn out to be relatively well oxygenated compared to other aquatic habitats, most of which occur in fresh water and, thus, most air-breathing fishes are also freshwater fishes (Graham 1997).

Diaz and Breitburg (2009) cover the development of aquatic hypoxia in a previous edition of this series, so this topic will just be briefly summarized here. Aquatic hypoxia/anoxia develops due to various combinations of: (1) aquatic respiratory rates exceeding photosynthetic rates, (2) poor or no mixing at the aerial/aquatic interface, (3) poor light penetration due to shading or turbidity, (4) isolation of water bodies, and (5) various combinations of the above (Junk 1984; Wetzel 2001; Diaz and Breitburg 2009). In temperate to polar regions, the most common scenarios resulting in hypoxia/anoxia involve isolation of the water body from the oxygen-rich atmosphere. Other temperate fish habitats subject to hypoxia include soft sediments that do not mix well with the water column and many swamp and marsh habitats such as sphagnum bogs.

Hypoxic and anoxic waters form in tropical waters through a diversity of processes that generally deplete oxygen faster and are harder to characterize than temperate systems (Junk 1984). In addition to hypolimnetic isolation due to thermal stratification, there are large annual rainfall and water level fluctuations that create flooded forests, seasonal lakes, remnant river channels and bring nutrient pulses to existing water bodies. The combinations of: (1) high temperature; (2) waters that can be nutrient rich; (3) dense terrestrial vegetation that can block sunlight and wind; (4) dense surface vegetation that can also block sunlight and wind but can also contribute photosynthetic oxygen to the water; and (5) a dense biota that can influence the water chemistry as much as physical factors, all create a mosaic of hypoxic and anoxic aquatic habitats across the tropics. It is common for tropical waters of the Amazon flooded forest (*varzea*) to have their top 10 cm be the only predictable aquatic oxygen source for months at a time (Val and Almeida-Val 1995). It is also not uncommon to find waters that cycle between near oxygen saturation conditions during the day and complete anoxia at night (Junk 1984).

2. EVOLUTION OF AIR BREATHING IN FISH

Against this backdrop of worldwide hypoxic habitats a number of fish lineages have taken advantage of the much richer and more predictable source of oxygen in the atmosphere by evolving the ability to breathe air. Extant air-breathing fishes include several marine species, several groups of temperate freshwater air breathers and a large number of small intertidal species that will obtain oxygen from the air when air exposed, but are not particularly specialized for air breathing (Graham 1997; Chapman and McKenzie 2009). However, the majority of specialized air-breathing fishes are found in tropical freshwaters (Graham 1997). Graham (1997) points out that since most of these fishes still breathe water, “air-breathing fishes” is not the most accurate term, but appears to be a term in use by the majority of workers in this field and will be adopted here. There is some speculation that air breathing in fish originated in salt water and that even tetrapod air breathing had a marine origin (Shultze 1999), yet the most parsimonious origin for lungfish and tetrapod air breathing is tropical swamp-like habitats where most specialized air-breathing taxa are found today (Graham and Lee 2004). Graham and Lee (2004) count more than 370 air-breathing fish species distributed among 49 fish families, but these numbers are certain underestimates due to poorly described families like the Loricariidae (Graham 1999). The Neotropical catfish family Loricariidae is the most diverse siluriform family and occupies most hypoxia-prone habitats in the Neotropics. Loricariids comprise 83 genera with over 825 nominal species, 709 of which are considered valid (Armbruster 2006). Although air-breathing is not synapomorphic in this family (Armbruster 1998), most loricariids examined to date will facultatively breath air upon exposure to hypoxia using their gut as an ABO (Gee 1976; Graham 1997), or show morphological evidence of air-breathing capabilities (Armbruster 1998). As the loricariids and other speciose air-breathing families like the Callichthyidae, Trichomycteridae, Gobidae, among others, are examined in more detail, it is likely that the number of extant air-breathing fish species will exceed 1,000. Despite extensive study of a few air-breathing fish species such as the lungfishes (Dipnoi), the morphology and physiology of gas exchange has not been studied in the vast majority of these air-breathing fish.

Of the more than 370 confirmed air-breathing species, members of the families listed in Table 10.1 have been confirmed to use elements of their alimentary tract proper (esophagus, stomach or intestine) as a specialized ABO. Since the Siluriform families listed in Table 10.1 are among the poorest described taxonomically and are already listed at 1,026 species by the All Catfish Species Inventory (2009) with an estimated 305 newly

Table 10.1

Diversity and number of species that potentially use a region of the gastrointestinal tract for air breathing. Species number data for Siluriforms come from the All Catfish Species Inventory (2009) and Froese and Pauly (2010) for the other families. Estimates of the number of undescribed species were not available for all families

GI region used for air breathing	Family	No. of species in that family	Estimated # of undescribed species in that family
Esophagus	Umbridae	5	0
	Blenniidae	420	?
	Synbranchidae	15	?
Stomach	Loricariidae	673	205
	Trichomycteridae	176	55
Intestine	Cobitidae	110	?
	Callichthyidae	177	45

discovered species yet to be described, fishes that use their alimentary tract to breathe air could eventually account for the majority of all air-breathing fish species. Lungs were the presumed original ABO in fishes and date to the earliest gnathostomes of the Devonian period (360–387 MYA; Perry 2007). Once the gas bladder appeared as an organ of buoyancy in fish evolution, it appears to have canalized ABO development and was frequently exploited for a respiratory function (Graham 1997). This was facilitated by a pneumatic duct connecting the gas bladder to the esophagus in the ancestral physostomous condition as well as the requisite musculature and valves for filling the bladder. Since a respiratory gas bladder is the only ABO other than lungs found in extant representatives from this early phase of fish evolution, we can assume that whenever selection for exploiting abundant atmospheric oxygen arose, a gas-filled organ with a direct connection to the atmosphere was a convenient target for selection. Once the physoclistous condition evolved and the pneumatic duct lost, or the swim bladder became encased in bone (as in the loricarioids; Schaefer and Lauder 1986), it appears that the gas bladder was less available as an ABO (a constraint was lifted) and natural selection could act on other body parts. Thus in teleosts, a diversity of ABOs has evolved, including the alimentary tract that is the subject of this chapter (Graham 1997). GAB fishes fall into two general categories: (1) facultative air breathing (FAB), which refers to those animals that only breath air when oxygen in the aquatic medium does not meet biological requirements, and (2) continuous air breathing (CAB), which refers to those animals that do not suffocate when denied access to air but still breathe air continuously when allowed access to the surface, even in

normoxic water (Graham 1997; Chapman and McKenzie 2009). A GAB fish that is an obligate air breather has yet to be described.

2.1. Evolution of the Gut as an ABO

Considering the phylogenetic location of the families in Table 10.1, each evolution of the gut proper (esophagus, stomach or intestine) as an ABO (hereafter gut air-breathing, GAB) appears to be a unique evolutionary event (Fig. 10.1). Armbruster (1998) suggests, based on morphological evidence mapped onto the phylogenies of Schaefer and Lauder (1986) and de Pinna (1993), that just within the loricariids and scoloplacids, there may have been as many as five separate origins of GAB. The respiratory diverticula emanating from the esophagus in another loricariiid (*Loricarichthys*) (Silva et al. 1997) may be yet another unique evolutionary origin of GAB. This proclivity for GAB to evolve suggests some distinct advantages to using the gut for this purpose that overwhelm any perceived disadvantages. One might argue that a more parsimonious interpretation is that a common loricarioid ancestor was a GAB fish and that the frequent reappearance of GAB in the descendent trichomycterids, loricariids (scoloplacids) and callichthyids (Fig. 10.1) are atavisms, since these are

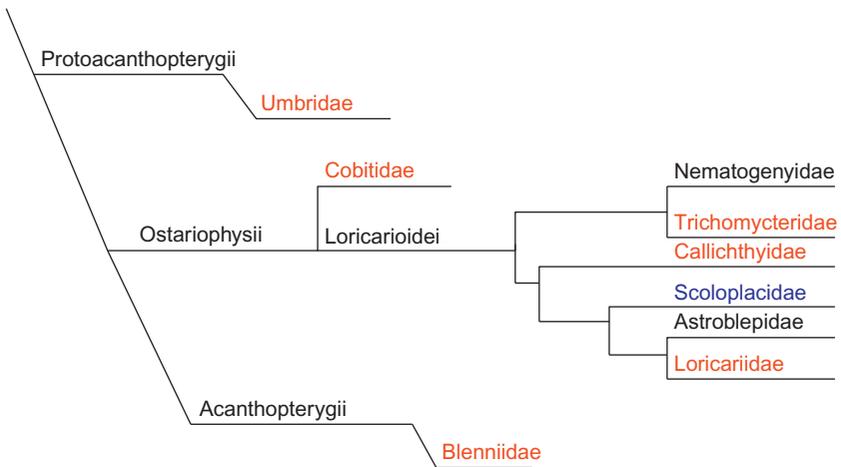


Fig. 10.1. Phylogenetic distribution of known or suspected gut air-breathing (GAB) fish families. Families in red have at least one species with published documentation of gastrointestinal tract oxygen extraction from the air. Families in blue are suspected of gut air breathing based on histological evidence. Families in black have not been demonstrated to breathe air. Ostariophysan relationships were drawn from the All Catfish Species Inventory (2009).

thought to be more likely to occur than *de novo* evolutionary innovations (Riegler 2008). This latter interpretation appears unlikely considering that the callichthyids use their hindgut for respiration whereas the other two families (and presumably the scoloplacids) use their foregut and there is no evidence for homology between the structures or even within many of the foregut breathers (Armbruster 1998). Certainly the evolution of esophageal ABOs in *Dallia* (Umbridae) and *Lipophrys* (Blennidae) and the evolution of an intestinal ABO in the loaches (Cobitidae) were independent evolutionary events. Interestingly, a synapomorphy for the loricarioidea that encompasses all of the GAB catfish families as well as the scoloplacids (Fig. 10.1) is a bony encapsulation of the swim bladder that may constrain its use as an ABO or organ of buoyancy (Schaefer and Lauder 1986).

Aside from obtaining access to the large amount of oxygen in the atmosphere, which is true of any air-breathing structure, the question then arises as to why the gut evolved into an ABO so frequently. One argument could be that portions of the gut already function as a transport epithelium and therefore must satisfy the constraints of the diffusion equation for some substances:

$$D = \Delta C * S / d$$

where D is the rate of diffusion, ΔC the difference in concentration between the gut lumen and the adjacent epithelial cell, S is the surface area of diffusional contact and d is the distance separating the two compartments. Since small fatty acids and some carbohydrates are generally absorbed in vertebrate guts by diffusion, the argument would be that the criteria for effective oxygen uptake by diffusion was already present and would involve relatively minimal evolutionary change for use as an ABO. This hypothesis would carry more weight if all gut air breathers used their intestines, the usual site of diffusional nutrient uptake, or if GAB fishes did not require substantial morphological remodeling to their gut (Sections 3 and 4) to breath air. However, the fact that taxa exploit regions of the gut for air breathing that were not originally specialized for foodstuff absorption (e.g. esophagus and stomach; Table 10.1) suggests that other criteria were important in driving the frequent evolution of the gut as an ABO.

A second hypothesis for the frequent evolution of GAB is that since the musculature, skeletal structures and cavities for ingesting and directing food from the mouth through the gastrointestinal (GI) tract were already present and had already been used to ingest air in the filling of physostomous swim bladders, this facilitated the evolution of gut air breathing. However, this same morphology and physiology can be used to fill the buccal cavity and pharyngeal region with air and thus does not explain why some fish evolved

transport of the air to the GI tract as opposed to exploiting the head region as an ABO which many other fish taxa have done (Graham 1997).

Since many of the GAB families are benthically oriented fishes, the answer to the frequent evolution of GAB may lie in buoyancy. Air in the head region would make the head more buoyant than the center of mass and tend to lift it off the substrate away from sources of benthic food and possibly increase visibility to predators or potential prey. As Gee (1976) discussed for buoyancy in general, asymmetric head buoyancy could also make it difficult to hold position in lotic waters. Displacing air to the GI tract would bring it closer to the center of mass and minimize buoyancy asymmetries. GAB fish generally hold on to air until taking a subsequent breath even after most of the oxygen is depleted (e.g. Gee and Graham 1978; McMahon and Burggren 1987), and Gee (1976) found that in a number of air-breathing loricarioids, the buoyancy attributable to air in the gut far surpassed buoyancy attributable to air in the swim bladder. Thus, buoyancy attributable to respiration represents a significant component of the animal's "buoyancy budget," especially for CABs, and could be envisioned as a target for natural selection. Certainly for the loricariids, where many species use an oral sucker to remain inverted under logs or rocks in the water column, the possession of a gut ABO would seem advantageous to a head region ABO. A head region ABO would presumably require extensive vascularization of both the dorsal and ventral buccal surfaces to accommodate extraction of oxygen in both normal and inverted positions, respectively. Thus, buoyancy issues and problems with maneuvering/positioning in the benthic environment may have been key factors favoring the frequent evolution of gut ABOs.

