Air breathing fish

Unit-I, Zoo-301

By

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What Constitutes Fish Air Breathing?

- An air-breathing fish may swim to the water surface, gulp air and then dive, or it may crawl onto land and either gulp air or passively exchange gases with the atmosphere across several exposed respiratory surfaces.
- Air breathing is one of several adaptive responses utilized by fishes dwelling in habitats where 0_2 supplies may be severely depleted.
- Others are behavioral avoidance of hypoxic areas, which in some cases may include a seasonal migration or aquatic surface respiration (ASR), in which a fish swims up to ventilate its gills with the thin layer of air-saturated surface water
- fish in hypoxic water instinctively swam to shallower water and eventually to the surface itself to obtain more 0_2 by ASR.

Different Natural Fish Activities Likely Associated with Aerial Respiraton, with Selected Examples of Genera or Families Fitting Each Category

I. Leaving water
   A. Crawling on land to migrate, feed, find a mate, burrow, defend a territory, avoid turbulence
      1. Many amphibious species: *Periophthalmus, Mnierpes, Gobionellus, Andamia, Alticus*
      2. Some freshwater species are amphibious or migrate: *Hoplerythrinus, Monopterus, Synbranchus, Anabas, Clarias, Anableps, Rivulus*, and some *Fundulus*
      3. Some intertidal marine species emerge from hypoxic water: *Blennius, Clinocottus, Helcogramma*
   B. Laying eggs above the water line
      1. Freshwater: *Brycon, Copella*
      2. Marine: *Leuresthes, Hubbesia* (only females emerge), *Mallotus* (some populations)
   C. Tolerating air exposure
      1. During low tide: *Tomicodon, Anoplarchus, Xiphister, Apodicthys* and others
      2. During the dry season: *Monopterus, Protopterus, Mastacembelus, Clarias* and others
      3. Surviving in the stalls of a tropical fish market: various species
   D. Flying through air
      1. Freshwater: *Gastropelecus*
      2. Marine: *Cypselurus, Exocetus*

II. Gulping air at the surface
   A. Nearly all species with physostomous gas bladders : Clupeidae, Cyprinidae
   B. Bottom or demersal fish in hypoxic water: *Achirus* (possibly aquatic surface respiration, ASR)
   C. During surface feeding: *Poecilia, Mugil*
   D. During ASR: *Cyprinus, Carassius*, some Gobiidae and Eleotrididae

Types of air breathing fishes

Classification of Air-Breathing Fish **Types Based** on Behavior and Factors Affecting Respiration, with Selected Examples for Each **Group**

I. Amphibious air breathers
   A. Active on land (volitional exposure): *Periophthalmus, Mnierpes, Entomacrodus, Andamia*
   B. Inactive on land (enforced exposure)
      1. Endure brief exposure: *Tomicodon, Blennius, Xiphister, Pholis*
      2. Estivators: *Protopterus, Synbranchus, Mastacembelus*

II. Aquatic air breathers
   A. Facultative: *Ancistrus, Hypostomus*
   B. Continuous
      1. Obligatory: *Arapaima, Anabas*
      2. Non-obligatory: *Hoplosternum, Piabucina, Erythrinus*

Amphibious Air Breathing

- These fish breathe air mainly during the periods they are out of water. They emerge from water for various reasons: to feed, rest, orientate, escape predators, and even court and hold territories.
- Amphibious air breathers are mainly found in the littoral zones of marine habitats. Many of these (e.g., mudskippers, *Periophthalmus*) are highly active on land whereas others appear to endure air exposure while stranded during low tide and awaiting the return of water.
- become amphibious air breathers when they are stranded by the disappearance of habitat water, as commonly occurs in certain areas during the tropical dry season.
- These fishes often become confined in mud burrows until rains come, and to endure low water conditions as well as the absence of food, they enter hypometabolic or even estivating states.

Amphibious Air Breathing

- These fish, which remain in water and surface periodically to gulp air, are divided into two air-breathing types: facultative and continuous.
- Facultative air breathers do not normally breathe air in normoxic water but need to adopt this mode when exposed to conditions unfavorable for aquatic respiration (hypoxia, hypercapnia) or in response to increased 02 requirements (as a result of changes in water temperature or activity).
- Continuous air breathers take air breaths at more or less regular (but not highly predictable) intervals, at all times, and under all aquatic conditions from hyperoxia to hypoxia.

Amphibious Air Breathing

- Continuous air breathers take air breaths at more or less regular (but not highly predictable) intervals, at all times, and under all aquatic conditions from hyperoxia to hypoxia.
- Their frequency of air breathing is regulated by factors affecting their need for aerial 02 such as aquatic hypoxia, water temperature, and activity level, although the use of inspired gas for buoyancy and digestive functions may also be important.
- Continuous air breathers can be further separated into two types: obligatory and non-obligatory
- Obligatory air breathers are not able to survive on the quantity of 02 obtained by aquatic respiration, even in normoxic water, and thus always need supplemental aerial oxygen.
- By contrast, non-obligatory, continuous air breathers do not require air breathing to survive while in normoxic water.

Classification of Fish Air-Breathing Organs

A. Lungs and Respiratory Gas Bladders of the More Primitive Bony Fishes

Lungs

Protopterus, Lepidosiren, Neoceratodus, Polypterus, Erpetoichthys

Respiratory Gas Bladders

Lepisosteus, Atractosteus, Amia, Arapaima, Heterotis, Pantodon, Gymnarchus, Notopterus, Papyrocranus, Xenomystus, Megalops, Phractolaemus, Erythrinus, Hoplerythrinus, Lebiasina, Piabucina, Pangasius, Gymnotus, Umbra

B. Air-Breathing Organs of the More Advanced Teleosts

Organs in the Head Region

Buccal and Pharyngeal Epithelial Surfaces

Electrophorus, Hypopomus, Sicyases, Alticus, Mnierpes, Entomacrodus, Periophthalmus, Periophthalmodon, Boleophthalmus, Scartelaos, Gillichthys, Channa, Monopterus, Synbranchus, Ophisternon, Blennius, Gobius

Branchial and Opercular Epithelial Surfaces

Mudskippers, *Pseudapocryptes*, Synbranchidae

Pouches Formed Adjacent to the Pharynx

Channa, Monopterus

Branchial Diverticulae

Heteropneustes, Clarias, Anabantoids

Gills

Hypopomus, Mnierpes, Synbranchus, Mastacembelus

Organs Located along the Digestive Tube

Pneumatic Duct

Anguilla

Esophagus

Dallia

Stomach

Loricariidae, Trichomycteridae

Intestine

Cobitididae, Callichthyidae

C. Skin

Erpetoichthys, Anguilla, Misgurnus, Clarias, Heteropneustes, Electrophorus, Neochanna, Xiphister, Sicyases, Mnierpes, Alticus, Coryphoblennius, Blennius, Periophthalmus, Boleophthalmus, Dormitator, Mastacembelus, Macrognathus, Monopterus, Synbranchus, Ophisternon

T Y P E S O F
AIR-BREATHING ORGANS

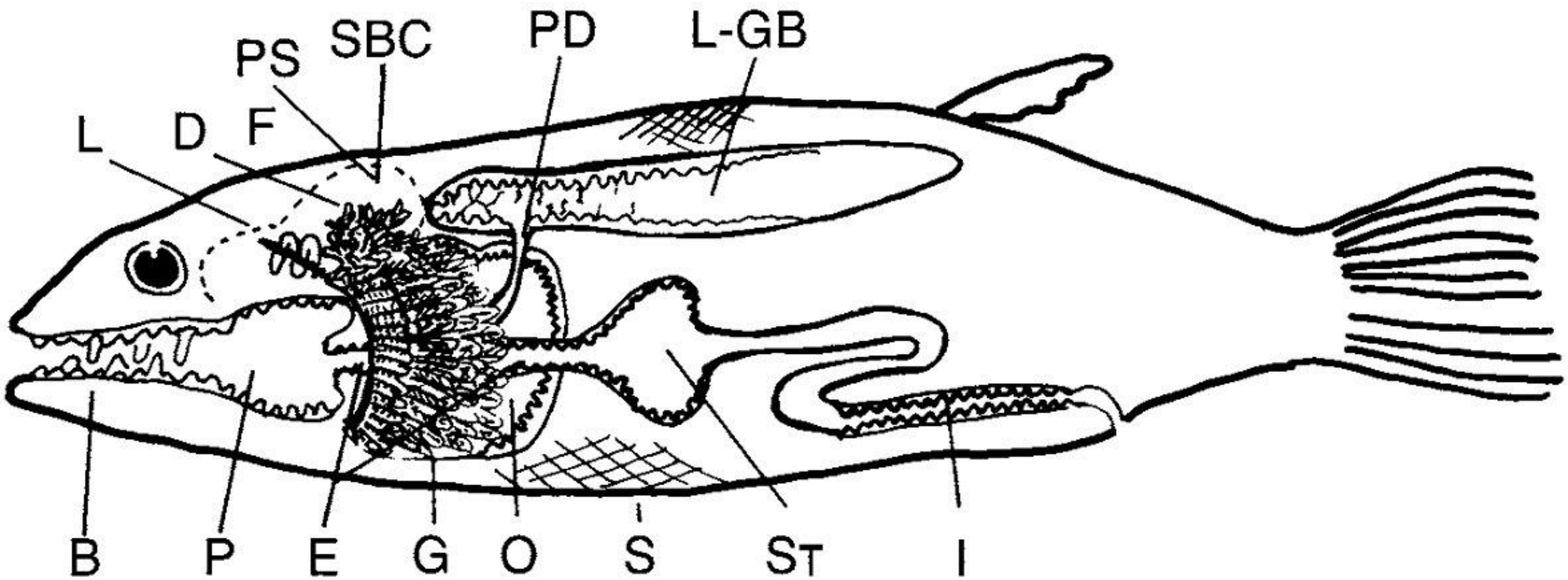


FIGURE Generalized air-breathing fish *"Aerorespirichthys"* illustrating the ABOs presently known, including: Modified epithelial surfaces in the buccal (B), pharyngeal (P), esophageal (E), and opercular (O) chambers, as well as the gills (G), skin (S), stomach (ST), and intestine (I). Modified spaces include, the suprabranchial chamber (SBC), or pharyngeal sacs (PS). Modified chambers include the pneumatic duct (PD), and the lung or respiratory gas bladder (L-GB). Projections into these spaces include the labyrinth (L), dendrites (D), and gill fans (F).

T Y P E S O F
AIR-BREATHING ORGANS

- Three categories based on structure, position, and degree of development
- I. Derivatives of the digestive tube including
- a. the lung and physostomous gas bladder (Physostomous swim bladders are directly connected to the gastrointestinal tract so that fish with these swim bladders, such as herrings, must “gulp” air to inflate their swim bladder and “burb” or “fart” air to deflate them.) having a respiratory function and other sections of the digestive tube including the esophagus, pneumatic duct, stomach, and intestine.

T Y P E S O F
AIR-BREATHING ORGANS

- Three categories based on structure, position, and degree of development
- II. Areas in and near the head, such as the buccal, pharyngeal, and opercular chambers having a dense covering of respiratory epithelium and, in most cases, an enhanced surface area, due to either or both an added chamber volume and the projection into it of branchial-arch extensions having a covering of respiratory epithelium.
- III. Other organs such as the gills and skin having structural the structural modifications promoting aerial gas exchange.