A final potential explanation for the frequent evolution of gut ABOs relates to diet. Many of the species in these gut air-breathing families are herbivorous or detritivorous (e.g. the majority of the loricarioids), so it is possible that ancestral forms were as well. Thus, one scenario is that dietary-driven changes to the GI tracts of ancestors facilitated (pre-adapted) evolution of gut ABOs. Lobel (1981) outlined four basic types of herbivory in fishes: (1) acid lysis in a thin-walled stomach; (2) trituration in a gizzard-like stomach; (3) trituration with pharyngeal jaws; and (4) microbial fermentation in the hindgut. It is entirely possible that morphological changes to the gut that facilitated digestion, for example thinning of GI epithelia to facilitate absorption of end-products of symbiont fermentations (Kihara and Sakata 1997), could have helped promulgate use of the gut for air breathing. Little is known about the trophic ecology of most of the fishes in these groups or the evolution of their digestive tract morphology, but one factor may be the sheer size of the GI tract in herbivorous fishes. For example, Nelson et al. (2007) report an astounding 4-meter gut length

(relative intestinal length of 20) in *Hypostomus regani*, a herbivorous loricariid. Whether any morphological changes driven by diet predisposed the evolution of gut air breathing in these groups remains a matter of speculation. Interestingly, Carter and Beadle (1931) and Persaud et al. (2006a) show that the respiratory intestine of *Hoplosternum* (Callichthyidae) develops from a fully functional digestive gut, well after normal maturation of the gut.

2.2. Challenges in Using the Gut as an ABO

The use of the gut as an ABO carries with it a number of perceived disadvantages. Gut air breathing potentially compromises digestive function in fishes. Vertebrate digestive processes generally take place under anaerobic conditions (van Soest 1994) and many of the GABs are herbivorous or detritivorous and presumably require an anaerobic gut to facilitate energy extraction from fermentative processes, as seen in marine herbivorous fishes (Clements et al. 2009), although the extent of fermentative processes in these freshwater herbivores is largely unknown. Thus, the use of the gut as an ABO could oxygenate portions of the gut and compromise digestive performance. In addition, the specialized respiratory portions of the gut are not thought to be involved in either the secretory or absorptive components of the digestive process (Persaud et al. 2006b). Thus turning over some of the gut to respiration may require additional structures, or modifications to existing structures, to accommodate digestive requirements. Based on histological evidence, Podkowa and Goniakowska-Witalińska (2002) suggest, however, that some absorption may be occurring in the respiratory segment of the *Corydoras* (Callichthyidae) intestine. This idea was confirmed by Gonçalves et al. (2007) in *Misgurnus* (Cobitidae) who found evidence that transport proteins normally involved in the digestive absorption of glucose are expressed in the respiratory portion of the intestine.

Conversely, food in the GI tract could potentially compromise the respiratory function of the ABO. The thin epithelium necessary for efficient diffusive gas exchange (Section 3) would seemingly be vulnerable to damage by the acid, alkali, digestive enzymes and dietary items that are normal constituents of the vertebrate GI tract. In addition, the physical presence of food and digestive juices would tend to increase the diffusive distance for oxygen, potentially limiting oxygen uptake in a gut ABO. Finally, use of the gut as an ABO seemingly places digestion and respiration in competition for some of the interfacing morphology and physiology. For example, it is hard to imagine that transport of substances with large differences in viscosity such as air and digesta is best accomplished by the same arrangement of visceral smooth muscle. In addition, both respiration and digestion are

characterized by blood flows regulated in accordance with activity; simultaneous digestion and air breathing would seemingly place different regions of the GI tract in competition for the available blood (Fig. 10.2). Full perfusion of the fish GI tract generally occurs postprandially (Thorarensen and Farrell 2006). Although ventilation–perfusion matching has not been studied in gut air-breathing fishes, presumably perfusion of gut ABOs is maximized when fresh air is present as in other air-breathing fishes (Burggren and Johansen 1986), possibly diverting blood flow from digestion during air breathing. Thus, GAB fishes had a number of interesting morphological and physiological challenges to overcome to successfully evolve the multi-functional gut into an ABO. The number of times this has occurred and the evolutionary success of the groups (Table 10.1) would attest to the viability of the strategy.

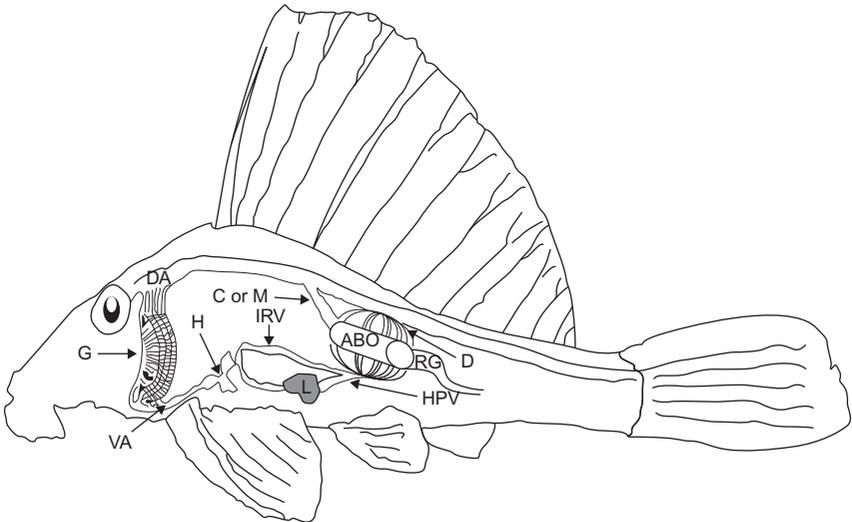


Fig. 10.2. General circulatory design among GAB fishes. Composite drawing incorporating the major features of all the different GAB fishes. Blood supply to the more anterior gut air-breathing organs (ABOs) (e.g. *Dallia* and *Ancistrus*) is via the coeliac artery whereas the more posterior intestinal ABOs tend to be supplied by the anterior mesenteric artery (e.g. *Misgurnus*) or directly from the dorsal aorta (e.g. *Callichthys* and *Hoplosternum*). ABO effluent blood travels back to the heart via the hepatic portal vein (Cobitidae) or the interrenal vein (all others). ABO = air-breathing organ; C or M = coeliac or anterior mesenteric artery; D = direct connection to the dorsal aorta through multiple vessels; DA = dorsal aorta; G = gills; H = heart; HPV = hepatic portal vein; IRV = interrenal vein; L = liver; RG = remaining gut; VA = ventral aorta.

3. MORPHOLOGY OF THE GUT AS AN AIR-BREATHING ORGAN

Across the families of GAB fish, common modifications of the GI tract consist of a reduction of digestive function and modification of features to facilitate respiration. The latter can be manifest as: (1) a high degree of vascularization; (2) capillaries embedded in an epithelium that is in direct contact with air; (3) a blood–air distance narrow enough for significant O₂ diffusion to occur; (4) increased surface area for gas diffusion to occur; (5) presence of surfactant producing lamellar bodies in epithelial cells; and (6) presence of muscular sphincters isolating the respiratory region from other regions of the GI tract. For the purposes of this review, we consider the esophagus, stomach, and intestine to be distinct regions of the gut proper.

3.1. Esophagus

Accounts of the esophagus serving as a respiratory region of the GI tract are limited to one species of umbrid (Crawford 1971, 1974), one species of blenniid (Laming et al. 1982; Pelster et al. 1988), although many blenniids have not been examined (Table 10.1), and a synbranchid (Liem 1967).

Though the majority of GAB fish are freshwater tropical species, the Alaska blackfish, *Dallia pecotralis* (Umbridae) inhabits the muskeg swamps of Alaska and Northern Siberia (McPhail and Lindsey 1970), and uses its esophagus as an ABO (Crawford 1974). *Dallia* possesses a highly vascularized swim bladder, but capillaries do not penetrate the inner epithelial lining of the swim bladder, and are separated from the epithelium by a layer of loose connective tissue and smooth muscle (Crawford 1974). This makes the swim bladder a good candidate for gas secretion (and certainly it may function in buoyancy regulation), but a poor candidate for gas absorption (Crawford 1974). However, the esophagus of *Dallia*, connected to the swim bladder at the pneumatic duct, is also highly vascularized but with extensive capillary penetration into the epithelial lining. Crawford's (1974) histological analysis revealed a blood–air barrier of < 1 μm which is similar to that reported in the ABO gas bladders of the bowfin, *Amia calva*, and the longnose gar, *Lepisosteus osseus* (Crawford 1971) (Table 10.2). Co-occurring with the extensive vascularization of the respiratory region of the esophagus was extensive folding of the mucosa, presumably for increasing surface area for gas absorption (Crawford 1974). In *Dallia*, gas absorption in the GIT is likely limited to the esophagus as there exists a distinct stricture between the near equally sized esophagus and stomach, and distal to the esophagus intraepithelial capillaries disappear and gastric glands appear (Crawford 1974).

Table 10.2
Air-blood diffusion distances and capillary density for the gut respiratory mucosal epithelium of gut air-breathing fishes

Respiratory region of the GI	Family	Species	Air-blood diffusion distance	Capillary density	Source
Esophagus Stomach	Umbridae	<i>Dallia pectoralis</i>	< 1 μm		Crawford 1971
	Loricariidae	<i>Ancistrus multispinnus</i>	0.6 μm	7/100 μm	Satora 1998
		<i>Hypostomus plecostomus</i>	0.25–2.02 μm ; arithmetic mean = 0.86 \pm 0.0046 μm (SE)	3–4/100 μm	Podkowa and Goniakowska- Witalińska 2003
		<i>Pterygoplichthys anisitsi</i>	Harmonic mean = 0.4–0.74 μm ; arithmetic mean = 1.52 \pm 0.07 μm (SE)		Cruz et al. 2009
Posterior intestine	Callichthyidae	<i>Hoplosternum thoracatum</i>	1–2 μm		Huebner and Chee 1978
		<i>Corydoras aeneus</i>	0.24–3.00 μm		Podkowa and Goniakowska- Witalińska 2002
	Cobitidae	<i>Lepidocephalichthys guntea</i>	0.86–1.08 μm	0.15/ μm^2	Yadav and Singh 1980
		<i>Lepidocephalichthys guntea</i>	2.6 μm		Moitra et al. 1989
		<i>Misgurnus anguillicaudatus</i>	11.9 \pm 0.4 μm	6.8/100 μm	McMahon and Burggren 1987
		<i>Misgurnus mizolepis</i>	0.7 \pm 0.11 μm		Park and Kim 2001

Lipophrys pholis (Blenniidae), an intertidal species of northern Europe, also uses its esophagus as an ABO. Gross observations of the esophagus consisted of a rich blood supply, many longitudinal folds, and visible separation from the buccopharynx and stomach by muscular sphincters (Laming et al. 1982). Following 3 h of forced air exposure, X-rays confirmed the presence of air bubbles in the esophagus, which was inflated to three times its pre-emersion size (Laming et al. 1982). Though Laming et al. (1982) did not report a blood–air diffusion distance, histological observation revealed that capillaries were embedded in the esophageal folds and were described as “superficial.”

Distinguishable from other regions of the GIT by the presence of many longitudinal folds and intraepithelial capillaries, the esophagus of *Monopterus albus* (Synbranchidae) may serve as an ABO (Liem 1967). Though blood–air diffusion distance was not measured, the capillaries are known to be embedded within the mucosal layer of the esophageal epithelium and are found only in the peaks of the papillary folds (Liem 1967).

3.2. Stomach

Reports of the stomach being used as an ABO are common for the Neotropical catfish families Loricariidae and Trichomycteridae. Attenuation of gastric activity in favor of oxygen uptake may have been feasible in these groups because of their exceptionally long, coiled intestines (Armbruster 1998; Nelson et al. 1999; Delariva and Agostinho 2001; Podkowa and Goniakowska-Witalińska 2003; Nelson et al. 2007) that could compensate for loss of stomach digestive function (Section 2.2).