T Y P E S O F
AIR-BREATHING ORGANS

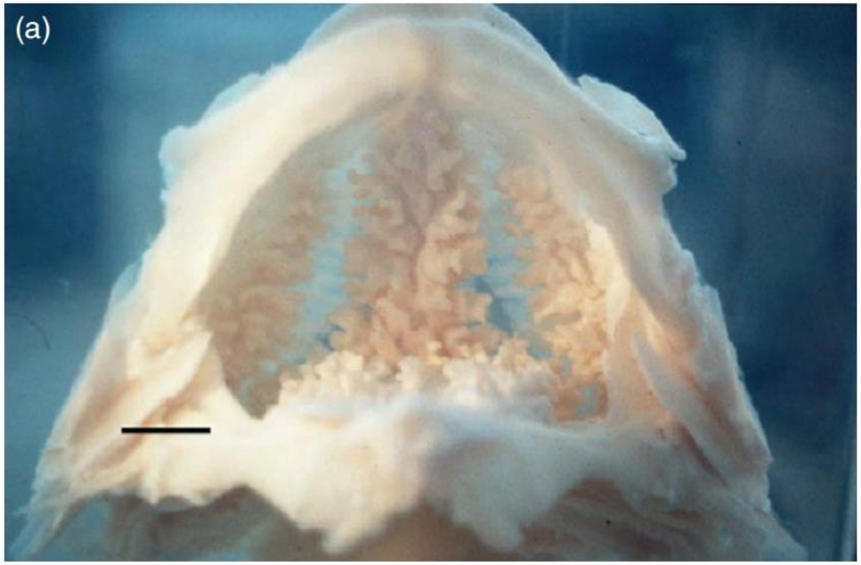
- LUNGS AND RESPIRATORY GAS BLADDERS
- Common features between these organs are-
- Embryonic origin as a small outpocketing from the ventral wall of the alimentary canal that persists and gives rise to ventrally positioned (i.e., closer to the ventral body wall) and paired organs
- The presence of a valvular glottis in the floor of the alimentary tract that guards the entrance to the lung
- The presence of a pulmonary circulation (i.e., afferent and efferent vessels leading more or less directly from the heart to the lungs and returning,

T Y P E S O F
AIR-BREATHING ORGANS

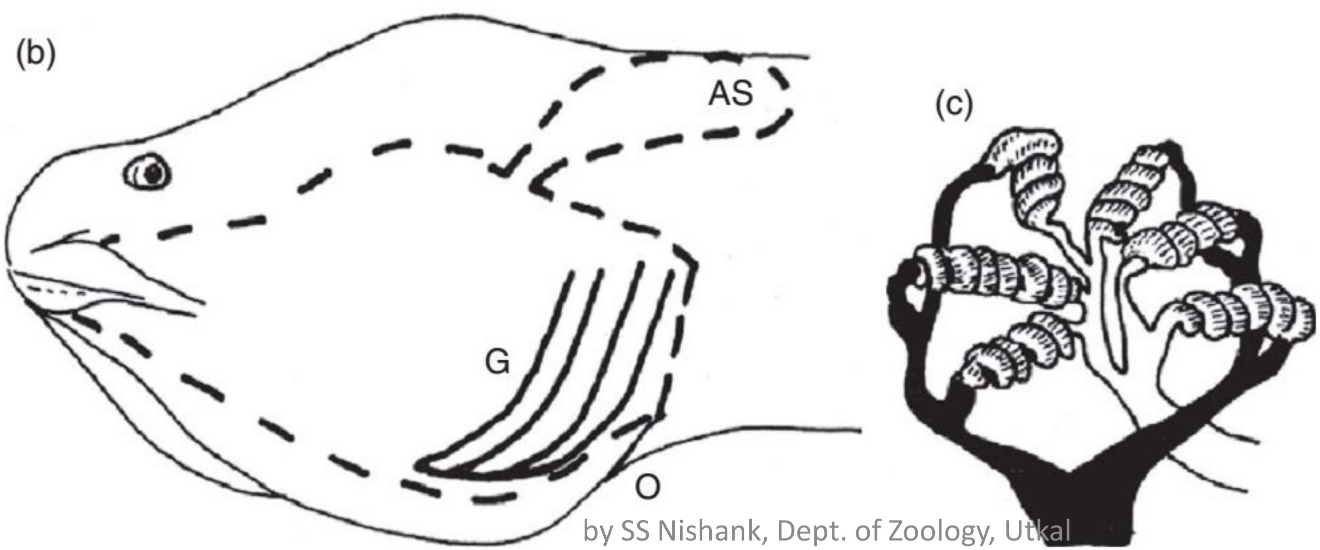
- LUNGS AND RESPIRATORY GAS BLADDERS
- Gas bladders by contrast:
- Have an embryonic origin from the side or dorsal aspect of the alimentary canal, occur higher in the body (for vertical stability in water), and are not paired
- Do not always have a glottis and may or may not retain an open pneumatic duct
- In most cases, receive blood in parallel with the systemic circulation and thus lack a specialized circulatory loop functionally equivalent to a pulmonary circulation

T Y P E S O F
AIR-BREATHING ORGANS: ABO in Head region

- large buccopharyngeal chamber volumes, reduced gills, an extensive respiratory epithelium covers nearly the entire interior of its mouth, from the jaw to the pharynx, and also covers the branchial arches and the inner walls of the operculum (e.g. *Electrophorus electricus* see figure)
- All of air-breathing gobies hold air in their mouths. *Gillichthys mirabilis* is both a facultative and amphibious air breather. It has vascular surfaces on the roof of its mouth and tongue. (All four mudskipper genera (*Periophthalmus,Periophthalmodon, Scartelaos, and Boleophthalmus*,)

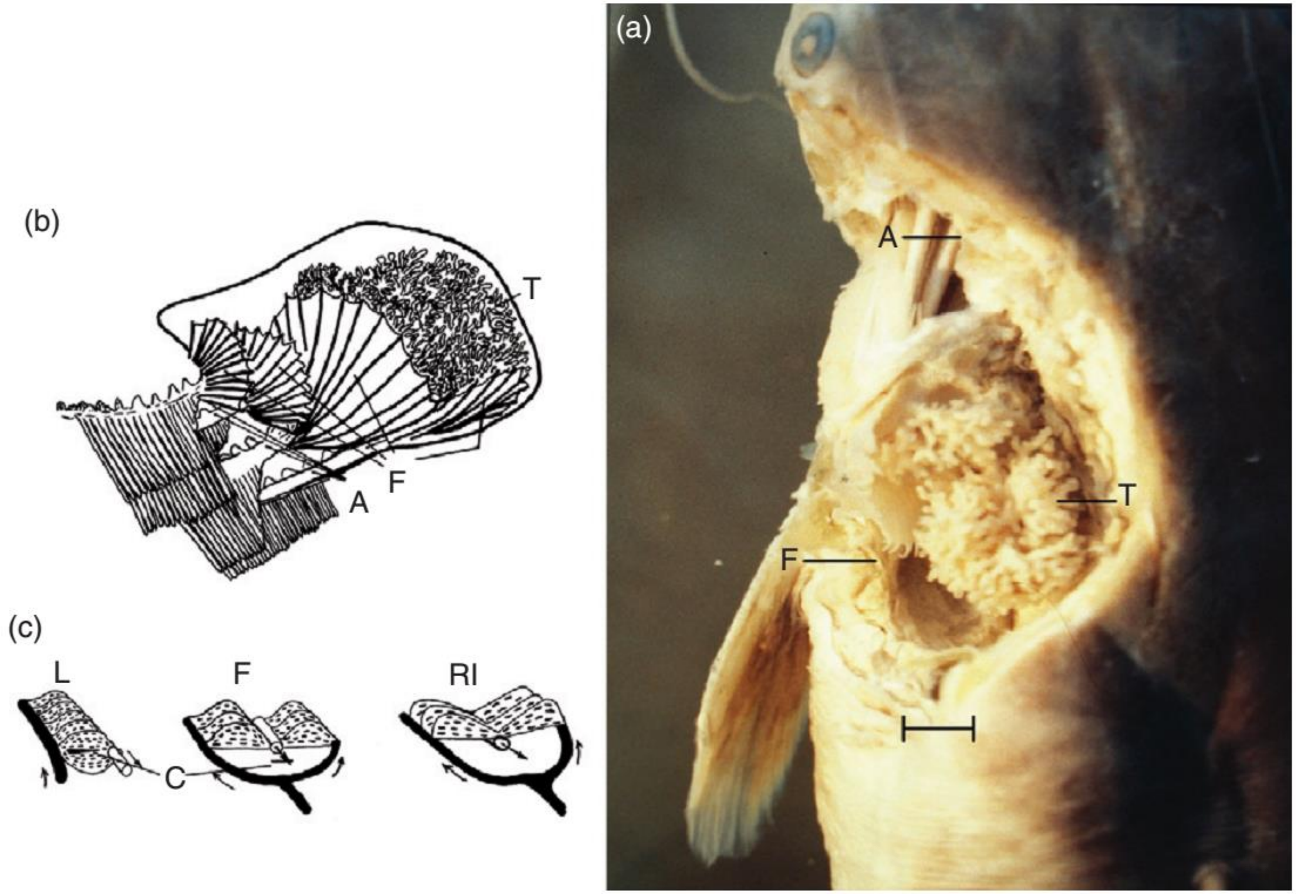


(a) Dorsal view of the lower jaw epithelium of *Electrophorus electricus*. Scale = 1 cm. (b) Side view of Monopterus cuchia with inflated ABO showing relative positions of the branchial chamber air sacs (AS), gill arches (G), and the position of the reduced opercular opening (O). (c) Capillary rosette detail.