3.2.1. GROSS MORPHOLOGY

Since the earliest observations in *Ancistrus* of Carter and Beadle (1931), it has been apparent that a thin-walled, translucent, highly vascularized stomach can function as an ABO in loricariids. This trend has been documented in many genera of loricariids (e.g. *Ancistrus*, *Hypostomus*, *Liposarcus*, *Pterygoplichthys*) (Carter and Beadle 1931; Carter 1935; Satora 1998; Souza and Intelizano 2000; Oliviera et al. 2001; Podkowa and Goniakowska-Witalińska 2003; Cruz et al. 2009), and is suggested in several closely related families (Gee 1976; Cala 1987; Armbruster 1998). Armbruster (1998) conducted the most extensive survey of GI gross morphology in loricarioids in which he scored modifications of the stomach for air breathing ranging from mere enlargement of the stomach to increasing degrees of stomach vascularization to the presence of one or two air-filled diverticula branching off the stomach. There are indications, however, that not all regions of a respiratory stomach may play an equal role in O₂ uptake.

Carter and Beadle (1931) described an elongated posterior region of the stomach in *Liposarcus* that was more vascularized than other regions.

3.2.2. REDUCED GASTRIC FUNCTION

Indications of respiratory function restricted to specific regions of the stomach can also be seen when examining the distribution of digestive glands. While the stomachs of both *Ancistrus* (Satora 1998) and *Pterygoplichthys* (Cruz et al. 2009) contain gastric glands, there is a reduced number in the corpus region of the stomach compared to the cardia and pylorus regions. In *Ancistrus*, capillaries were only embedded in the mucosal epithelia in the corpus region (Satora 1998), further suggesting that the corpus is the site of O₂ uptake. Cruz et al. (2009) reported a reduction in gastric glands coincident with a high degree of longitudinal folding of the mucosa in the corpus region. Furthermore, no regions stained positive for Alcian blue or for PAS indicating a lack of acid and neutral mucopolysaccharide production, respectively, in all regions of the stomach. This suggests that digestion occurs elsewhere in the GI tract (Cruz et al. 2009). Similarly, only a weak positive Alcian blue reaction was seen in the entire stomach mucosal surface of *Hypostomus* and the PAS reaction was negative (Podkowa and Goniakowska-Witalińska 2003). These authors also noted that food was never observed in the stomach of *Hypostomus*, also suggestive of the hypothesis that most digestion is occurring elsewhere in the GI tract.

Carter and Beadle (1931) were the first to report a reduction in digestive glands in *Ancistrus*. This observation was corroborated in *Liposarcus* by Oliveira et al. (2001) who described the stomach mucosa as non-glandular simple cuboidal epithelia. No food was observed in the stomach of any specimens despite regular feeding throughout captivity in the Oliveira et al. (2001) study. The epithelial mucosa develops into many folds and projections distal to the stomach, providing more surface area in the intestine for nutrient absorption (Oliveira et al. 2001).

3.2.3. VASCULARIZATION

A short blood–air barrier is essential for the diffusion of O₂ from the stomach lumen into surrounding capillaries. Reports of capillaries embedded within the stomach mucosa include *Ancistrus* (Satora 1998; Satora and Winnicki 2000), *Liposarcus* (Oliveira et al. 2001), *Hypostomus* (Podkowa and Goniakowska-Witalińska 2003), *Pterygoplichthys* (Cruz et al. 2009), and *Ancistrus*, *Hypostomus*, *Peckoltia*, *Pterygoplichthys*, and *Megaloancistrus* (Souza and Intelizano 2000). The shortness of the blood–air barrier is illustrated in Fig. 10.3 where it is evident that, in *Ancistrus*, the gut lumen is separated from a capillary erythrocyte by only

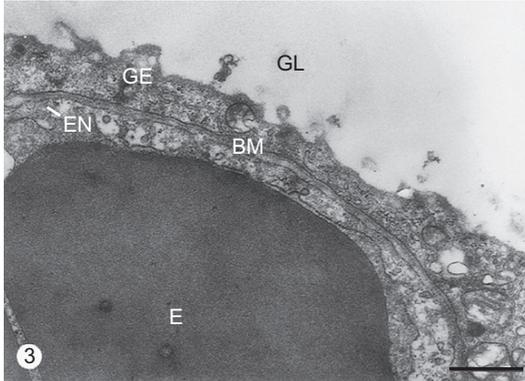


Fig. 10.3. Transmission electron micrograph of the corpus region of the stomach of *Ancistrus Multispinnis* (Loricariidae). The air space is top/right. BM = basement membrane; E = erythrocyte; EN = capillary endothelium; GE = gastric epithelium; GL = gastric lumen. The scale bar = 1 μ m. Taken from Satora (1998).

three layers: (1) the gastric epithelium, (2) the basement membrane, and (3) the capillary endothelium. Published diffusion distances and capillary densities are summarized in Table 10.2.

Though all studies of stomach ABOs describe a dense capillary network for O₂ uptake, few have investigated the type of capillaries embedded within the mucosa. Visceral capillaries, normally associated with the GI tract, are characterized by an endothelium varying in thickness and containing many pores, while alveolar capillaries, such as those found in mammalian lungs, are characterized by a flattened endothelium with a continuous basement membrane lacking pores (Jasinski 1973). Satora and Winnicki (2000) liken the capillaries in the stomach mucosa of *Ancistrus* to the alveolar type in that the endothelium is flattened and the basement membrane is nearly continuous except for the existence of sparse pores, leading the authors to speculate that the stomach mucosa capillaries evolved from the visceral type to accommodate a respiratory function. In contrast, the capillary endothelium within the *Hypostomus* stomach mucosa contains “relatively numerous” pores and more closely resembles the visceral capillary type (Podkowa and Goniakowska-Witalińska 2003).

3.2.4. SURFACTANT PRODUCTION

Epithelial cells resembling mammalian type I and II pneumocytes are found in all known fish lungs and gas bladders (Graham 1997). These cells contain surfactant-producing lamellar bodies thought to aid in gas absorption by decreasing surface tension among other suggested functions

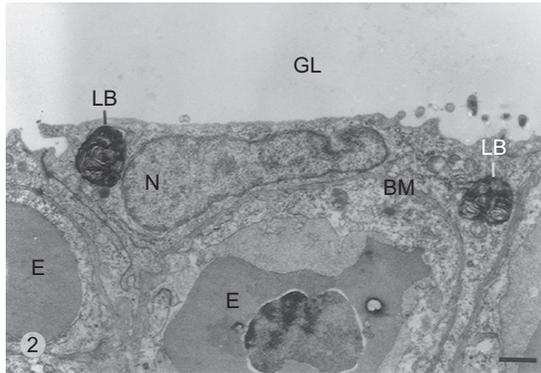


Fig. 10.4. Transmission electron micrograph from the corpus region of the stomach of *Ancistrus multispinnis*. Lamellar bodies (LB) are visible beneath the epithelial cell surface. BM = basement membrane; E = erythrocyte; GL = gastric lumen; N = nucleus. Scale bar = 1 μm . Taken from Satora (1998).

(Daniels and Orgeig 2003). Satora (1998) was the first to document the presence of lamellar bodies in the cytoplasm of stomach epithelial cells, less than 0.5 μm from the gut lumen in *Ancistrus* (Fig. 10.4). The presence of type I pneumocyte-like cells, specific to the corpus of the stomach mucosa, was later confirmed (Satora and Winnicki 2000). In the latter study, however, the authors reject the possibility that the abundant amount of surfactant produced in the stomach of *Ancistrus* reduces surface tension since the stomach is not vesicular like the alveoli of mammalian lungs. They instead favor the idea that the surfactant may serve to protect against desiccation and oxidative stress. Since then, lamellar bodies have also been documented in the stomach epithelial cells and gastric glands of *Hypostomus* (Podkowa and Goniakowska-Witalińska 2003) and *Pterygoplichthys* (Cruz et al. 2009). These authors favor the idea that surfactant aids in O_2 uptake.

3.3. Posterior Intestine

Gut air breathers in the families Cobitidae and Callichthyidae have been shown to use the intestine as an ABO (Table 10.1).

3.3.1. GROSS MORPHOLOGY

Similar to the stomach ABOs of loricariids and trichomycterids, the respiratory intestine of several cobitids and callichthyids has been described as thin-walled, translucent, and highly vascularized. This is seen in the posterior two-thirds of the intestine in *Lepidocephalichthys* (Cobitidae)

(Yadav and Singh 1980; Moitra et al. 1989). Additionally in this species, collagen fibers are present in lieu of the tunica propria in the respiratory segment of the intestine, allowing greater expandability to hold more air (Yadav and Singh 1980). In *Misgurnus* (Cobitidae), the distal 60% of the GI tract is estimated to be involved in O₂ uptake as the intestinal epithelia become thinner and more heavily vascularized in this region (McMahon and Burggren 1987).

The stomach and anterior intestine of *Corydoras* (Callichthyidae) are muscular, opaque and easily discernible from the thin-walled, translucent, air-filled posterior intestine, which occupies 30–40% of the entire intestine length (Kramer and McClure 1980; Podkowa and Goniakowska-Witalińska 2002). Kramer and McClure (1980) measured gas bubbles seen in the posterior intestine that occupied an average of 48% of the length of the entire intestine (range 21–69%) in experimentally induced air-breathing *Corydoras* (Callichthyidae). Huebner and Chee (1978) estimated that 50% of the GI tract of *Hoplosternum* (Callichthyidae) is dedicated to respiration, as it appears smooth, thin-walled, highly vascularized, and contained gas bubbles.

3.3.2. MUCUS PRODUCTION AND THE PRESENCE OF FOOD IN THE RESPIRATORY INTESTINE

There is a disparity between cobitids and callichthyids regarding the abundance of mucus-producing goblet cells in the respiratory intestinal epithelia. Sparse goblet cells are seen in the respiratory intestine of *Misgurnus* (Cobitidae) (Jasinski 1973) and *Lepidocephalichthys* (Cobitidae) (Yadav and Singh 1980; Moitra et al. 1989). Park and Kim (2001) reported a reduced density of goblet cells in the posterior intestine of *Misgurnus* (Cobitidae) relative to that seen in the esophagus and stomach. Numerous goblet cells are reported in the respiratory intestine of *Hoplosternum* (Callichthyidae) (Huebner and Chee 1978) and *Corydoras* (Callichthyidae) (Podkowa and Goniakowska-Witalińska 2002). The advantages of mucus may include lubrication for the passage of digesta and protection of the thin-walled, highly vascularized posterior intestine from desiccation and mechanical damage, but excessive mucus may increase gas diffusional distance.

Though numerous goblet cells in the respiratory intestine may be advantageous, it may not be a necessity, as seen in *Misgurnus*, where fecal matter emerges from the anterior spiral intestine already enclosed in a mucus pouch (McMahon and Burggren 1987). The respiratory intestines of the cobitids *Misgurnus* (Wu and Chang 1945) and *Lepidocephalichthys* (Yadav and Singh 1980) are usually filled with air and digesta are rarely seen, although Huebner and Chee (1978) observed fecal pellets between gas bubbles in the respiratory intestine of the callichthyid *Hoplosternum*.

3.3.3. VASCULARIZATION

Capillary penetration into the intestinal mucosa creating a short blood–air barrier for O₂ absorption has been recorded for the respiratory intestine of several species (Table 10.2). McMahon and Burggren (1987) examined the stomach, anterior, mid, and posterior intestine of *Misgurnus* and found a significant decrease in the blood–air barrier distance and a significant increase in capillary density progressing posteriorly along the GI tract. Histological preparations confirmed infiltration of capillaries into the posterior intestinal mucosal epithelium of *Misgurnus* (Jasinski 1973; Park and Kim 2001), *Hoplosternum* (Huebner and Chee 1978), and *Corydoras* (Podkowa and Goniakowska-Witalińska 2002).

Jasinski (1973) classified infiltrating capillaries seen in *Misgurnus* as the alveolar type based on the observations of flattened capillary endothelium, a continuous basement membrane, and only occasional pores. Though Podkowa and Goniakowska-Witalińska's (2002) description of *Corydoras* capillaries is similar to Jasinski's (1973) description of *Misgurnus*, they classify the infiltrating capillaries in the respiratory intestine of *Corydoras* as the visceral type, suggesting that some nutrient absorption does take place here. In order to better classify capillary type in the future, pore numbers should be quantified.

3.3.4. SURFACTANT PRODUCTION

Goblet cells and their secretions into the intestinal lumen may protect against desiccation and oxidative stress, but the existence of surfactant producing lamellar bodies in the respiratory intestinal epithelia has only been confirmed in *Misgurnus* (Jasinski 1973) and *Corydoras* (Podkowa and Goniakowska-Witalińska 2002).