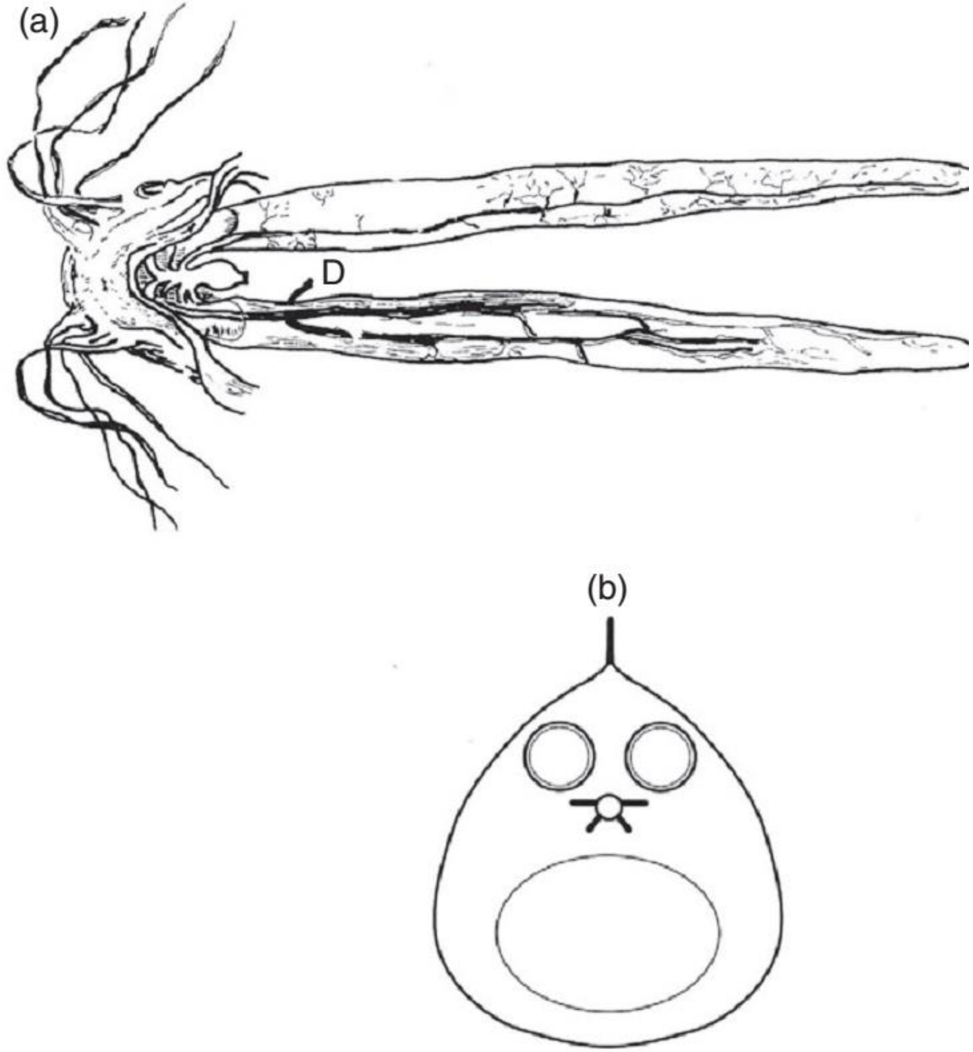


T Y P E S O F
AIR-BREATHING ORGANS: Suprabranchial Chambers

- A sac or space extending from the top of the branchial chamber, the suprabranchial chamber (SBC), enhances the ABO volume and surface area.
- In catfish genera, *Clarias, Heterobranchus,* and *Dinotopterus* paired SBCs extending from the skull to beyond the pectoral girdle. In addition, gill filaments at the dorsal end of all four gill arches are fused to form fans that partially seal the lateral side of the SBC and serve as valves for ventilation. (see Fig. 7)
- The Indian catfish (*Heteropneustes fossilis*) also has large, paired SBCs bordered by gill fans. SBC area is expanded by paired tubes that extend into the body musculature to a distance of about one-half body length. The respiratory epithelium covering the SBC and the inner surface of the fans are also formed by modified gill lamellae. Contraction of musclesheets surrounding the SBC projections causes exhalation (Fig 8).



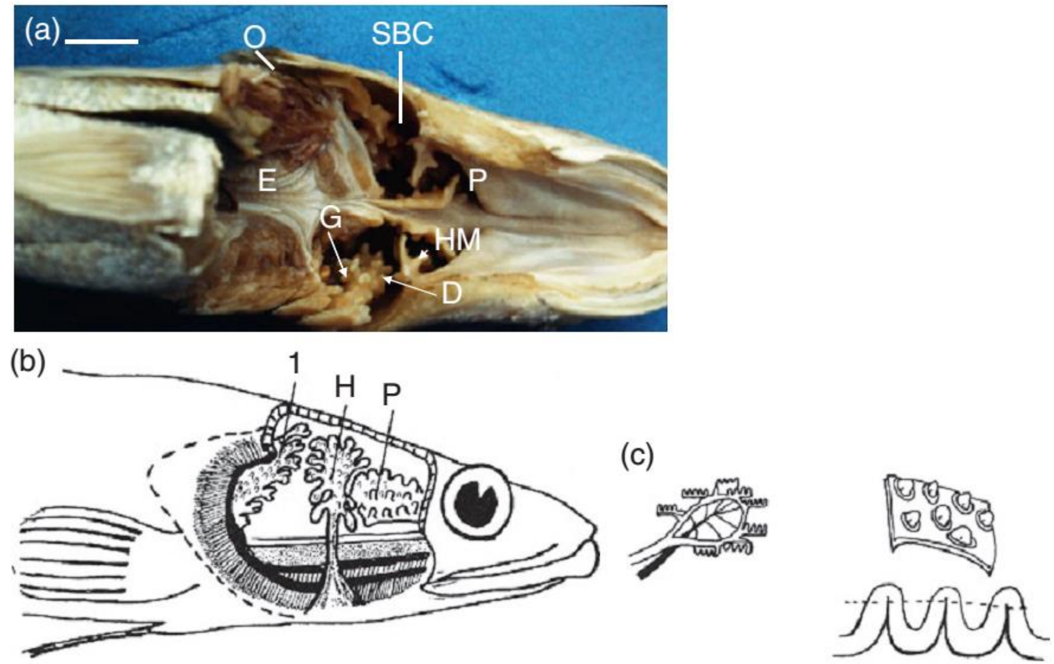
(a) Dorsal view of the SBC of a 35-cm *Clarias gariepinus* showing the two respiratory trees (T), gill fans (F), and gill arches (A). Scale = 2 cm. (b) Side view of the same features. (c) Probable stages in the transition of clariid gill lamellae (L) into gill fans (F) and the respiratory epithelium rows occurring on the dendrites, fans, and SBC walls.



(a) Modified drawing of the SBC of *Heteropneustes fossilis* made by J. Hyrtl in 1854. (b) Transverse body section showing air-sac penetration into the body myotomes.

T Y P E S O F
AIR-BREATHING ORGANS: Suprabranchial Chambers

- In Anabas testudineus, the large, paired SBCs extend from behind the eye to the pectoral girdle. Protruding into each is the labyrinth, a bony element formed by the epibranchial of gill arch 1. The respiratory epithelium covering the labyrinth and the SBC forms parallel rows of capillaries having ring-shaped endothelial cells.
- In *Channa micropeltes* the vascular structure of respiratory epithelium covering SBC forms islets, featuring rosettes of spiraling capillary loops, different segments of which emerge into the ABO (Fig. 10)



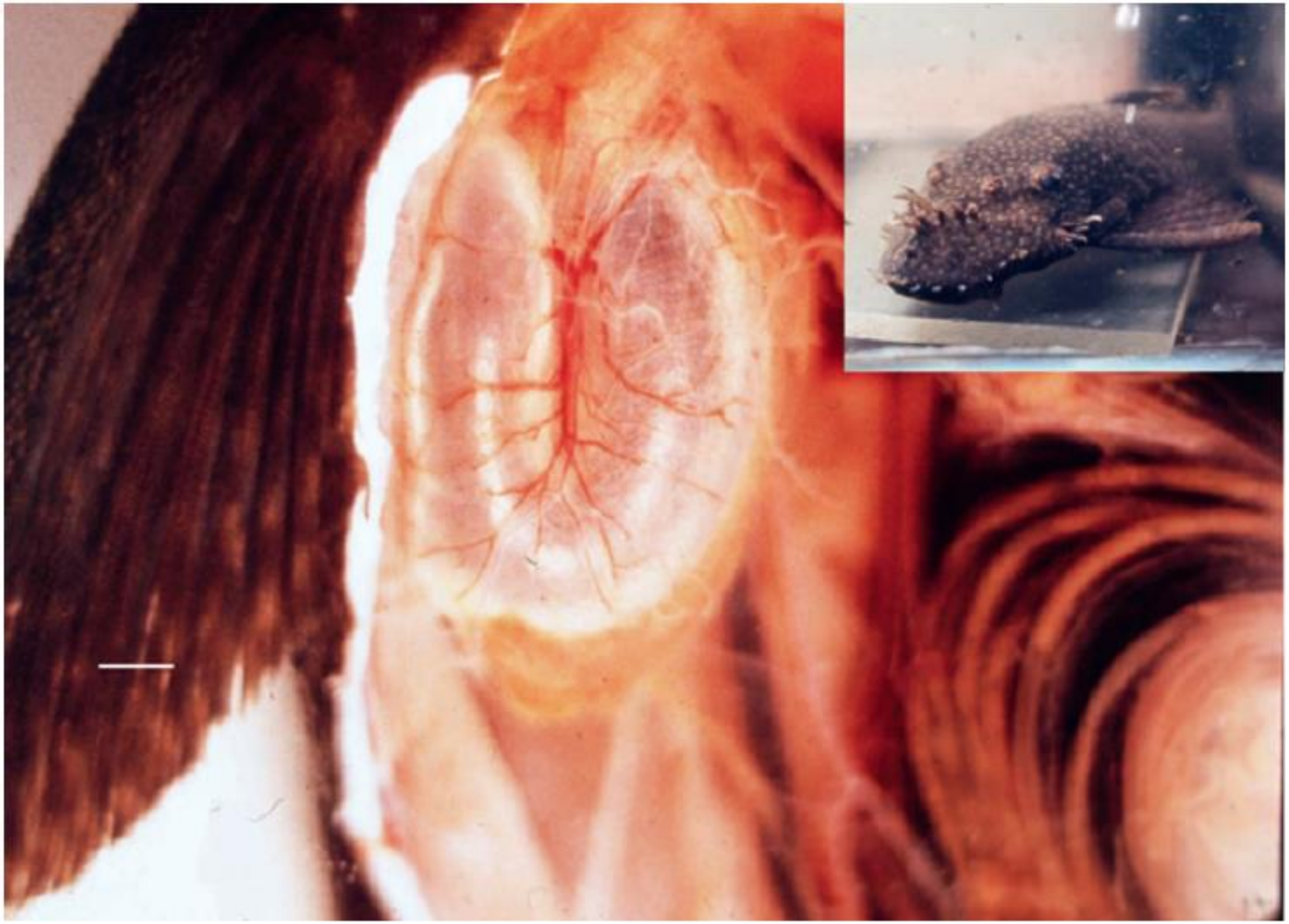
(a) Ventral view of the SBC of a 30-cm *Channa micropeltes*. Head was sectioned at level of the esophagus (E) and roof of mouth to show openings into the SBC. O, operculum; G, gill arches; D, dendrites on arches 1 and 2. Dendrites also on hyomandibular (H) and parasphenoid (P) bones. Scale = 1 cm. (b) Side view showing dendrite penetration into the SBC. (c) Detail for the capillary rosettes and spiraling.