4. CIRCULATORY MODIFICATIONS ASSOCIATED WITH USE OF GUT ABOs

The potential for air-breathing fishes to lose oxygen to hypoxic waters across their gills has been extensively considered (e.g. Graham 1997) and will not be heavily reiterated here. Figure 10.2 shows the general circulatory plan of fishes with GABOs. Because oxygenated venous blood emanating from the ABO next encounters capillaries in the gills (or the liver and then the gills (Cobitidae)), oxygen will be lost to the water across the gill secondary lamellae if the water PO₂ is lower than that of the blood. Thus, the ability to shunt oxygenated blood away from the gill secondary lamellae during simultaneous aquatic hypoxia and air breathing could be favored by natural

selection. Fernandes and Perna (1995) and Crawford (1971) present histological evidence for the possibility of shunting in *Hypostomus* and *Dallia*, respectively, and blood chemistry studies showing CO₂ retention in *Hypostomus* during air breathing (Wood et al. 1979) also imply shunting, but to our knowledge there has yet to be direct physiological demonstration of shunting oxygenated blood away from the gill gas exchange surface of GAB fish while breathing air. Interestingly, some GAB fish do not alter their rate of branchial ventilation upon breathing air in hypoxic water and some appear to actually increase gill ventilation under air-breathing conditions (Section 5.1.2).

The major variation in circulatory design among GAB fishes is the ABO drainage returning to the heart either via the hepatic portal circulation (Cobitidae) or the systemic circulation (all others) (Carter and Beadle 1931; Graham 1997; Fig. 10.2). Venous return through the systemic circulation is perceived as advantageous because bypassing the capillary beds of the liver will facilitate a more even corporal distribution of oxygen and avoid a pressure drop between the ABO and the heart (Fig. 10.2). Systemic venous return also exposes the ABO effluent to more direct suction from the heart during cardiac relaxation than would the hepatic portal return pathway (Olson 1994). In addition to the differential return paths to the heart, there is some variation in the path arterial blood takes to the ABO among the different groups, supporting contentions of independent evolutionary origins for GAB among the different taxa (Section 2.1). Although all GABOs are supplied with blood from branches of the dorsal aorta (Fig. 10.2), the more anterior gut ABOs tend to be supplied by branches of the coeliac artery (e.g. *Dallia* (Crawford 1971) and *Ancistrus* (Carter and Beadle 1931)) whereas the more posterior intestinal ABOs tend to be supplied by the anterior mesenteric artery (e.g. *Misgurnus* (McMahon and Burggren 1987)) or directly from the dorsal aorta (e.g. *Callichthys* and *Hoplosternum* (Callichthyidae); Carter and Beadle 1931). Yadav and Singh (1980) report the presence of a possible shunt vessel between the ventral aorta and the intestinal ABO in *Lepidocephalus* (Cobitidae), but this vessel has not been reported by other workers nor has its physiological function been investigated.

An additional major circulatory adjustment found in GAB fishes is the intrusion of the capillaries of the ABO into the gut luminal epithelial layer (Section 3). The normal position for capillaries of the GI tract would be in the *lamina propria*, basal to the gut epithelium. Although this capillary position functions perfectly well for the diffusive uptake of some foodstuffs such as small fatty acids (Fänge and Grove 1979), apparently, rates of diffusive oxygen uptake with such an arrangement were insufficient as the ABOs evolved, so a general histological finding is that capillaries have

migrated into the epithelial layer, but do not directly abut the luminal surface of the gut (Fig. 10.3). Table 10.2 presents estimated diffusional distances for gut ABOs from a number of histological studies. The ranges reported fall within those of other fish ABOs and are in the range of mammalian lung diffusive distances (Weibel 1984). Capillary densities of gut ABOs are typical for fish ABOs in general (Podkowa and Goniakowska-Witalińska 2002, 2003; Cruz et al. 2009). The Cruz et al. (2009) study of *Pterygoplichthys* (Loricariidae) is the only known estimate of the diffusing capacity of a gut ABO. Cruz et al. (2009) found the diffusing capacity of this stomach ABO to be higher than for most other fish ABOs, but lower than published values for the lungs of lungfish (*Lepidosiren* and *Protopterus*). This estimated diffusing capacity of a gut ABO (Cruz et al. 2009) is also substantially below estimates for lungs of similar-sized mammals (Weibel 1984).

5. PHYSIOLOGY OF GUT AIR BREATHING

5.1. Ventilation

5.1.1. VENTILATION OF GUT AIR-BREATHING ORGANS (GABOs)

Surprisingly, there are no studies on the mechanics of GABO inflation. Most authors describe inspiration as “gulping,” presumably a negative buccal cavity pressure derived from buccal and perhaps opercular cavity expansion as described for other air-breathing fishes (Liem 1989). A further assumption is that positive pressure is then generated by buccal cavity contraction with both oral and opercular valves closed, driving the air posteriorly to the ABO as detailed for lungs and swim bladder ABOs (Liem 1989). Expiration and air transport through the GI tract are equally as mysterious in GAB fishes. Crawford (1971) comments on the presence of a well-developed esophageal skeletal musculature that may be involved in expelling gas from the *Dallia* (Umbridae) esophagus; however, there is no confirmation of this. Likewise, Gradwell (1971) discusses three ways that *Plecostomus* (Loricariidae) could exhale while submerged: (1) hydrostatic pressure alone in conjunction with elastic recoil and appropriate valving; (2) contraction of visceral smooth muscle of the respiratory stomach; and (3) positive abdominal cavity pressure developed through contraction of the *rectus abdominis* skeletal muscle, but there has been no experimental differentiation among these alternatives. The two families with intestinal ABOs (Callichthyidae and Cobitidae) have a unique transport problem. Since they exhale through their vent (Gee and Graham 1978; McMahon and Burggren 1987), they must transport air the entire length of the GI tract.

While this unidirectional transport of air potentially minimizes respiratory dead space, it raises a new problem of coordinating transport of air with transport of digesta. Both of these families have a transitional zone between the digestive and respiratory portions of their intestine (McMahon and Burggren 1987; Persaud et al. 2006b) that is richly endowed with smooth muscle and appears to function in compacting the digesta and possibly encasing it in mucus. This compacted digesta would then minimally interfere with gas exchange in the respiratory (posterior) segment of the intestine. Persaud et al. (2006b) found that depriving two callichthyids of access to the surface in normoxic water caused them to curtail feeding activity and diminish the transport of digesta posteriorly. Since Persaud et al. (2006b) and other authors (e.g. Gee and Graham 1978) have noted the synchronous release of air from the vent immediately following inspiration, Persaud et al. (2006b) propose that the column of air present in the guts of these continuous air-breathing fishes is necessary for normal digesta transport. Furthermore, Persaud et al. (2006b) claim that the amount of visceral smooth muscle in the respiratory portion of the intestine is insufficient for peristaltic transport of air. Thus, the pressure generated by the buccal/opercular pump speculatively provides the force for inspiration, air transport, digesta transport across the respiratory zone of the intestine and expiration in intestinal GAB fishes.

5.1.2. GILL VENTILATION DURING AIR BREATHING

The general pattern of branchial ventilation in fish exposed to progressive hypoxia is to defend arterial PO_2 (oxygen regulation) by increasing total gill ventilation (Holeton 1980; Fig. 10.5). This is manifested by either increases in ventilatory frequency f_v (Affonso and Rantin 2005) or ventilation volume V_t (Nelson et al. 2007) with the latter considered more common, possibly as an energy-saving strategy (Mattias et al. 1998; Fig. 10.5). As environmental oxygen falls to levels where this strategy waxes futile, the animal ceases oxygen regulation at a point called the critical oxygen tension (P_cO_2) and metabolic rate begins to drop in concert with environmental $[O_2]$ (oxygen conforming) or the animal switches to air-breathing to maintain oxygen regulation if it has evolved that capacity (Fig. 10.5). As an animal starts using atmospheric oxygen, the prediction is that gill ventilation should diminish if not stop. Fish expend substantial energy, around 10% of their resting metabolic rate, in ventilating their gills (Holeton 1980; Glass and Rantin 2009), and although air-breathing fish generally still use their gills or skin to eliminate CO_2 (Johansen 1970), the potential loss of O_2 to the water across the secondary lamellae would seem to make ventilating the gills in hypoxic water generally counterproductive. Indeed, fish from one of the GAB taxa that completely emerges (*Lipophrys*)

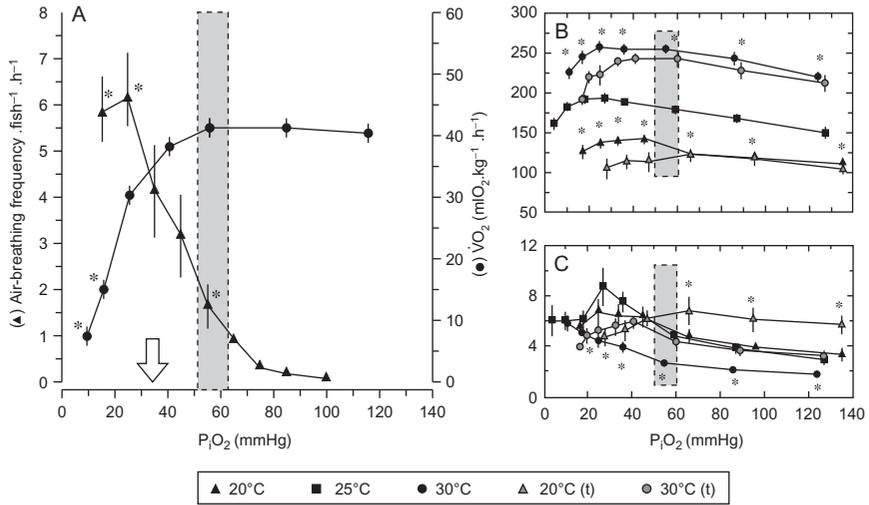


Fig. 10.5. (A) Air-breathing frequency (▲) of 50 *Hypostomus regani* exposed to progressive hypoxia and allowed free access to the surface and aquatic mass-specific oxygen consumption (●) of 17 *Hypostomus regani* exposed to progressive hypoxia but denied access to the surface. The stippled bar designates the range of PO_2 over which air breathing normally commences (Mattias et al. 1998). (B) Respiratory frequency (breaths·min $^{-1}$) (f_R ; top panel) and (C) tidal volume (ml·kg $^{-1}$ ·min $^{-1}$) (V_T ; bottom panel) of *Hypostomus regani* exposed to progressive hypoxia over a period of 9 h and denied access to the surface. Closed symbols represent animals chronically acclimated to a temperature whereas the stippled symbols represent animals acutely transferred to the experimental temperature. Each symbol represents the mean for that group ± 1 SE. The stippled bar designates the range of PO_2 over which air breathing would normally commence (modified from Nelson et al. 2007).

has been reported to cease branchial ventilation upon leaving the water (Laming et al. 1982), although Pelster et al. (1988) claim that ventilation continues during emersion in a tidal fashion with the opercular valve closed. The situation is also unclear and certainly not generalizable to those GAB fishes that remain submersed. Some investigators have reported cessation of branchial ventilation in loricariids (Gradwell 1971; Wood et al. 1979) but these were visual observations and appear to have been erroneous. Graham (1983) reports a 20% drop in gill f_v in air-breathing *Ancistrus* when acclimated to hypoxic water, but Gee and Graham (1978) report a 33% increase in *Hoplosternum* gill f_v when induced to increase its frequency of air breathing through aquatic hypoxia and Affonso and Rantin (2005) report a 31% increase in hypoxic *Hoplosternum* gill f_v when not allowed to breathe air, although *Hoplosternum* has also been reported to have poorly developed gill secondary lamellae (Carter and Beadle 1931). Finally, no change in the rate of gill ventilation with air breathing has been reported for both foregut breathers *Hypostomus* (Nelson et al. 2007) and hindgut breathers *Misgurnus*

(Cobitidae) (McMahon and Burggren 1987). Although V_t has not been measured in GAB fish while air breathing, we have to conclude at this juncture, based upon f_v measurements alone, that reduced gill ventilation while air breathing is not a general strategy GAB fish have employed to either save energy or reduce O_2 loss to hypoxic water.

5.2. Gas Exchange and Metabolic Rate in GAB Fishes Breathing Air

Although the attempt to characterize the gas composition of GABOs dates to the nineteenth century (Jobert 1877), there is a surprisingly small amount of information on gas exchange in GAB fishes. Despite this, a general consensus has emerged that GABOs are only minimally involved in CO_2 excretion. Regardless of whether the fish is a foregut breather (*Ancistrus* Loricariidae) (Carter and Beadle 1931; Graham 1983) or hindgut breather *Misgurnus* (Cobitidae) (McMahon and Burggren 1987) or *Hoplosternum* (Callichthyidae) (Carter and Beadle 1931), the general finding is for very minimal amounts or no CO_2 to be released via the ABO. The high capacitance of water for CO_2 (Schmidt-Nielsen 1997) allows for efficient CO_2 excretion by the gills and skin. Blennies, represented by *Lipophrys pholis* are the only GAB fish that are classified as amphibious and have had their plasma CO_2 measured under emersion conditions (Pelster et al. 1988). (Note: *Hoplosternum* have been reported to migrate over land between ponds (Carter and Beadle 1931), *Misgurnus* have been reported to endure droughts in dry burrows (Ip et al. 2004) and some Loricariids will self-emerge in the laboratory (J. A. Nelson personal observation).) Pelster et al. (1988) report a 53% rise (from 2.43 to 3.71 mmHg) in plasma PCO_2 in emersed *Lipophrys pholis*, consistent with the general vertebrate emersion expectation (Schmidt-Nielsen 1997), but do not report ABO [CO_2]. Based on this limited physiology, GABOs do not appear to be significant organs of CO_2 excretion.

The frequent evolution of GAB (Section 2.1) most likely transpired to provide supplementary oxygen to animals when dissolved oxygen became limiting. Other proposed functions such as buoyancy (Gee 1976) and propelling of digesta (Persaud et al. 2006b) appear to be secondary functions (see below) and possible exaptations (Gould and Vrba 1982). Almost without exception, GAB fish exposed to hypoxia do not go hypometabolic when allowed to breathe air and instead retain oxygen regulation and normal levels of activity (Fig. 10.5). Rates of air breathing will thus be complex functions of metabolic rate and all of its inherent variance and problems in accurately assessing. Metabolic rate in fishes depends on size, species and multiple additional factors including experimental and environmental variables such as stress level, temperature and water chemistry

(Nelson and Chabot 2010). Thus, attempts to characterize ABO ventilation rates across GAB fishes would be premature and disingenuous based upon the limited information available. The same can be said for respiratory partitioning (the fraction of oxygen contributed by aerial versus aquatic respiration) under various conditions and rates of oxygen uptake from the ABO; the number of studies are so few, and the probability of experimental and environmental effects overwhelming the results so real, that there can be little heuristic value in creating generalizations here. Graham (1983) for *Ancistrus* (Loricariidae) at 25°C and McMahon and Burggren (1987) for *Misgurnus* (Cobitidae) at 20°C give the most detailed accountings of changes in ABO gas composition over time, and the reader is referred to these if more detailed information is desired. The following consideration of gas exchange in GAB fishes follows the organization of Table 10.1.

5.2.1. ESOPHAGEAL GAS EXCHANGE

For esophageal breathers (Table 10.1), Crawford (1971) showed that three individual *Dallia* (Umbridae) maintained normal metabolic rates below an $[O_2]$ of 2 mg/l by supplementing aquatic respiration with air breathing. Likewise, Laming et al. (1982) show that metabolic rates of *Lipophrys* (Blenniidae) stay relatively constant throughout cycles of immersion/emersion and that skin oxygen consumption is only a minor contributor to oxygen uptake, suggesting that the GABO is able to maintain normal resting rates of oxygen consumption in emergent members of this species.

5.2.2. FOREGUT (STOMACH) GAS EXCHANGE

Of the two stomach-breathing families (Table 10.1), gas exchange has only been studied in the loricariids. Cala et al. (1990) report that the hypoxia-exposed trichomycterid *Eremophilus* must increase its air-breathing frequency to survive, but there have been no studies of actual gas exchange in this family. The loricariids that have been studied conform to the general facultative air-breathing (FAB) pattern (Section 5.1.2; Fig. 10.5). As environmental $[O_2]$ drops, metabolic rate is regulated until a P_wO_2 between 25 and 60 mmHg is reached (Graham and Baird 1982; Graham 1983; Nelson et al. 2007), at which time, many loricariids begin breathing air with their stomachs (Gee 1978; Graham and Baird 1982; Graham 1983; Mattias et al. 1998; Nelson et al. 2007). Graham (1983) demonstrated utilization of the oxygen component of air in the loricariid ABO by showing a progressive decline in $[O_2]$ of ABO gas with breathhold length in *Ancistrus*. Oxygen uptake from the ABO can also be inferred from the sub-atmospheric gut oxygen levels reported by Carter and Beadle (1931) for *Ancistrus* and Nelson et al. (2007) for *Hypostomus*. Graham (1983) also showed that increased oxygen demand in *Ancistrus* was met entirely through increases in air-breathing frequency (f_v); ventilation volume

(V_t) of air breaths remained constant throughout changes in air-breathing demand in this species. Interestingly, *Ancistrus* acclimates to 2–3 weeks of hypoxia by expanding the size of its ABO 25% and increasing its ability to extract oxygen from the ABO (Graham 1983). Although most authors report no air breathing from loricariids in normoxic water, MacCormack et al. (2006) report surfacing (presumably air-breathing) behavior that was independent of environmental $[O_2]$ in a telemetered loricariid (*Glyptoperichthyes*) held in cages in a natural environment. This observation, coupled with observations that another loricariid genus (*Panaque*) will voluntarily emerge in normoxic water (Nelson personal observation), suggests that our understanding of air-breathing behavior and ventilation dynamics in GAB loricariids will benefit from more studies on additional species under field-relevant conditions.

5.2.3. HINDGUT (STOMACH) GAS EXCHANGE

Both families of intestinal air breathers (Table 10.1) appear to be continuous, but not obligate air breathers (Gee and Graham 1978; Kramer and McClure 1980; McMahan and Burggren 1987). Wu and Chang (1945) claim that *Misgurnus* (Cobitidae) abandons continuous air breathing at low temperature, and it is possible that McMahan and Burggren (1987) did not lower temperature enough (10°C) to observe this effect, but based on the currently available information, it seems safest to classify both the callichthyids and cobitids as CAB fishes. This implies that some other physiological function such as buoyancy (Gee 1976), digesta transport (Persaud et al. 2006b) or enhanced scope for activity (Gee and Graham 1978; Almeida-Val and Farias 1996) is served by breathing air in these fishes. However, since representatives from both families conform to the FAB pattern of responding to aquatic hypoxia with increased ventilation of their ABO to regulate metabolic rate (Gee and Graham 1978; McMahan and Burggren 1987), we conjecture that these factors were secondary to aquatic hypoxia in driving the original evolution of intestinal respiration. McMahan and Burggren (1987) found that when *Misgurnus* was exposed to aquatic hypoxia, it increased the rate of intestinal ventilation entirely through increases in f_v . Changes in aerial V_t were not involved, similar to what Graham (1983) reported for stomach-breathing *Ancistrus* (Section 5.2.2). Gee and Graham (1978), Kramer and McClure (1980), and Affonso and Rantin (2005) also report increases in f_v with progressive aquatic hypoxia in three species of intestinal-breathing callichthyids. McMahan and Burggren (1987) estimated an $\sim 70\%$ turnover of ABO air (30% deadspace) with each subsequent breath in *Misgurnus* intestines. Interestingly, they report no correlation between gas composition of the ABO and breath interval durations ranging from 5 min to 1 h, suggesting that the available oxygen is extracted from the air relatively rapidly and very little gas exchange occurs

subsequently. Jucá-Chagas (2004) reports that the intestinal breathing *Hoplosternum* (Callichthyidae) can extract more oxygen per unit body mass from an air breath than either a gas-bladder-breathing erythrinid (*Hoplerythrinus*) or a lungfish (*Lepidosiren*).

5.3. Gut Air-breathing Ventilatory Drive

Manipulations of the gas composition of the aquatic and aerial medium by Gee and Graham (1978) and McMahon and Burggren (1987) conclusively show that representatives from neither intestinal air-breathing family (Table 10.1) are sensing the chemical composition of the gas in the ABO to set ABO ventilation rate, although ABO volume may play a role (Gee and Graham 1978). The main factors that appear to set the rate of aerial ventilation in GAB fish are P_wO_2 and metabolic rate (Kramer and McClure 1980; Graham and Baird 1982; McMahon and Burggren 1987). McMahon and Burggren (1987) report a modest sensitivity of *Misgurnus* (Cobitidae) f_v to water PCO_2 as do Graham and Baird (1982) for stomach-breathing *Ancistrus* and *Hypostomus*, but the primary drive for ventilation appears to be chemosensation of P_wO_2 as evidenced by the inverse relation of f_v with P_wO_2 in all species measured. This would accord well with Oliviero et al. (2004) who found ventilation of a gas-bladder ABO in the erythrinid *Hoplerythrinus* to be driven by O_2 chemoreceptors on the gills. Graham and Baird (1982) report no change in the threshold P_wO_2 for air breathing to commence even after hypoxia acclimation had produced improvements in the size and extraction efficiency of the ABO, also strongly suggestive of environmental chemosensation of P_wO_2 setting this parameter. In contrast, Brauner et al. (1995) show a leveling off of the f_v/P_wO_2 relationship in *Hoplosternum* (Callichthyidae) such that reductions in P_wO_2 below 100 mmHg did not elicit further increases in f_v . Brauner et al. (1995) also demonstrated an inverse relation between f_v and pH and a direct relationship between f_v and water hydrosulfide (HS^-) concentration in this species and suggest that these latter two variables (indicative of water parcels that have gone anaerobic) may be as important as P_wO_2 in setting rates of ABO ventilation in nature.

Rates of aerial ventilation in GAB fishes are also sensitive to metabolic demand influenced by changes in temperature, size or activity level. McMahon and Burggren (1987) report a linear increase in ABO ventilation between 10° and 30°C ($Q_{10} \sim 2$ for 10°–20°C and $Q_{10} \sim 1.5$ for 20°–30°C) for *Misgurnus* and Graham and Baird (1982) report a steady increase in f_v between 20° and 30°C ($Q_{10} \sim 1.4$) for *Ancistrus*. Sloman et al. (2009) found that smaller, and therefore metabolically more active, *Hoplosternum* (Callichthyidae) had a higher P_wO_2 air-breathing threshold during exposure

to progressive hypoxia than larger animals when held in isolation. This relationship disappeared when animals were held in groups, casting doubt upon the field relevance of the former result, but still suggestive of the idea that metabolic demand may partially drive ABO ventilation rate. Conversely, Mattias et al. (1998) found no relationship between body mass (M_b) and air-breathing threshold in 50 *Hypostomus regani* over a 600 g size range. Perna and Fernandes (1996) also found no effect of size on air-breathing threshold for *Hypostomus plecostomus* over an 83 g size range. Activity appears to correlate with air-breathing frequency in CAB callichthyids, but has not been studied in other GAB fish taxa. Gee and Graham (1978) found a significant correlation between air-breathing frequency and activity in two species of CAB callichthyids (*Hoplosternum* and *Brochis*). Kramer and McClure (1980) also found significant relationships between activity and f_v in a third species of callichthyid (*Corydoras*), but only at three of the five depths they tested. Boujard et al. (1990) report a robust circadian cycle in *Hoplosternum* wherein feeding, activity and air-breathing activity all peaked during the hours of darkness in these nocturnal fish, and Sloman et al. (2009) report a significant relationship between activity and air-breathing in *Hoplosternum*, but only when in groups. Almeida-Val and Farias (1996) found one species of CAB (*Hoplosternum*) to have an exceptionally high rate of tissue oxygen consumption suggesting that CAB may have evolved to support high tissue rates of ATP turnover, but since an FAB foregut-breathing loricariid (*Liposarcus*) had the lowest rate of tissue ATP turnover among analyzed species this is not a general property of GAB fishes.