T Y P E S O F
AIR-BREATHING ORGANS: Digestive Tube

- Esophagus
- The amphibious blenny *Lipophrys pholis* holds air in its esophagus, which has longitudinal folds containing many capillaries. The esophagus of the blackfish, *Dallia pectoralis*, is richly endowed with capillaries positioned within 1 mm of the surface along area-increasing micro-ridges formed by cuboidal epithelium.
- Pneumatic Duct
- The gas bladder of the eel *A. anguilla* (also other species) is physostomous; has a gas gland, the vascularized area within the gas-bladder wall that slowly secretes O2 into the organ for buoyancy. Anguilla has a pneumatic duct, this structure's esophageal opening is gated by a sphincter valve, which may limit air ventilation. The pneumatic duct is richly vascularized, and absorbs O2 from the gas bladder, which supplies respiration. While out of water Anguilla makes use of this oxygen supply and also breathes through its gills and skin

T Y P E S O F
AIR-BREATHING ORGANS: Digestive Tube

- Stomach
- Anatomical studies show a stomach ultrastructure comparable to lungs and gas bladders in having a large number of capillaries but relatively few digestive cells near the inner surface. In Liposarcus spinosus, (= Ancistrus sp.), a dense capillary mesh forms in the corpus region but not in either the cardiac or pylorus regions (Figure 11).



Air-filled stomach ABO of *Liposarchus* (= *Ancistrus*) *spinosus* on the right side of the abdomen. Note right pectoral fin and spiral intestine. Scale = 0.5 cm. (Inset) Fish exhaling air.

T Y P E S O F
AIR-BREATHING ORGANS: Digestive Tube

- Intestine
- Intestinal air breathing evolved independently in two groups, the New World catfishes (Callicthyidae, Callichthys asper, Hoplosternum thoracatum) and the Old World loaches (Cobitididae, Lepidocephalichthys guntea, Misgurnis anguillicaudatus).
- In both the groups, swallowed air is passed through the digestive intestine and into the posterior, respiratory section. Once O2 is removed from this gas, it is ejected from the anus, usually at the same instant that new air is gulped.
- In both the families, the digestive intestine has the important added function of compressing and then enclosing the feces in mucus clumps to minimize their size and maximize air contact in the respiratory surface.
- In *Hoplosternum thoracatum*, the respiratory intestine is perfectly aligned with the body axis and functions in buoyancy control. During air exposure, the intestine of the amphibious marine Chilean clingfish (*Sicyases sanguineus*) contains air and the vessels of this organ are engorged with blood;

T Y P E S O F
AIR-BREATHING ORGANS: Digestive Tube

- Gills
- The contribution of gills to aerial respiration cannot be quantified because most species that hold air in their branchial chambers also have a respiratory epithelium lining that chamber's surface.
- Although the walls of the branchial chambers of the amphibious blennies (*Entomacrodus nigricans*) and rockskippers (*Dialommus macrocephalus*) lack a prominent respiratory epithelium, oxygen partial pressure (PO2)measurements indicate that branchial oxygen consumption rate (V_O2) takes place in air, which implicates the gills in this process.

Modifications Related to Air Breathing

- Respiratory modifications of gills for amphibious air breathing include larger cartilaginous support rods in the filaments, which are often curved to reduce contact with adjacent filaments and thus lessen the chance of coalescence and collapse out of water.
- Among aquatic air breathers, reductions in gill area resulting from the diminution or the complete absence of filaments from some branchial arches are a specialization that increases air-breathing efficiency and is most common in species that use continuous aquatic air breathing or are obligate air breathers.
- On the other hand, the gill area of many facultative air breathers is not reduced and comparable to the gill areas of non-air-breathing species e.g. facultative Australian lungfish (Neoceratodus).

Modifications Related to Air Breathing

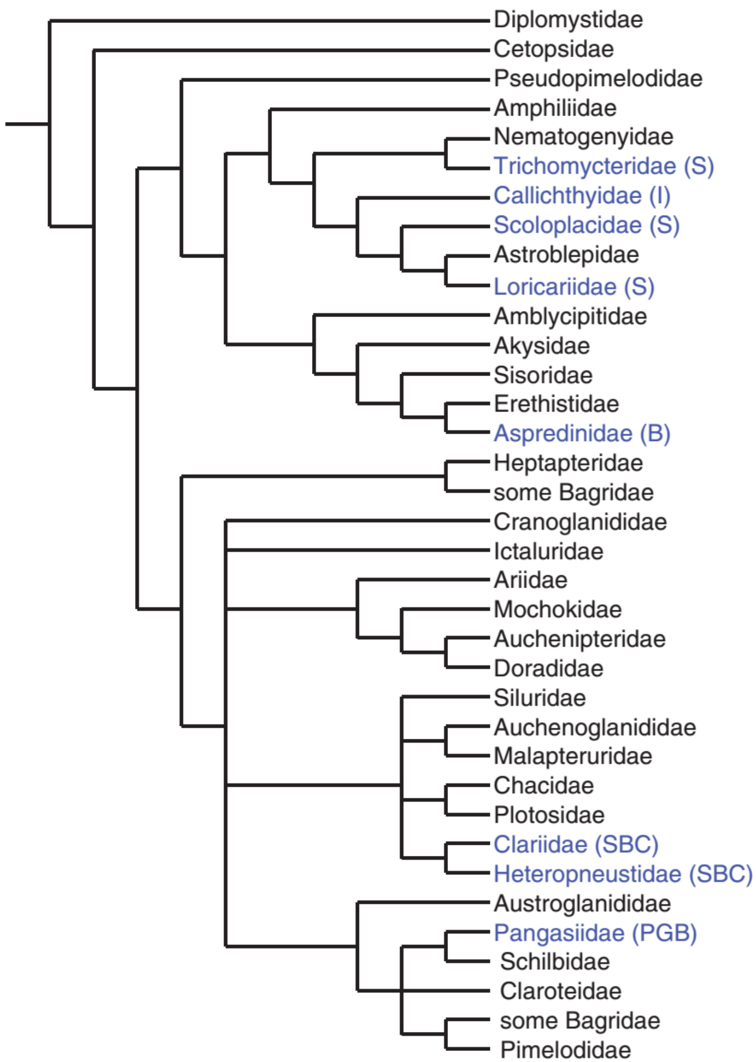
- Skin as ABO
- Fish skin is a less effective gas-exchange organ than either the gills or ABO because of its greater thickness, the added diffusion barriers of scales and mucus, and low perfusion and ventilation potentials.
- Fish skin is metabolically active; the epidermis contains a living epithelium as well as sensory and secretory cells, all of which receive nutrition via dermal capillaries.
- Specializations for skin respiration in amphibious airbreathing fishes include the presence of epidermal capillaries (reduce air–blood diffusion distance) along the dorsal body surface (this area is readily exposed to air and makes less contact with the substrate).
- mudskippers, obtain about half of their O2 via the skin, air–blood diffusion distances can be less than 5 mm along the dorsal-body surface
- In Kryptolebias (= Rivulus) marmoratus, which is totally reliant on skin respiration in air, capillaries on its dorsal body surface are within 1 mm of the body surface.

Modifications Related to Air Breathing

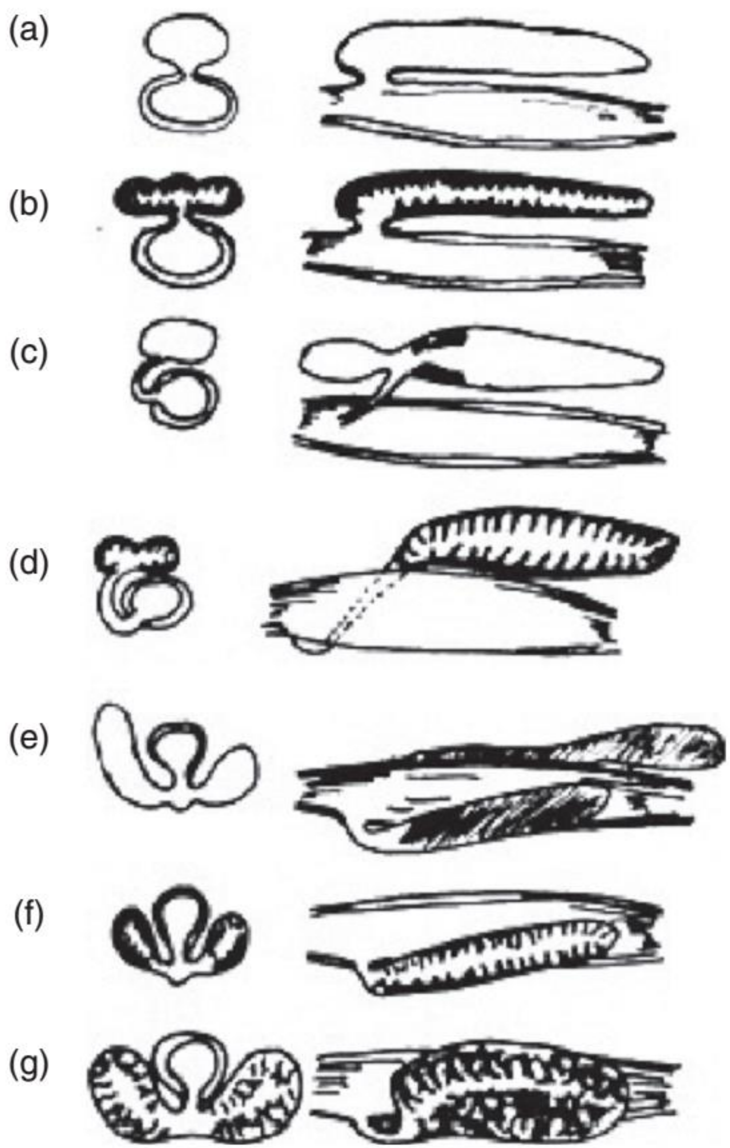
- Skin as ABO
- Among aquatic air breathers, the most dramatic application of cutaneous respiration occurs in the eleotrid, *Dormitator latifrons*. In hypoxic water, this fish hyperinflates its physoclistous gas bladder and becomes positively buoyant, thus emerging its forehead to expose a dense capillary network that is engorged with blood and functions for aerial respiration.

Overhead view of a large number of *Dormitator latifrons* aggregated at a dam in Panama. Each fish is positively buoyant and has its aerial-respiratory frontal skin patch exposed to air.

The Types of Air-Breathing Fishes



Phylogenetic relationships within the order Siluriformes showing the families in which air breathing occurs (blue) and their
ABO type in parentheses: B, buccal chamber;
I, intestine; PGB, pulmonoid gas bladder;
S, stomach; SBC, suprabranchial chamber.



Modified version of Bashford Dean's illustration of the evolutionary progression of gut and lung or gas bladder position in fishes and tetrapods. Double-layered structure is gut. Dark or striated areas are respiratory epithelium. (a) Sturgeon (no aerial respiration). (b) *Lepisosteus* and *Amia.* (c) *Erythrinus;* pneumatic duct (note its left side origin). (d) *Neoceratodus;* ventrally originating pneumatic duct ascends right side. (e) *Polypterus*; note smaller left lung. (f) *Lepidosiren* and *Protopterus.* (g) Tetrapods.

strategies employed by air-breathing fishes to defend against endogenous ammonia toxicity during exposure to terrestrial conditions (emersion).

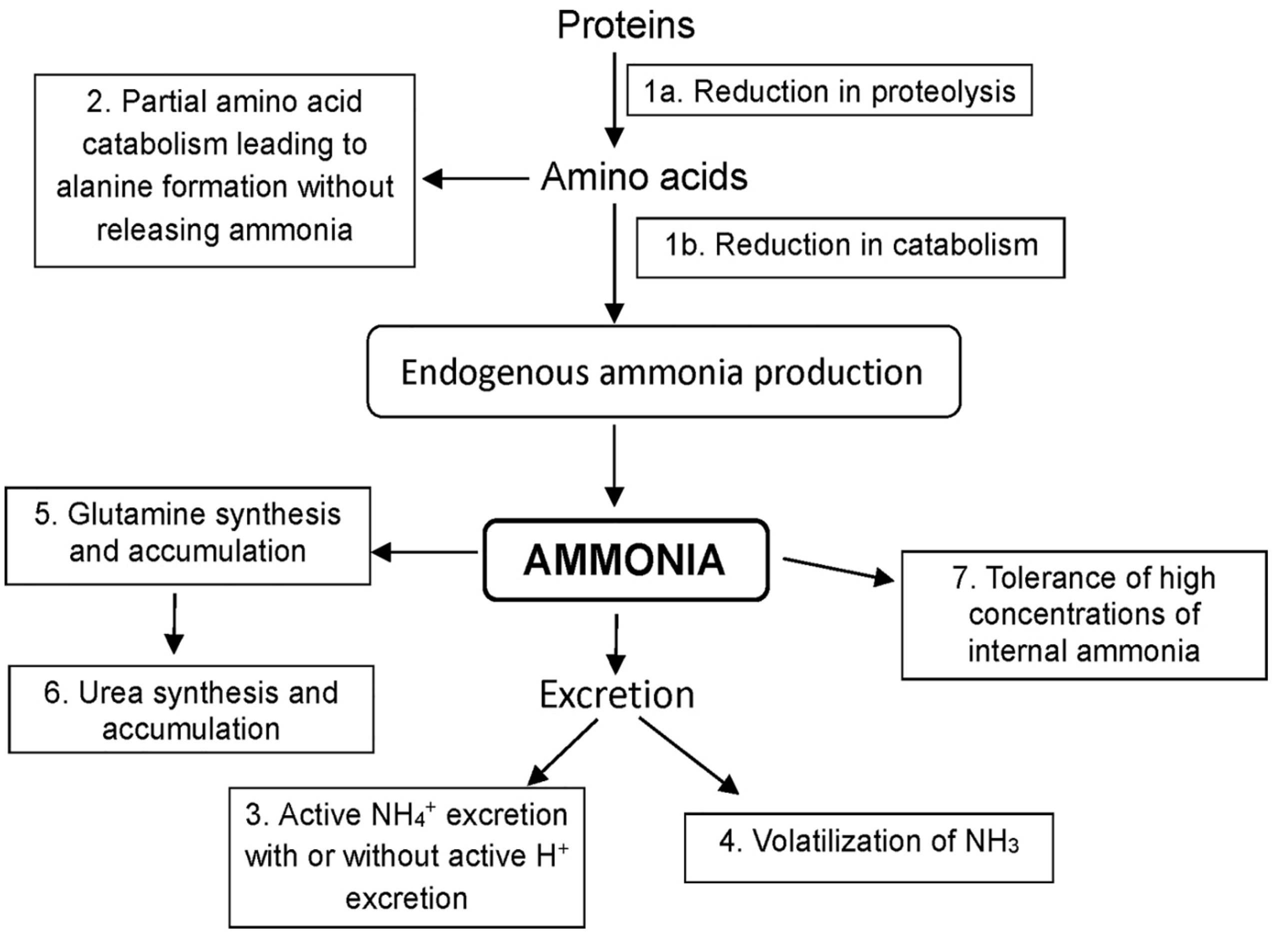
- Fishes in water excrete ammonia as the major nitrogenous waste through gills, but gills of air-breathing fishes are modified for air-breathing or largely replaced by air-breathing organs.
- Notably, fishes emerged from water can no longer excrete ammonia effectively because of a lack of water to flush the gills
- In fishes, a major portion (40–60%) of the dietary nitrogen intake is excreted as nitrogenous wastes within 24 h.
- Fully aquatic fishes are predominantly ammonotelic in water as they excrete > 50% of the nitrogenous waste as ammonia. The primary organ of ammonia excretion in fishes is the gill.
- Rhesus glycoproteins (Rhag, Rhbg and Rhcg) are crucial NH_3 (and NH_4^+) channels in ammonotelic fishes. At the gill, erythrocytic Rhag can facilitate NH_3 efflux from erythrocytes into plasma.
- When out of water, airbreathing fishes are confronted with problems of ammonia intoxication.

Deleterious effects of ammonia in fish

- Ammonia is toxic to fishes because of multiply reasons. At the organismal level, it causes hyperventilation, hyper-excitability, coma, convulsions and, eventually, death of the fish.
- At the branchial level, NH_4^+ can affect certain transporters and hinder ionoregulation by replacing K^+, and interfere with the operation of Na^+/K^+ -ATPase and $Na^+:K^+:2Cl^-$ cotransporter.
- At the cellular level, ammonia can interfere with energy metabolism, as it can impair the tricarboxylic acid cycle, by inhibiting pyruvate dehydrogenase, isocitrate dehydrogenase, or α-ketoglutarate dehydrogenase.
- In the central nervous system, NH_4^+ can substitute for K^+ to activate the background K^+ channel and affect the resting membrane potential, disruption of electrochemical gradients.

Strategies adopted by air-breathing fishes to defend against ammonia toxicity during emersion

- air-breathing fishes generally display seven ammonia-defense strategies (Fig. 1), with four major themes including reduction in ammonia production, continuous excretion of ammonia, detoxification of ammonia, and tolerance of high levels of internal ammonia.



Seven strategies employed by air-breathing fishes to defend against endogenous ammonia toxicity during exposure to terrestrial conditions (emersion).

Reduction in protein degradation and amino acid catabolism

- These include mudskippers, marble goby, four-eyed sleeper, weather loach, wamp eel, and African lungfishes

Partial amino acid catabolism forming alanine

- Certain amino acids can be converted to glutamate; they include arginine, glutamine, histidine and proline. Through the transamination reaction catalyzed by alanine aminotransferase, glutamate can react with pyruvate to produce α-ketoglutarate and alanine without the release of ammonia.
- As partial amino acid catabolism allows certain amino acids to be used as an energy source without releasing ammonia, it is a major strategy adopted by fishes which are active on land. These include giant mudskipper, climbing perch , and small snakehead.

Active ammonia excretion

- the most effective way to avoid ammonia toxicity in fishes during emersion is to excrete ammonia continuously despite the lack of water to flush the branchial and cutaneous surfaces.
- However, only a few air-breathing fishes with modified gill structures or accessory air-breathing organs are capable of active ammonia excretion. These include giant mudskipper, climbing perch, and African sharptooth catfish.

Volatilization of ammonia

- some air-breathing fishes can volatilize NH_3, and hence excrete ammonia continuously, during emersion.
- While the temperate intertidal blenny, Blennius pholis, can excrete 8% of the total ammonia as NH_3 gas during emersion at 13 °C, several tropical air-breathing teleosts, including weather loach, can volatilize a substantial amount of ammonia at temperatures close to 30 °C while on land.

Glutamine synthesis

- This strategy involves the detoxification of endogenous ammonia to glutamine. NH_4^+ can react with glutamate with the hydrolysis of ATP to form glutamine catalysed by glutamine synthetase.
- Glutamate can be synthesized de novo from α-ketoglutarate and NH_4^+ in the presence of NADH (one mole of NADH is equivalent to three moles of ATP), catalyzed by glutamate dehydrogenase. Taken together, the formation of one mole of glutamine removes two moles of ammonia.
- If ammonia detoxification starts with NH_4^+ and α-ketoglutarate and ends in glutamine, every mole of ammonia detoxified would result in the hydrolysis of two moles of ATP-equivalent .
- In fish brains, glutamine formation plays a major role in ammonia detoxification. Hence, fish brains often show the largest increases in glutamine concentration in response to ammonia toxicity.

Urea synthesis

- only the ornithine-urea cycle takes part in ammonia detoxification through de novo urea synthesis.
- Fishes are described as ureogenic only when they possess a functional ornithine-urea cycle with at least a low rate of urea synthesis. Fishes which excrete > 50% of nitrogenous waste as urea-N are regarded as ureotelic.
- African lungfishes are ureogenic, but they are ammonotelic in water under normal circumstances.
- Ureogenic fishes possess carbamoyl phosphate synthetase III which uses glutamine as a substrate . Overall, the synthesis of one mole of urea requires the hydrolysis of five moles of ATP in ureogenic fishes. As urea synthesis in fishes is energy intensive, many air-breathing teleosts do not adopt ureogensis as a major strategy to ameliorate ammonia toxicity during emersion. They include mudskippers, marble goby, four-eyed sleeper, weather loach, small snakehead, African sharp tooth catfish. By contrast, African lungfishes (sarcopterygians), possess a functional ornithine-urea cycle and utilize ureogenesis as an essential mechanism to defend against ammonia toxicity on land.

Tolerance of high levels of internal ammonia

- Some air-breathing fishes adopt the strategy to accumulate and tolerate high concentrations of ammonia in their tissues during emersion, although ammonia is not always evenly distributed within their bodies. Some of them accumulate high levels of ammonia in the muscle, while others can tolerate relatively high concentrations of ammonia in the brain.
- Mammalian brains can tolerate only ∼1 μmol g^{-1} of ammonia, beyond which encephalopathy would develop. Hence, air-breathing fishes with high brain ammonia tolerance, like mudskippers (> 14 μmol g^{-1} of brain ammonia) and swamp eel (> 3 μmol g^{-1} of ammonia in the brain).

Some air-breathing fishes display various combinations of the seven strategies to deal with ammonia during emersion

- The combination of these strategies adopted can be correlated to the behavior of the fish, the frequency and duration of terrestrial exposure, and/or the nature of the environment in which it lives.
- Examples: Mudskippers, small snakehead and the four-eyed sleeper , African lungfishes
- The giant mudskipper, *Periophthalmodon schlosseri*, adopts the strategies of reduction in amino acid catabolism in conjunction with partial amino acid catabolism leading to the formation of alanine. This allows the giant mudskipper to use proteins and amino acids as energy sources to support movement on land without producing ammonia.
- When exposed to terrestrial conditions under a dark:light regime, contents of several essential amino acids, including isoleucine, leucine, proline, serine, lysine and valine, increase in the tissues of P. schlosseri.
- When kept out of water, P. schlosseri can continuously excrete ammonia into the water trapped in the fenestrae of the branchial interlamellar fusions.

Some air-breathing fishes display various combinations of the seven strategies to deal with ammonia during emersion

- Through partial amino acid catabolism and the resulting alanine formation, P. schlosseri can reduce its dependency on glycogen for energy supply, and sustain a high metabolic rate for an extended period on land.
- During the first 24 h of terrestrial exposure, the Oriental weather loach, *Misgurnus anguillicaudatus* suppress proteolysis and amino acid catabolism to transiently impede ammonia production. Alanine accumulates during this period, indicating the usage of certain amino acids to sustain muscular activities on land through partial amino acid catabolism
- During terrestrial exposure, the skin of M. anguillicaudatus is a probable site of NH3 volatilization.