5.4. Cardiovascular Response to Gut Air Breathing

Although there is a fairly rich literature on cardiovascular responses to air breathing in fish, most of this literature relates to lungfishes and several other large (mostly swim bladder ABO) species (Graham 1997). There is very little cardiac, and no vascular, information on GAB fishes while breathing air. GAB fishes can exhibit an almost immediate reflex bradycardia when exposed to hypoxia as shown in the loricariid *Hypostomus* by Nelson et al. (2007) (Fig. 10.6). This is presumably the same generalized, although not universal, vagally mediated reflex bradycardia response to hypoxia seen in water-breathing fishes (Taylor 1992). This hypoxic bradycardia appears to have a metabolic component, as Nelson et al. (2007) report a more established hypoxic bradycardia at 30°C than at either 20°C or 25°C. The development of a significant bradycardia in loricariids during progressive hypoxia, when metabolic rate remains unchanged (Nelson et al. 2007), suggests that the cardiac response to hypoxia may be somewhat

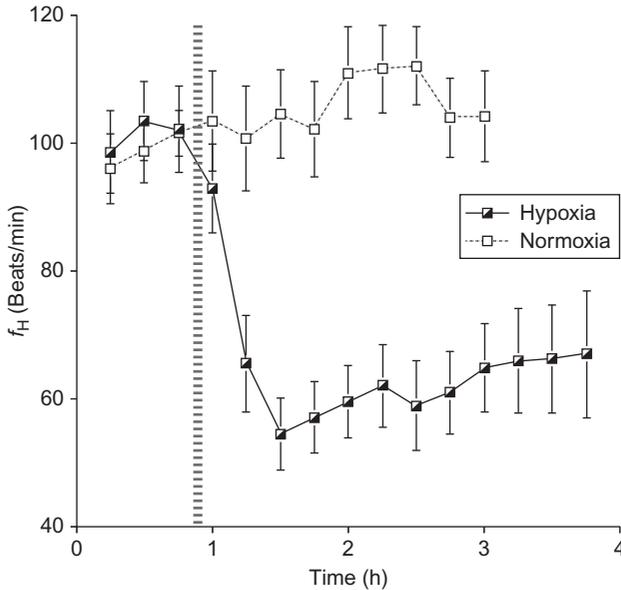


Fig. 10.6. Heart rate (f_H) in *Hypostomus regani* exposed to 20 mmHg PO₂ for 3 h (half-closed symbols) or normoxic conditions for 3 h (open symbols). Each symbol represents the mean for that group ± 1 SEM. The striped bar designates the onset of hypoxia. Hypoxia exposure immediately initiated an approximate 50% reduction in heart rate that gradually recovered over time. Mean heart rate was significantly lower in the hypoxia-exposed animals throughout the exposure period (MANOVA $P < 0.001$), although individual animals would briefly elevate their heart rate back to control levels or even higher when surfacing to breath air (modified from Nelson et al. 2007).

similar to that for carp (*Cyprinus carpio*) at 15°C (Stecyk and Farrell 2002), where a reduction in f_H is somewhat compensated for by increases in stroke volume. Reimmersion of emergent, air-breathing *Lipophrys* could be considered a descent into hypoxic conditions and does result in a transient 37% bradycardia, but this is followed almost immediately by a 15% tachycardia that is sustained for at least 10 min (Laming et al. 1982).

The precepts of ventilation–perfusion matching dictate that inflation of the ABO by air-breathing fish in hypoxic water should produce an increase in cardiac output coincident with diversion of blood to the ABO (Johansen 1970). This is often, but not universally, manifest by an immediate post-breath tachycardia in air-breathing fishes (Table 6.5 in Graham 1997). The only pre- and post-breath heart rates published for hypoxic GAB fishes are for loricariids. Nelson et al. (2007) report an average 34% increase in heart rate immediately post-breath in *Hypostomus*, similar to the 32% air-breath tachycardia reported by Graham (1983) for the co-familiar *Ancistrus*. Nelson

et al. (2007) also report a large individual variance in post-air-breath tachycardia that was somewhat related to an animal's predilection to breath air. Interestingly, emersion from normoxic water produces a transient bradycardia in the GAB blenny, *Lipophrys* (Laming et al. 1982; Pelster et al. 1988).

5.5. Blood Chemistry of Gut Air-breathing Fishes

Perhaps the most heavily studied aspect of air-breathing fish physiology is the properties of their hemoglobins. Thus, the literature is replete with blood chemistry information, often collected at one time of the year at a single location (e.g. Powers et al. 1979). These types of measurements are often the basis for speculation about the action of natural selection on hemoglobin, but as Graham (1997) points out, without standardized collection conditions or methodology for analyzing hemoglobin, the foundations on which these adaptive scenarios are built perhaps are weak or non-existent. Wells (1990) also provides cautionary evidence against painting adaptive scenarios based upon differences in hemoglobin amount or properties. Graham (1997) provides an extensive review of the blood chemistry of all air-breathing fishes, for which, in this case, much of the information comes from GAB fishes.

From an oxygen transport perspective, there are two major issues for the blood of a GAB fish. First, there is the problem of venous admixture with the (presumably saturated) blood leaving the ABO (Fig. 10.2) and, second, there is the potential loss of O₂ to hypoxic water at the gills (Section 4). The amphibious blenny *Lipophrys* (Blenniidae) or any other GAB fish that emerses has the additional challenge of CO₂ accumulation. The blood of GAB can be generally characterized as having a moderate to low P₅₀ with coincident low erythrocyte [NTP] (Powers et al. 1979; Graham 1997; Marcon et al. 1999). However, since many of the GAB fishes acclimatize/acclimate to hypoxia by increasing blood oxygen affinity at least partially through reductions in erythrocyte [NTP] (Graham 1983, 1985; Wilhelm and Weber 1983; Val et al. 1990), reported values will be heavily dependent on the environmental conditions at the time of collection. The high-oxygen-affinity blood may be associated with the general occupancy of hypoxic habitats by these fishes, but is in contrast to the hypothesis that air-breathing fish should have reduced blood oxygen affinity. Riggs (1979) summarized the extensive data set from the second 1976 *Alpha Helix* expedition and concluded that there was no evidence for a right shift in the blood oxygen equilibrium curves of air-breathing fishes, although Morris and Bridges (1994) expanded that data set and provide some modest evidence for a right shift across all measured air-breathing fish.

The blood of GAB fishes can be further generalized as having a moderate to strong Bohr effect and no Root effect (Focesi et al. 1979; Powers et al. 1979; Bridges et al. 1984). The Bohr effect would seem maladaptive, at least in the case of one GAB loricariid *Liposarcus*, which appears not to tightly regulate their plasma pH in the face of hypercarbic acidosis (Brauner et al., 2004); in this case, the Bohr effect would exacerbate both the desaturation of hemoglobin in ABO effluent and the potential loss of O₂ to hypoxic water during gill transit by blood under acidotic conditions. The general absence of a Root effect in the GAB fishes would seemingly support the swim bladder inflation function of this property as GAB fishes generally have reduced swim bladders and swim bladder function (Gee 1976; Schaefer and Lauder 1986).

The blood of GAB fishes can also be characterized, with the exception of the amphibious *Lipophrys* (Bridges et al. 1984), as having a high volume of erythrocytes (hematocrit; Hct) with a coincident high blood hemoglobin concentration ([Hb]) (Graham 1997). These values are also subject to hypoxia acclimation/acclimatization in some loricariids (Graham 1983, 1985; Val et al. 1990) although Graham (1985) also demonstrated a lack of [Hb]/Hct acclimation in one callichthyid (*Hoplosternum*) and one loricariid (*Loricaria*). Interestingly, Sloman et al. (2009) show that there was no relationship between blood [Hb] or Hct and surfacing behavior in a species of *Hoplosternum*. Fernandes et al. (1999) and Nelson et al. (2007) show that changes in blood erythrocytic content begin almost immediately upon hypoxia exposure in *Hypostomus*. *Hypostomus regani* exposed to three hours of hypoxia or eight hours of graded hypoxia were characterized by having significantly higher [Hb] and smaller erythrocytes that contained more hemoglobin per erythrocyte than normoxic animals (Fernandes et al. 1999; Nelson et al. 2007). This result is most likely due to the hypoxic animals releasing a store of erythrocytes to enhance oxygen transport because the time is too short for new erythrocyte production. Val et al. (1990) also reported a higher cell hemoglobin concentration in another loricariid exposed to hypoxia for 30 days or captured from hypoxia-prone habitats. However, Weber et al. (1979) reported cell swelling and decreased cell hemoglobin concentrations in loricariids exposed to hypoxia for 4–7 days, suggesting that there may not be a generalized loricariid or GAB blood chemistry response to hypoxia or that stress interacts to differential degrees with hypoxia in laboratory settings. Although most of the GAB fishes carry multiple forms of hemoglobin, there is presently no evidence that air-breathing fishes generally adjust the relative expression of various hemoglobin isoforms in response to hypoxia or air breathing (Almeida-Val et al. 1999).

6. BEHAVIORAL ECOLOGY OF GUT AIR BREATHING

Considering the stochasticity of oxygen availability in most of the environments occupied by GAB fishes (Section 1), it is not unreasonable to assume that most of the ecology and behavior of these organisms will be influenced by environmental oxygen availability (Kramer 1987), yet experimental verification is mostly lacking. Predator–prey dynamics are undoubtedly a function of environmental $[O_2]$ whether a fish is a water, air or bi-modal breather (Domenici et al. 2007). The increased aquatic ventilation required in hypoxic habitats (Section 5.1.2) will increase an animal's energetic requirements and potentially its detectability by both potential predators and prey. Certainly, the diminished scope for activity under hypoxia (Chabot and Claireaux 2008) could compromise predator–prey performance; however, the diminished feeding activity and scope for growth in hypoxic water (Chabot and Claireaux 2008) may be just as important on a different time scale.

The evolution of air breathing solved some of these problems for GAB fishes, but opened up several new ones (Kramer 1987). Air breathing could expose animals to a new class of aerial predators. In a direct test of this hypothesis, Kramer et al. (1983) showed that air-breathing fishes (one GAB fish) were more vulnerable to predation from a green heron (*Butorides striatus*) when forced to breath air than were water-breathing fishes under similar conditions. Kramer and McClure (1980) offer some evidence that an hypoxic GAB fish (*Corydoras*) is less likely to surface the deeper they reside and Power (1984) provides evidence from the field that GAB loricariids will avoid shallow waters where they are vulnerable to avian predation despite an abundance of food. These results, coupled with observations of synchronized air-breathing behavior in several GAB fishes (e.g. Gee and Graham (1978), Kramer and Graham (1976) and Sloman et al. (2009) for *Hoplosternum*; Kramer and Graham (1976) for *Ancistrus*) suggest that the evolution of gut air breathing may be associated with anti-predator behaviors to compensate for the increased visibility to surface predators or to aquatic predators that are potentially more adept at detecting and capturing an animal while surfacing, or both. Indeed, many GAB fishes have adopted a nocturnal lifestyle where they are less likely to be visible to visual predators when most active. Boujard et al. (1990) demonstrate nocturnal maxima of activity, feeding and air breathing in *Hoplosternum* that very quickly tracked experimental changes to the timing of the daylight cycle. Likewise, MacCormack et al. (2006) report only nocturnal surfacing (presumably air-breathing) behavior in the loricariid (*Glyptoperichthyes*) telemetered and held in cages in a natural environment.

Considering the potential interactions between digestive and respiratory function when the gut is used for both (Section 2.2), there is surprisingly little information on the partitioning between feeding activity and aerial respiration in GAB fishes. Persaud et al. (2006b) found that two callichthyids would stop eating when denied access to air and propose that air breathing is essential to move digesta through the poorly muscled hindgut. Presumably air pressure is also used to propel sperm caudally in the *Corydoras* (Callichthyidae) that fertilize their eggs by ingesting sperm (Kohda et al. 1995). Nelson et al. (2007) found no predilection between fed or starved *Hypostomus* to breath air or any differences between fed and unfed animals in other physiological parameters upon hypoxia exposure. Kramer and Braun (1983) report that air-breathing frequency after feeding in *Corydoras* (Callichthyidae) is variably dependent on P_wO_2 . Above 50% saturation there was a decrease in air-breathing frequency after feeding whereas at a P_wO_2 of 44 mmHg there was no change and at a P_wO_2 of 24 mmHg there was an increase in air-breathing frequency (Kramer and Braun 1983). Certainly our understanding of how GAB fishes balance their digestive and respiratory gut functions is in its infancy.

7. AMMONIA VOLATILIZATION BY THE GI TRACT

Most fish are ammonotelic, that is, they excrete waste nitrogen as molecular ammonia or ammonium ion (NH_4^+). This is the least energetically costly method of nitrogen excretion and in circumneutral waters of low $[NH_3]$ is thought to occur largely by passive diffusion of NH_3 to the water aided by diffusional trapping of NH_3 as NH_4^+ through acidification of the surface boundary layer (Moreira-Silva et al. 2010). This mechanism of nitrogen excretion is no longer available to animals that emerge or inhabit waters of high $[NH_3]$ where the diffusive gradient would be lowered or reversed. Thus, amphibious fishes have adopted a variety of strategies to tolerate higher body $[NH_3]$, reduce endogenous NH_3 production, develop alternative modes of NH_3 excretion or employ various combinations of these strategies (Ip et al. 2004). One alternative mechanism of NH_3 excretion that has been demonstrated in emersed fish is the release of NH_3 gas to the atmosphere, or ammonia volatilization (Frick and Wright 2002; Tsui et al. 2002). Tsui et al. (2002) show a progressive increase in NH_3 volatilization with time of emersion in *Misgurnus*. They conclude that volatilization is occurring in the gut because NH_3 volatilization ceased in animals that were not allowed access to the surface and because emersed and NH_3 -exposed fish had a significantly more alkaline anterior intestine than controls (Tsui et al. 2002). This would be

an exciting new function for the gut of air-breathing fishes and might help explain the frequent evolution of GABOs (Section 2.1). Unfortunately, this finding has yet to be confirmed by other investigators and since Moreira-Silva et al. (2010) also demonstrate a significant increase in the membrane fluidity of gills in emersed *Misgurnus* that would aid in NH_3 loss to the atmosphere, the role of the gut in NH_3 excretion clearly represents an interesting area for further studies.