Control of air-breathing in fishes: Central and peripheral receptors

Control of air-breathing in fishes

- environmental and systemic factors can stimulate air-breathing responses in fishes with bimodal respiration, and these may be controlled by peripheral and central chemoreceptors.
- The systemic factors that stimulate air-breathing in fishes are usually related to conditions that increase the O2 demand of these animals (e.g. physical exercise, digestion and increased temperature),
- while the environmental factors are usually related to conditions that impair their capacity to meet this demand (e.g. aquatic/aerial hypoxia, aquatic/aerial hypercarbia, reduced aquatic hidrogenionic potential and environmental pollution).
- It is now well-established that peripheral chemoreceptors, innervated by cranial nerves, drive increased air-breathing in response to environmental hypoxia and/or hypercarbia. These receptors are, in general, sensitive to O2 and/or CO2/H+ levels in the blood and/or the environment. Increased air-breathing in response to elevated O2 demand may also be driven by the peripheral chemoreceptors that monitor O2 levels in the blood.

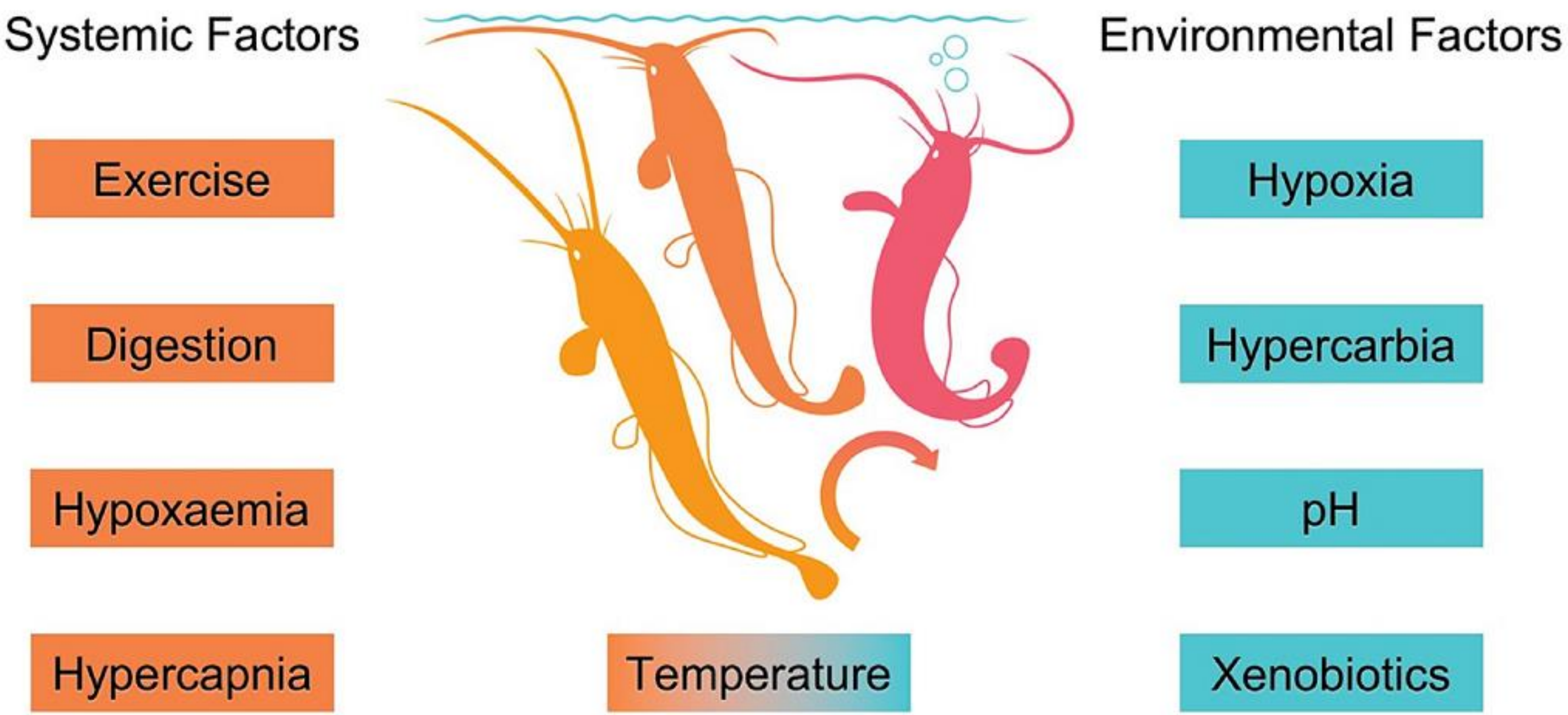
Control of air-breathing in fishes

- Aquatic surface respiration (ASR) reflex may have favored the selection of air-breathing based on the following hypotheses:
- (1) ASR allowed individuals to survive in waters under severe hypoxia;
- (2) some individuals inadvertently came into contact with the air during ASR (e.g. by inhaling it), which provided conditions for O2 uptake from the air across vascularized epithelia, making it possible to select them as air-breathing organs (ABO) and
- (3) ASR exposes the animals to predation, so individuals with the capacity to gulp and hold air could protect themselves from predators by temporarily returning to the depths, hence further favoring the evolution of adaptations for true aerial respiration

Control of air-breathing in fishes

- Fishes possess specialized chemosensitive cells, located in the central and/or peripheral nervous system, capable of monitoring the partial pressure of O2 (PO2) or CO2 (PCO2), as well as the hydrogen ionic potential (pH), in the blood and/or the environment (internally and/or externally oriented chemoreceptors). These chemoreceptors modulate a wide range of behavioral and physiological adjustments that favor the survival of fishes during situations of hypoxia/hypoxaemia (i.e. reduced levels of O2 in the environment or in the body, respectively) and hypercarbia/hypercapnia (i.e. increased levels of CO2 in the environment or in the body, respectively),
- There are differences in the location, distribution and orientation of these chemoreceptors among species, and their functions may vary depending on the specificity of these cells.

Control of air-breathing in fishes



Systemic and environmental factors with effects on air-breathing behavior in fishes. Note that temperature can be both a systemic factor and an environmental factor.

Control of air-breathing in fishes - Stimulators of reflex air-breathing responses

- Several factors stimulate air-breathing behaviors in fishes, which can be classified as either "systemic" or "environmental".
- Systemic factors are states of the organism that increase O2 demand for aerobic metabolism, in particular warming, exercise and digestion, which then stimulate overall ventilatory activity.
- Environmental factors, on the other hand, are external conditions that increase the animals' O2 demand; challenge respiratory gas exchange, and/or damage the fragile epithelium of the gill lamellae. This includes warming, hypoxia, hypercarbia, pH and pollutants.
- In species that are obligate airbreathers such factors will alter the intensity of aerial respiration whereas, in facultative air-breathers, such factors can trigger the air breathing behavior as well as modulate its intensity.

Control of air-breathing in fishes - Systemic factors

- Increase in physical exercise leads to increase in air-breathing frequency in all facultative species that have been studied, namely Amia calva, Clarias gariepinus, Gymnotus carapo, Hoplosternum littorale, Lepisosteus oculatus, Megalops cyprinoides, Neoceratodus forsteri, and Pangasianodon hypophthalmus.
- Food consumption also causes a transient increase in obligate air-breathing fishes when feeding in normoxic water, but this phenomenon is also expected to occur in facultative air-breathing fishes
- An increase in temperature is a combined systemic/environmental factor that stimulates air-breathing behavior in fishes because it increases the demand for O2 in the tissues and requires increased O2 delivery. An increase in air-breathing frequency associated with temperature elevation in *Channa argus, Megalops atlanticus* and *Umbra limi* demonstrating that the stimulatory influence of temperature on this behavior is not a mere consequence of aquatic hypoxia.

Control of air-breathing in fishes - Systemic factors

- There is some indirect evidence that ‘internal’ respiratory drive, in the spiny catfish C. gariepinus, and individuals with higher intrinsic metabolic rates and O2 demands spontaneously breathed more air in normoxia. In bimodal breathing fishes, this venous hypoxaemia may cause inescapable chemoreflexive stimulation of air-breathing, that increases with intensity as they exercise harder.

Control of air-breathing in fishes - Environmental factors

- Fishes with facultative aerial respiration (both Actinopterygii and Sarcopterygii) typically shift from gill ventilation to air-breathing as O2 levels in water fall. This transition has been described in numerous species, namely A. calva, Anabas testudineus, Ancistrus chagresi, C. gariepinus, Erpetoichthys calabaricus, Heteropneustes fossilis, Hoplerythrinus unitaeniatus,
- This response is elicited either by external or internal [if environmental hypoxia induces hypoxaemia] O2 chemoreceptors
- However, the actinopterygian and sarcopterygian species just cited, as well as the obligate air-breathing teleosts C. argus and Monopterus cuchia, show an increase in air-breathing frequency when exposed to aerial hypoxia, which may have been triggered by hypoxaemia through internally oriented chemoreceptors or by external chemoreceptors that monitor the PO2 of air in the ABO.

Control of air-breathing in fishes - Environmental factors

- Aquatic hypercarbia can increase the frequency of aerial respiration in several species of fish with obligatory or facultative air-breathing, such as A. chagresi, E. calabaricus, H. unitaeniatus, H. plecostomus, L. paradoxa, N. forsteri, P. aethiopicus, P. dolloi, S. marmoratus and T. Trichopterus
- airbreathing reflexes can be triggered by internal and/or external chemoreceptors sensitive to CO_2/H^+
- aerial hypercarbia can also increase air-breathing frequency in some air-breathing fishes, such as C. gariepinus, E. electricus, L. paradoxa, P. aethiopicus, Protopterus annectens and T. trichopteru
- The pH of water influences several physiological processes in fishes, including respiratory gas exchange and the excretion of nitrogenous wastes. Water pH is inversely proportional to water PCO_2, and a reduction in environmental pH may lead to a respiratory acidosis that compromises O_2 uptake in these animals

Control of air-breathing in fishes - Environmental factors

- Therefore, to avoid this effect, fishes with aerial respiration show an increase in the frequency of this behavior when in contact with water with reduced pH
- In A. calva, infusions of HCl into the dorsal aorta caused significant declines in blood pH and O2 content and elicited air-breathing responses. When, however, the animals were held in hyperoxic water, the infusions only caused a decline in pH and there were no air breathing responses.
- Brauner et al. (1995) found, that an increase in air-breathing frequency in H. littorale was a direct consequence of elevated water acidity and not of higher aquatic PCO2.
- Finally, another environmental factor that can stimulate airbreathing in fishes is aquatic pollution. Contaminants in aquatic environments can be of anthropic origin or even natural, such as the hydrogen sulfide (H2S) that is mainly produced by bacterial sulfate reduction in sediments and anaerobic decomposition of organic matter.

Control of air-breathing in fishes - Environmental factors

- These compounds can stimulate aerial respiration in fishes for a variety of reasons. Hydrogen sulfide, for example, can reduce the affinity of hemoglobin for O_2 and impair the electron transport chain reaction by binding to cytochrome-c oxidase, which may lead to both hypoxaemia and an impaired ability to produce ATP, that in turn triggers an increase in air-breathing frequency.
- Other pollutants, on the other hand, may irritate the gill epithelium of the animals, inducing changes in gill morphology (such as an increase in the number of interlamellar cells, cell hyperplasia and a greater production of mucus) that inhibits both xenobiotics absorption and branchial gas exchange– a situation that may increase the requirement for air breathing.

Systemic and environmental factors and its effects on air-breathing behavior in various species of fish.

	Species	Physical Exercise	Digestion	Increased Temperature	Aquatic Hypoxia	Aerial Hypoxia	Aquatic Hypercarbia	Aerial Hypercarbia	Reduced Environmental / Blood pH	Contaminants (H_2S)
FACULTATIVE	*Amia calva* (A)	+[30]		+[9, 12]	+[9]				+[26]	
	Anabas testudineus (A)				+[8]					
	Ancistrus chagresi (A)			+[19]	+[19]		+[19]			
	Clarias gariepinus (A)	+[52]			+[45, 51]			+[16]		
	Erpetoichthys calabaricus (A)				+[22]		+[22]			
	Gymnotus carapo (A)	+[49]								
	Heteropneustes fossilis (A)				+[10]					
	Hoplerythrinus unitaeniatus (A)				+[40, 44]		+[43]			
	Hoplosternum littorale (A)	+[15]			+[15, 29, 37]				+[29]	+[29, 37]
	Hypostomus plecostomus (A)				+[19]		+[19]			
	Hypostomus regani (A)				+[31]					
	Lepisosteus oculatus (A)	+[30]			+[20]	+[20]		nc[20]		
	Lepisosteus osseus (A)			+[11]	+[24]					
	Megalops atlanticus (A)			+[32]	+[32]					
	Megalops cyprinoides (A)	+[36, 41]			+[36]					
	Misgurnus anguillicaudatus (A)			+[25]						
	Neoceratodus forsteri (S)	+[2]			+[27, 35]	nc[5]	+[5]			
	Pangasianodon hypophthalmus (A)	+[50]			+[46, 54]		nc[54]			
	Rhinelepis strigosa (A)				+[28]					
	Synbranchus marmoratus (A)				+[21] / nc[3]		+[3]			
	Umbra limi (A)			+[18]						
OBLIGATORY	*Channa argus* (A)			+[23]		+[23]				
	Channa striata (A)		+[14, 48]							
	Electrophorus electricus (A)				nc[7]	+[7]	nc[7]	+[7]		
	Lepidosiren paradoxa (S)			+[53]	nc[34]	+[34, 47, 53]	+[33, 38]	nc[33]/+[38]		
	Monopterus cuchia (A)				+[13]	+[13]	nc[13]			
	Protopterus aethiopicus (S)				nc[6]	+[6]	+[6]	+[1] / -[4]		
	Protopterus annectens (S)							+[16]		
	Protopterus dolloi (S)				nc[39]	+[39]	+[42]	-[4] / nc[42]		
	Trichogaster trichopterus (A)				+[17]	+[17]	+[17]	+[17]		

Note: (A) Actinopterygii; (S) Sarcopterygii; (H_2S) Hydrogen sulfide; (+) Stimulation; (-) Inhibition; (nc) No change; (blank) No data available.

Control of air-breathing in fishes - Peripheral receptors mediating air-breathing responses

- the location of peripheral chemoreceptors (gills, orobranchial cavity or elsewhere) and their orientation (external water or internal blood) are highly variable among fishes, whether unimodal or bimodal breathers.
- Considering unimodal and bimodal breathers, there is a trend whereby the receptors involved in triggering changes in heart rate and gill ventilation rate in response to hypoxia and hypercarbia are preferentially located in the gills, whereas those that produce increases in gill ventilation amplitude are more extensive, often also being found in extrabranchial locations.
- Also, the distribution of CO_2-sensitive chemoreceptors in the gills tends to be more restricted than O_2-sensitive chemoreceptors, and the location of the CO_2 receptors may differ from the O_2 receptors.

Control of air-breathing in fishes - Peripheral receptors mediating air-breathing responses

- The primary sites of peripheral O_2 sensing in fish appear to be the gills and orobranchial cavity.
- Chemoreceptors in the orobranchial cavity are innervated by branches of the Vth (trigeminal) and/or VIIth (facial) cranial nerves, those on the pseudobranch by branches of the VIIth and/ or IXth (glossopharyngeal) cranial nerves, and those on the gill arches by branches of the IXth and/or Xth (vagus) cranial nerves.
- Some of these chemoreceptors respond only, or preferentially, to changes in external (water) O_2, others respond only, or preferentially, to changes in internal (blood) O_2, and some respond to both
- Highly sensitive mechanisms to monitor O_2 and acid-base balance are important for the survival of all vertebrate species. In fishes, this requirement is primarily filled by endoderm-derived neuroepithelial cells (NECs) in the gills

Control of air-breathing in fishes - Peripheral receptors mediating air-breathing responses

- So, the predominant putative $O_2/CO_2/H^+$ chemoreceptors in fishes, NECs are mainly located on the gill filaments and secondary lamellae of all branchial arches and are innervated by afferent fibers of the central nervous system.
- The location, orientation and innervation of peripheral O_2-sensitive chemoreceptors involved in the control of gill ventilation rate, gill ventilation amplitude and air-breathing in fishes with bimodal respiration are summarized in Tables.

Control of air-breathing in fishes - Peripheral receptors mediating air-breathing responses

- Acute exposure of fish to aquatic hypercarbia typically elicits significant increases in gill ventilatory amplitude and/or gill ventilation rate, resulting in an increase in total gill ventilation. This is usually accompanied by a decrease in heart rate, and increase in systemic vascular resistance
- There is strong evidence that these responses arise from the stimulation of specific CO_2/H^+ chemosensitive NECs and are not dependent on changes in water or blood O_2 concentration
- At present, the cardiorespiratory responses to CO_2/H^+ in fish are believed to arise primarily from receptors distributed throughout the gill arches innervated by the IXth and Xth cranial nerves. It is clear that these receptors in the gills monitor the CO_2 in the water,
- The chemoreceptors involved in stimulating air-breathing in response to hypercarbia appeared to be branchial, distributed across all gill arches and responded specifically to changes in aquatic PCO_2.

Control of air-breathing in fishes - Peripheral receptors mediating air-breathing responses

- This would suggest that chemoreceptor groups with different orientations – external water versus internal blood – are involved in eliciting air-breathing responses to hypercarbia and hypoxia (respectively) in H. unitaeniatus.
- Although aquatic hypercarbia induces an increase in gill ventilation in most air-breathing fishes yet, in some species (such as H. unitaeniatus), if the increases in aquatic PCO2 are large enough, they can inhibit gill ventilation and stimulate air-breathing.

Location, orientation and innervation of peripheral O_2- and CO_2/pH-sensitive chemoreceptors involved in gill ventilation rate responses.

Species	Receptor Location	Orientation	Innervation	References
O_2 Chemoreceptors				
Amia calva (A)	Pseudobranch + All gill arches	E + I	VII, IX, X	McKenzie et al. (1991a)
Clarias gariepinus (A)	First gill arch	I	IX, X	Belão et al. (2015)
Hoplerythrinus unitaeniatus (A)	All gill arches	E + I	IX, X	Lopes et al. (2010)
Lepisosteus osseus (A)	All gill arches	I	IX, X	Smatresk (1986); Smatresk et al. (1986); Smatresk (1988, 1989)
Pangasianodon hypophthalmus (A)	First gill arch +?	E + I	IX, X,?	Thomsen et al. (2017); V.A. Armelin, M.T. Teixeira, M.T. Thomsen, L.H. Florindo, M. Bayley, and T. Wang, unpublished data.
CO_2/H^+ Chemoreceptors				
Hoplerythrinus unitaeniatus (A)	First gill arch	E	IX, X	Boijink et al. (2010)

Note: (A) Actinopterygii; (S) Sarcopterygii; (E) External – water – orientation; (I) Internal – blood – orientation; (?) Unknown; (VII) Facial nerve; (IX) Glossopharyngeal nerve; (X) Vagus nerve.

Location, orientation and innervation of peripheral O_2- and CO_2/pH-sensitive chemoreceptors involved in gill ventilation amplitude responses.

Species	Receptor Location	Orientation	Innervation	References
O_2 Chemoreceptors				
Amia calva (A)	Pseudobranch + All gill arches	E + I	VII, IX, X	McKenzie et al. (1991a)
Clarias gariepinus (A)	All gill arches	I	IX, X	Belão et al. (2015)
Hoplerythrinus unitaeniatus (A)	All gill arches + Extrabranchial	E + I	IX, X,?	Lopes et al. (2010)
Lepisosteus osseus (A)	All gill arches	I	IX, X	Smatresk (1986); Smatresk et al. (1986); Smatresk (1988, 1989)
Pangasianodon hypophthalmus (A)	First gill arch + ?	E + I	IX, X,?	Thomsen et al. (2017); V.A. Armelin, M.T. Teixeira, M.T. Thomsen, L.H. Florindo, M. Bayley, and T. Wang, unpublished data
CO_2/H^+ Chemoreceptors				
Hoplerythrinus unitaeniatus (A)	First gill arch	E	IX, X	Boijink et al. (2010)

Note: (A) Actinopterygii; (S) Sarcopterygii; (E) External – water – orientation; (I) Internal – blood – orientation; (?) Unknown; (VII) Facial nerve; (IX) Glossopharyngeal nerve; (X) Vagus nerve.

Location, orientation and innervation of peripheral O_2- and CO_2/pH-sensitive chemoreceptors involved in air-breathing responses.

Species	Receptor Location	Orientation	Innervation	References
O_2 Chemoreceptors				
Amia calva (A)	Pseudobranch + All gill arches	(E[a])	VII, IX, X	McKenzie et al. (1991a)
Clarias gariepinus (A)	First gill arch	E + I	IX, X	Belão et al. (2015)
Hoplerythrinus unitaeniatus (A)	All gill arches	(E[a]) + I	IX, X	Lopes et al. (2010)
Lepisosteus osseus (A)	All gill arches	E[a] + I	IX, X	Smatresk (1986); Smatresk et al. (1986); Smatresk (1988, 1989)
Pangasianodon hypophthalmus (A)	First gill arch +?	E + I	IX, X,?	Thomsen et al. (2017); V.A. Armelin, M.T. Teixeira, M.T. Thomsen, L.H. Florindo, M. Bayley, and T. Wang, unpublished data.
Protopterus aethiopicus (S)	All gill arches	(E[a]) + I	IX, X	Lahiri et al. (1970)
CO_2/H^+ Chemoreceptors				
Hoplerythrinus unitaeniatus (A)	All gill arches	E	IX, X	Boijink et al. (2010)
Lepidosiren paradoxa (S)	?	?	?	Amin-Naves et al. (2007a)

Note: (A) Actinopterygii; (S) Sarcopterygii; (E) External – water – orientation; (I) Internal – blood – orientation; (?) Unknown; (VII) Facial nerve; (IX) Glossopharyngeal nerve; (X) Vagus nerve.

[a] In *A. calva* and *H. unitaeniatus*, external NaCN stimulated air-breathing only if blood P_{O2} levels were low or if NaCN was injected internally as well. In *L. osseus*, external NaCN stimulated air-breathing, but such stimulation was stronger when the animals' blood P_{O2} levels were low. In *P. aethiopicus* the effects of external stimuli are equivocal.