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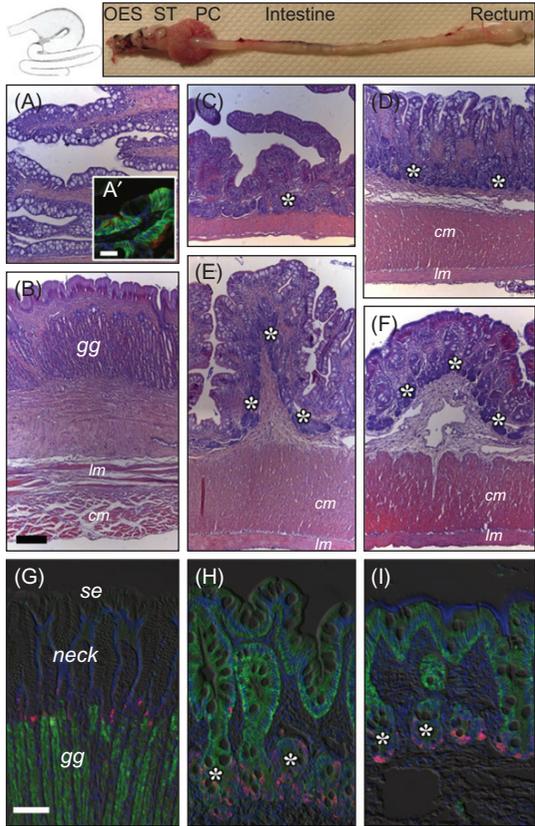


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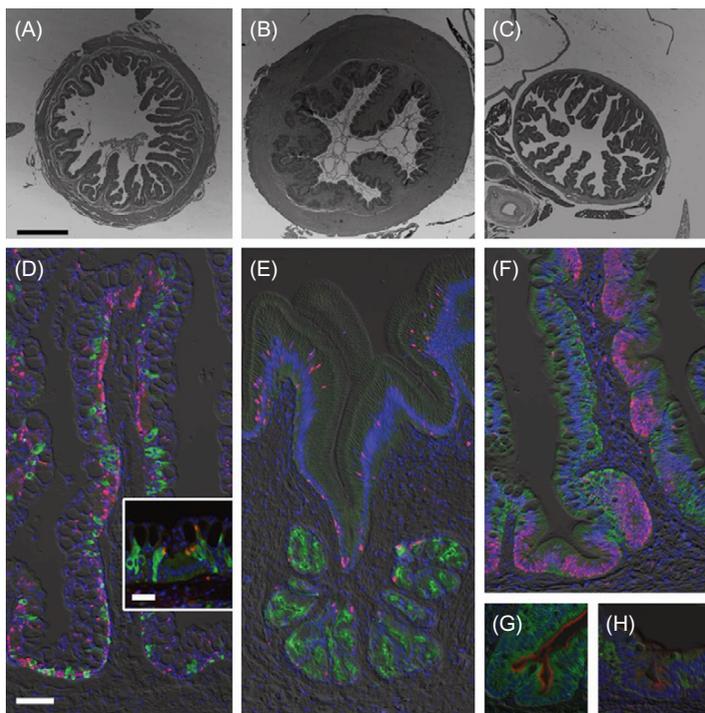


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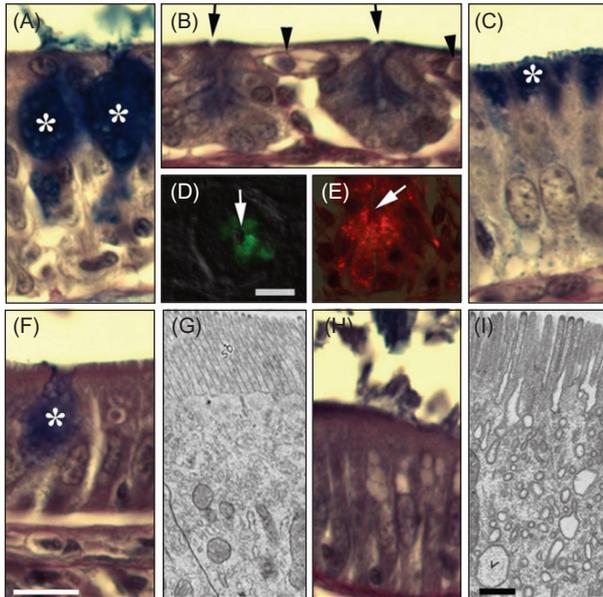
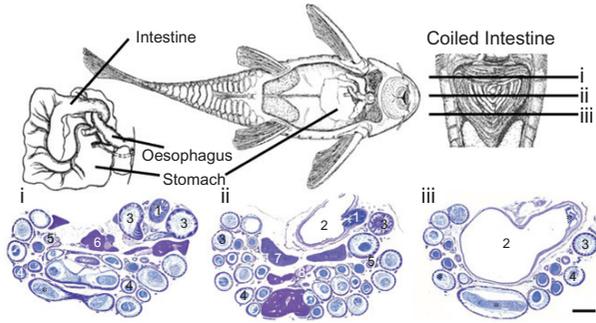


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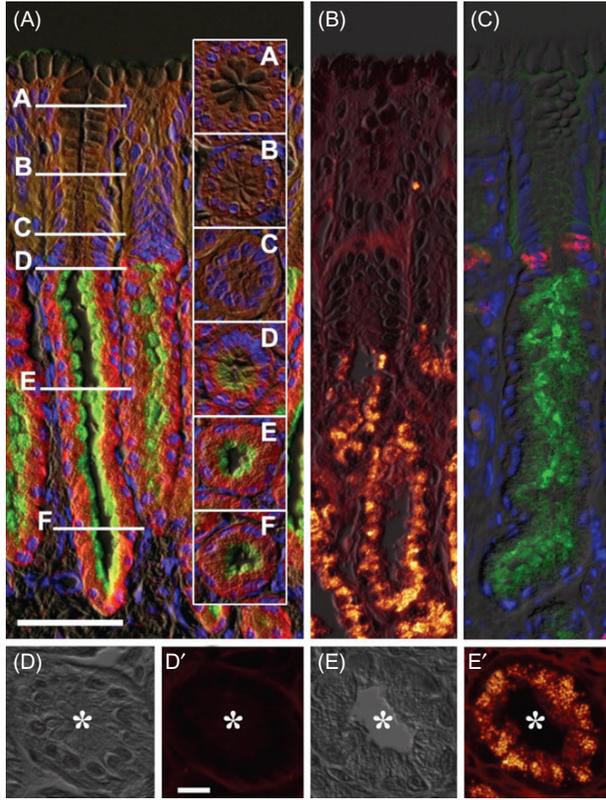


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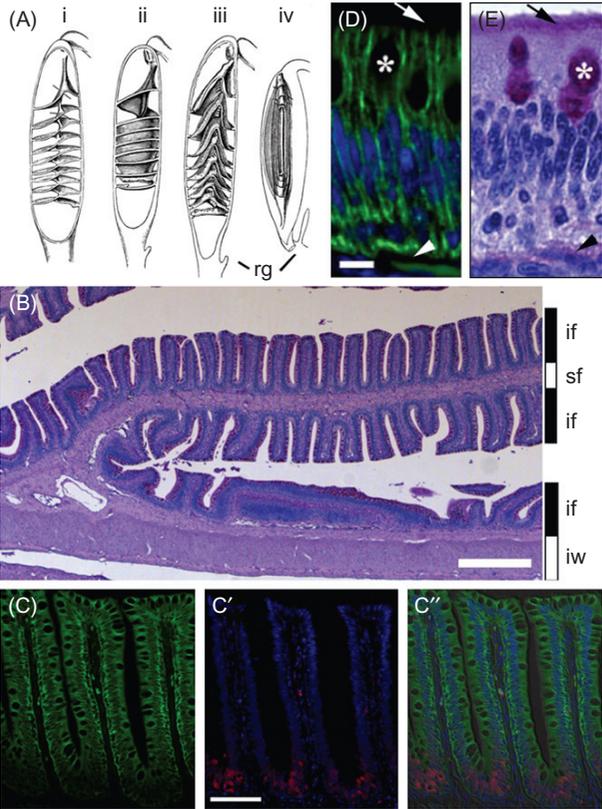


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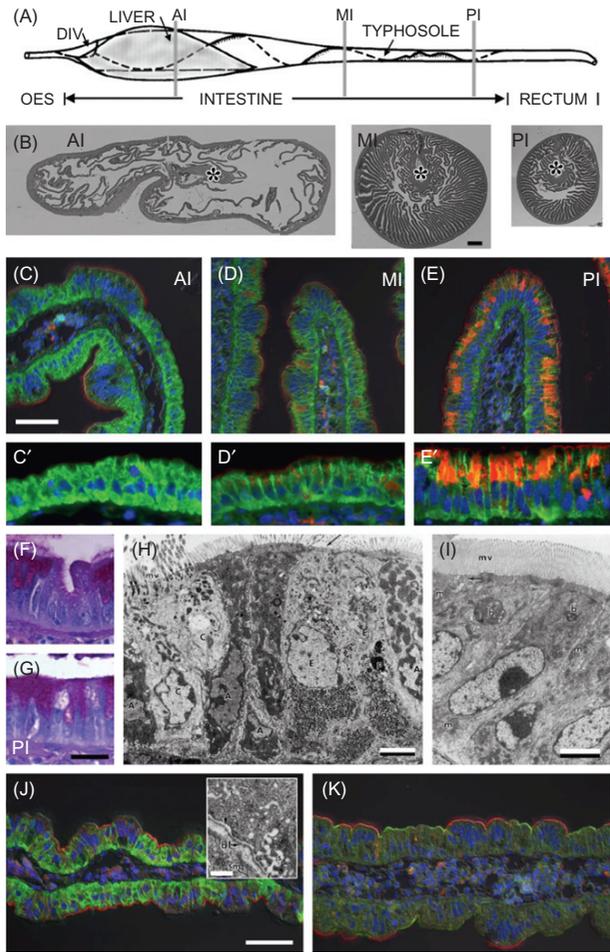


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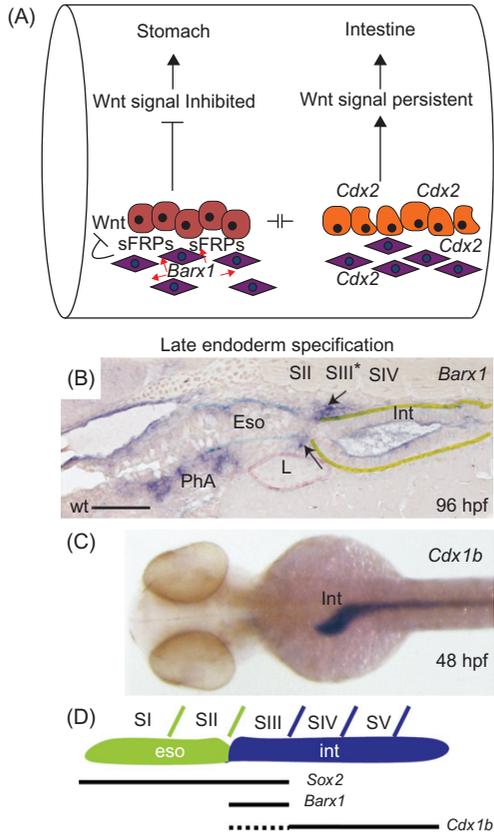


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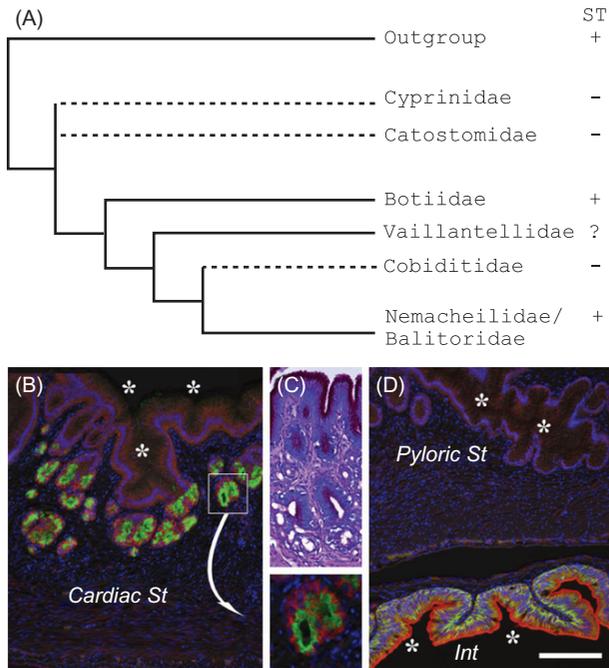