- Air breathing is an auxiliary respiratory mode that enables a fish to live in hypoxic waters or to become amphibious and to perhaps further utilize the mechanical processes integral to this adaptation in the augmentation of functions such as buoyancy, sound reception or production, and reproduction.
- Air breathing is an ancient trait that first evolved in fishes. While air breathing is an ancient fish trait, it has also evolved in a number of derived fish groups, including the modern teleosts.
- Air breathing occurs only in the bony fishes (Osteichthyes) where it is found in nearly 400 species distributed among approximately 140 genera in 50 families and spanning 18 orders.
- Air breathing is not known to occur in any fish group other than bony fishes.

Aquatic Air Breathers

- Aquatic air breathers remain in water (although some species doing this can also be amphibious air breathers) and there are two types, facultative and continuous.
- Facultative air breathers normally respire aquatically and use air breathing only when it is required by environmental conditions, principally hypoxia.
- Included among many facultative air breathers are the Australian lungfish Neoceratodus forsteri, nearly all of the genera of the South American suckermouthed armored catfishes (Loricariidae, e.g., Liposarcus chagresi and many other species) and other Amazon catfishes (Gymnotus carapo, Hypopomus brevirostris, and H. occidentalis), the swamp eel (Synbranchus marmoratus), the salmoniforms (Umbra limi and three other species and Dallia pectoralis), the estuarine goby (Gillichthys mirabilis), and the Asian eel goby (Odontamblyopus lacepedi and other species), which switches to air breathing only when its burrow water becomes hypoxic at low tide.

Aquatic Air Breathers

Some aquatic air breathers do this regularly even in normoxic water and are termed continuous air breathers. Continuous air breathing is common in species living in habitats where hypoxic water is either a chronic or frequent occurrence, and in many cases continuous air breathing is not solely for respiration but also functions to maintain the volume and wall tension of the ABO in order to serve additional and potentially multiple purposes such as buoyancy and either or both sound production and reception (e.g., featherbacks *Notopterus notopterus* and two other species, also *Papyrocranus afer* and *Xenomystus nigri*).

Obligate Air Breathers

- These fishes completely depend on and require access to aerial oxygen and, even if they are in water that is well oxygenated, they will have a reduced aerobic scope or possibly even drown if prevented from air breathing. Examples of obligatory air breathers include the four African lungfish (*Protopterus atheiopicus*, *P. amphibius*, *P. annectens*, and *P. dolloi*), the South American lungfish (*Lepidosiren paradoxa*), the Amazon osteoglossid (*Arapaima gigas*), the African butterfly fish (*Pantodon bucholzi*), the Atlantic tarpon (*Megalops atlanticus*), the silurid (*Pangasius sutchi*), some species of clariid catfishes (but results vary, *C. batrachus, C. lazera, C. gariepinus, C. macrocephalus*), the armored catfish *H. thoracatum*, the monotypic Amazon electric knifefish (*Electrophorus electricus*), several anabantoids including *Anabas testudinus*, *Osphronemus goramy*, *Trichogaster trichopterus* and *T. pectoralis*, and *Colisa fasciatus*), the swamp eel (*Monopterus cuchia*), and probably the seven other species in this genus), and probably some of the 12–14 species of snakehead (*Channa*), but this has not been studied.

Obligate Air Breathers

- Obligatory air breathing appears to be the consequence of developing such a proficient level of air-breathing specialization that the capacity for aquatic respiration using the gills is compromised.

Amphibious Air Breathing

- There are three grades of amphibious air breathers: species that endure seasonal exposure in drying mud, those that endure brief stranding by a receding tide, and those that volitionally emerge from the water.
- Fishes subject to long-term exposure in drying mud include the African and South American lungfish (Protopterus and Lepidosiren), swamp eels (Synbranchidae), armored catfish (Liposarcus, Hypostomus, and Callichthys), anabantoids (Anabas and Ctenopoma), snakeheads (Channa), clariid catfishes (Clarias).

Amphibious Air Breathing

- While amphibious air breathing is often associated with hypoxic stress and disappearance of water from a habitat, the natural behavior of a number of tropical and subtropical intertidal fishes such as the rockskipper Dialommus (= Mnierpes) macrocephalus, numerous blennies (Blennius pholis, Entomacrodus nigricans, Alticus kirki, and Andamia tetradactyla, there several species in each of these genera), and the mudskippers (Scartelaos histophorus, Boleophthalmus pectinirostris, Periophthalmus modestus, and Periophthalmodon schlosseri, there are numerous species in each genus) make frequent terrestrial sojourns for the purpose of exploiting resources above the water line.

The Evolution of Air Breathing

For the majority of air-breathing fishes a close link exists between this specialization and environmental hypoxia, suggesting that natural selection for air breathing has been driven largely by the cyclic occurrence, over geologic time, of severe environmental hypoxia (about 30–40% air saturation of water). For each group in which air breathing has evolved, selection has operated on a specific combination of factors that included genetic variation and the potential advantages in terms of inter-specific competition and ecological radiation through niche expansion afforded by increased hypoxia tolerance and air breathing.

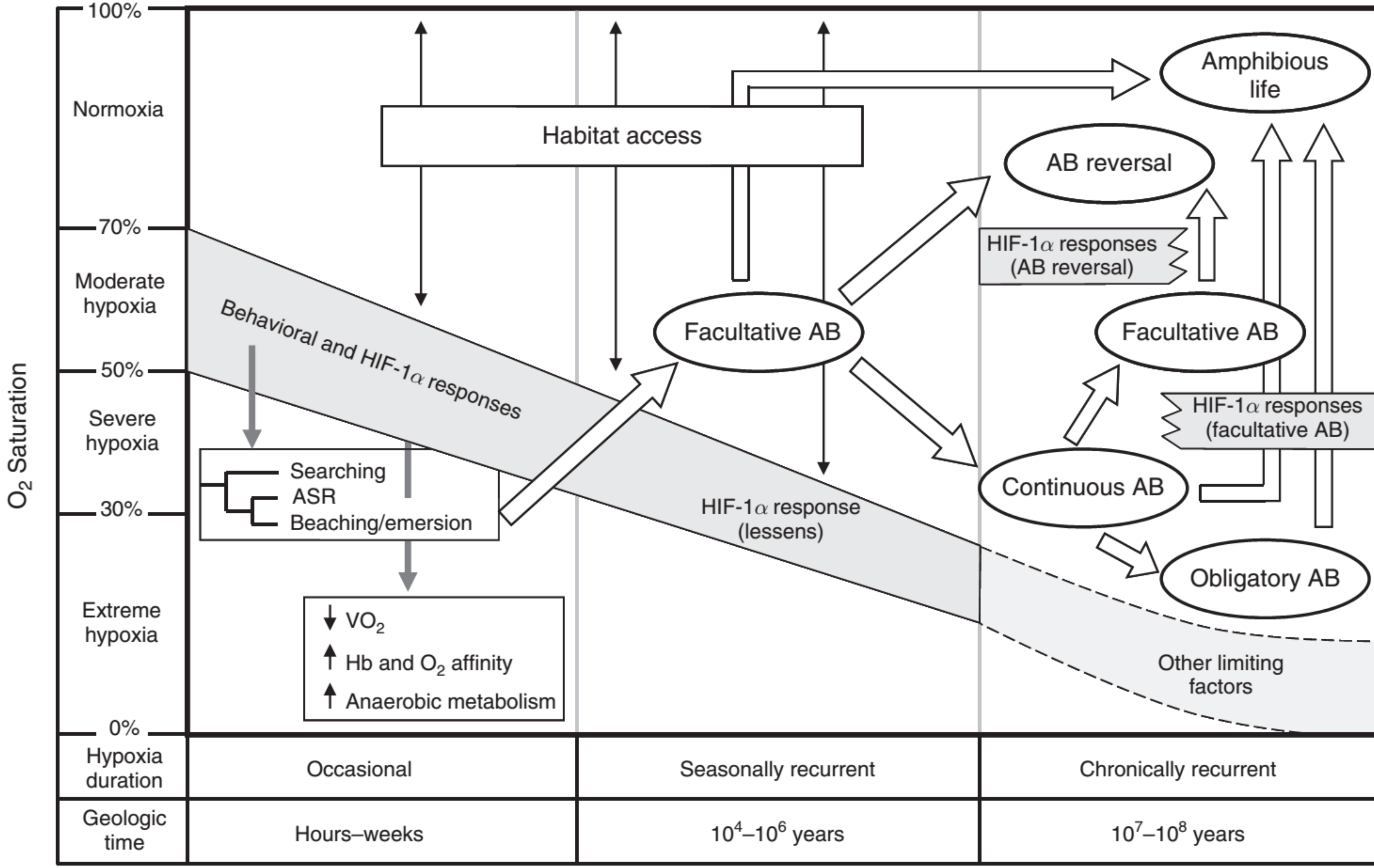


Figure 3 Integrated aspects of environmental hypoxia adaptation and the selective mechanisms operating over different periods of time leading to the evolution of air breathing and terrestriality in different fish groups and its effect of opening limited habitats for occupation and promoting radiation and diversification. Behavioral responses such as ASR that takes a fish close to the surface increased the potential for inadvertent air gulping may have been a major selective factor in the origin of air breathing. Specialization for hypoxia and air breathing would lead to down regulation of HIF-1α response mechanisms. Modified from Graham JB and Wegner NC (2010) Breathing air in water and in air: The air-breathing fishes. In: Nilsson GE (ed.) *Respiratory Physiology of Vertebrates: Life With and Without Oxygen*, pp. 174–220. Cambridge: Cambridge University Press.

Air Breathing and Natural History
Adaptive Radiations

Air breathing appears to have been an important factor in the radiation and diversification of certain groups. Many of the species in the families Callicthyidae and Clariidae, and all of the species in the five families comprising the anabantoid suborder (Anabantidae, Belontiidae, Helostomatidae, Osphronemidae, and Luciocephalidae), breathe air. Taken together, these groups comprise a large fraction of the total air-breathing fish diversity (about 14% of the families, 16% of the genera, and 39% of the species).

Air Breathing and Natural History
Adaptive Radiations

- Air breathing permits populations to expand into habitats where, because of adverse conditions, ecological success is assured through limited competition from non-air-breathers.
- Mud skippers have prominent eyes and a good visual acuity in air. Although their lateral line is reduced, mudskippers can hear airborne sound (250–600 Hz). Also, their physiology is specialized to limit desiccation, to allow osmoregulation in different salinities, and to modify nitrogen excretion for water conservation. Some species can also sense the O2 content of the air in their burrow. While most mudskippers retain the capacity for aquatic respiration, at least one species in the genus *Periophthalmodon* (*Pn. schlosseri*) is an obligatory air breather.

Air Breathing and Natural History
Adaptive Radiations

- Amphibious life poses a problem for vision because of the refractive differences of air and water. Solutions include, for some mudskippers, reduction of lens curvature to compensate for the added corneal refraction in air or, in *Dialommus macrocephalus* and some blennies (*E. nigricans*), flat corneas reduce aerial astigmatism and allow emmetropia in air without compromising aquatic accommodation.