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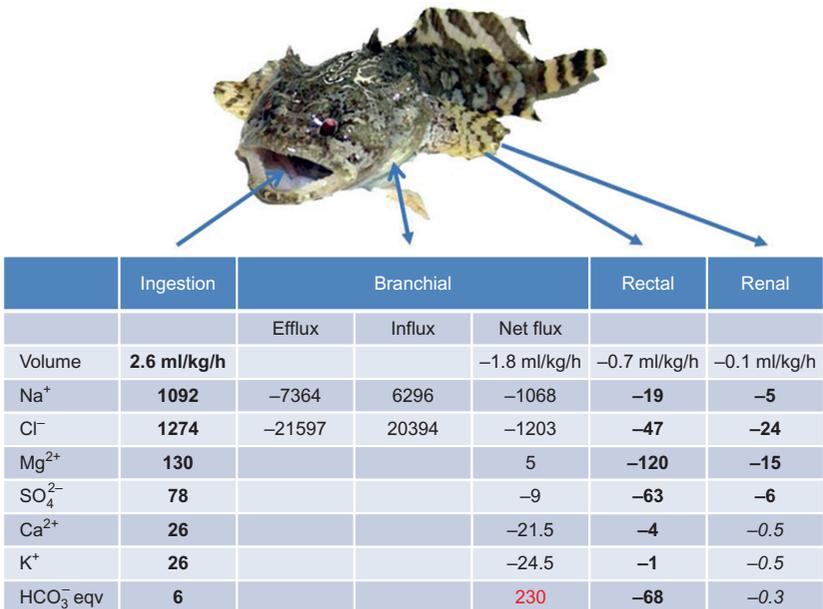


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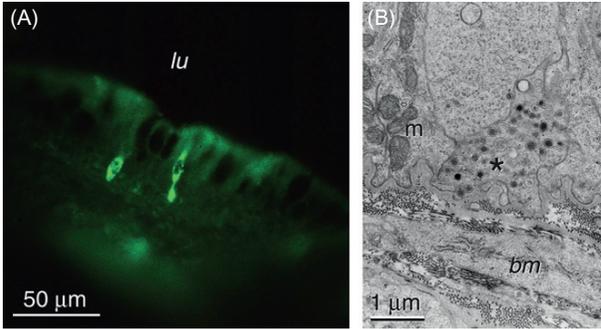


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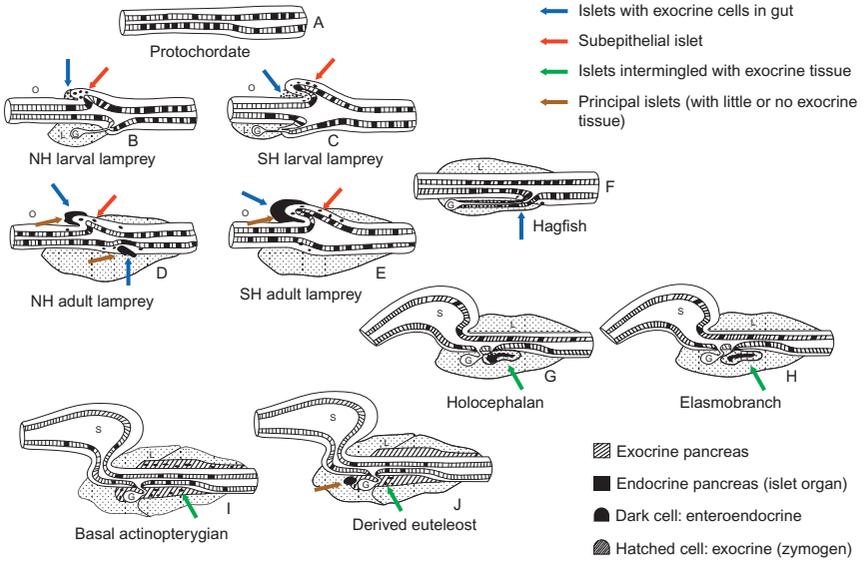


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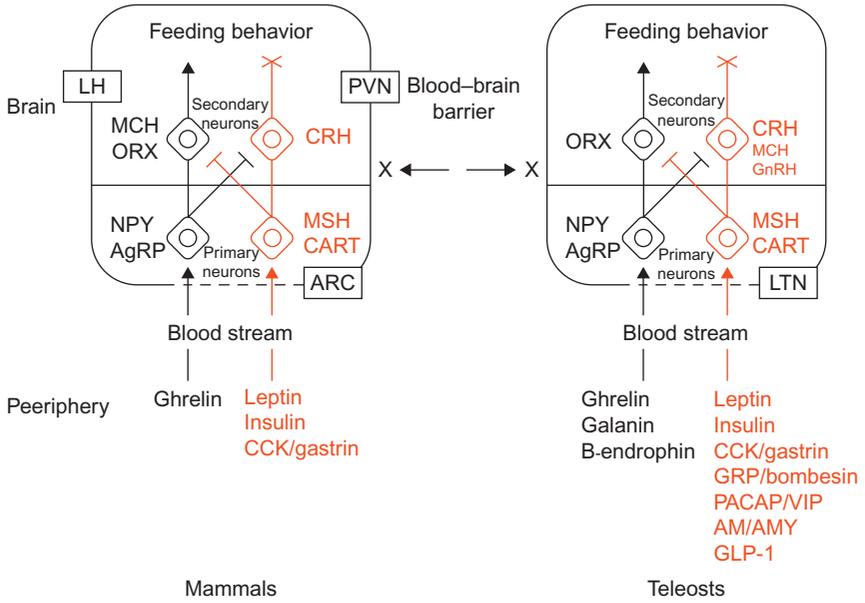


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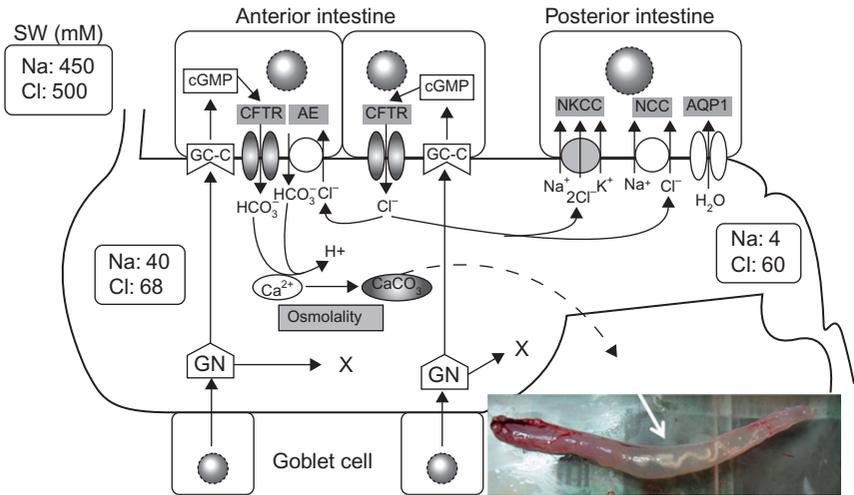


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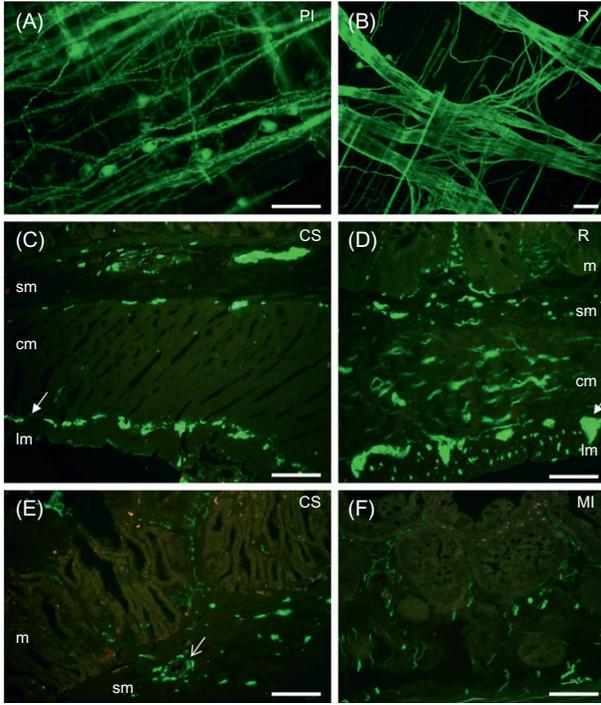


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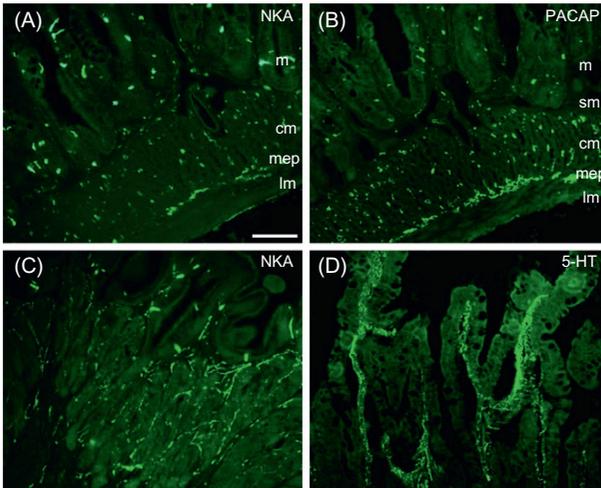


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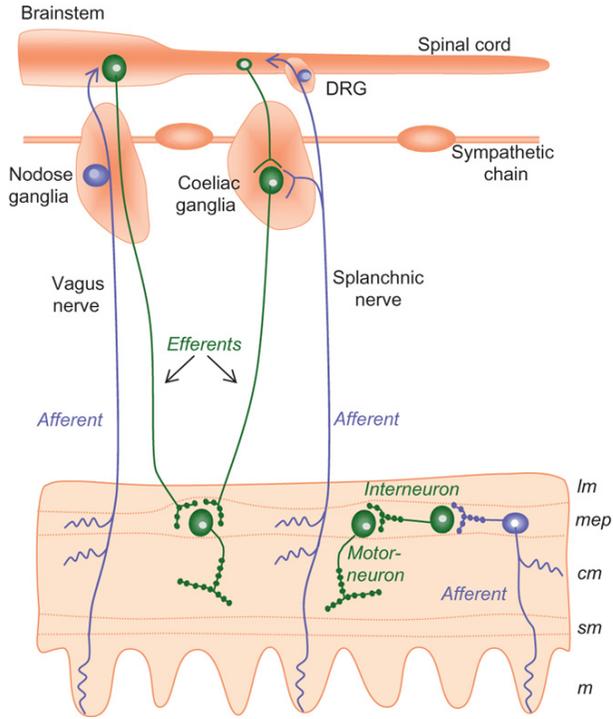


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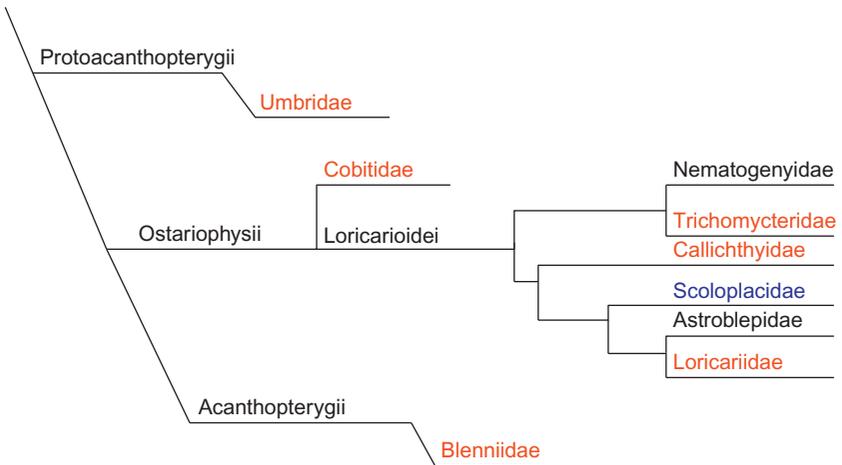


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