African amphibious fishes and the invasion of the land by the tetrapods

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Many species of amphibious fishes (fishes that live both in and out of water as normal parts of their life histories), belonging to a diverse array of families, occur in both freshwater and marine habitats in many parts of Africa. Some of the best studied forms are common in widely occurring intertidal habitats along much of the African seacoast. Several species of mudskippers (family Gobiidae, subfamily Oxudercinae) occur in mangrove areas and in other protected muddy or sandy habitats. A larger and more diverse group of blennies (family Blenniidae), some of which are called rockskippers, occur in mainly rocky habitats. The primary focus of this paper is on both the mud- and rockskippers. None of the living amphibious fishes are directly related to or descended from the ancient sarcopterygian fishes that appear to have been the ancestors of all tetrapods. However, studies of the biochemical, ecophysiological, functional morphological, and behavioural adaptations shown by the living forms for amphibious modes of life provide us with diverse examples of evolutionarily successful, functional suites of adaptations that might also have been used, in varying combinations, by ancestral forms that could have occupied similar habitats.

Introduction

Amphibious fishes may be defined as those fishes that live both in and out of water as normal parts of their life histories. Graham (1997) has exhaustively reviewed the published literature on air-breathing fishes in general and amphibious fishes in particular. With respect to amphibious fishes he points out the following.

The exact number of living amphibious species is unknown. There are at least 200 known species worldwide. Amphibious capacities are widely distributed phylogenetically, including at least one lamprey (in Australia), the three genera (six species — four African) of sarcopterygian lungfishes, and a very large and varied assortment of actinopterygian species. The actinopterygians include (this list is illustrative of the diversity, not exhaustive): at least one cladistian polypterid (family Polypteridae); several species of clingfishes (family Gobiesocidae); assorted catfishes (several families, including the walking catfishes of the family Clariidae); some eels (family Anguillidae); some sculpins (family Cottidae); a large number of blennies (family Blenniidae) and their relatives, especially the various rockskippers; and substantial numbers of gobies (family Gobiidae), especially the mudskippers of the subfamily Oxudercinae. Many, but not all, of these groups include African species.

Graham (1997) classifies these fishes into three functional categories: (i) fishes capable of surviving prolonged (seasonal) periods out of water buried in mud; (ii) fishes experiencing periodic (usually tidal) aerial exposures, during which they are usually relatively inactive; and (iii) fishes capable of volitional (that is purposeful) visits onto land, some of which can be quite long, and during which they are often very active. Group (i) fishes are almost all freshwater forms, well adapted to survive long, often hot, dry seasons. Most live in the subtropics or tropics. Group (ii) fishes are almost all marine intertidal species, usually living on rocky coastlines exposed to considerable wave activity. They often hide under rocks or in thick mats of seaweed. They occur from the tropics to the subarctic. Group (iii) fishes are widely distributed geographically, climatically, and in terms of habitats. They live in freshwater, brackish (especially estuarine), and marine environments. In marine environments they live in relatively protected habitats (e.g. mudskippers in mangrove areas) or in high-energy, exposed habitats (many rockskippers).

This phylogenetic, geographic, environmental, and behavioural diversity among amphibious fishes provides important background for the comparable diversity that exists among these organisms in terms of functional morphology and ecophysiology. Graham (1997), supplemented by Gibson (1993), Gordon & Olson (1995), and Martin (1995), provide extensive recent reviews of essentially all of the scientific literature on these topic areas. Therefore, in this paper I focus on the ecophysiological and behavioural adaptations for amphibious life shown by the best-studied, most fully terrestrial, members of group (iii), namely selected species of mudskippers and rockskippers. I also emphasize work done on African species.

My emphasis in this discussion is on basic science aspects. The ecophysiological and behavioural characteristics of these fishes are keys to two perspectives: (i) understanding of the major ways in which these animals survive and function in their own worlds; and (ii) viewing the diversity of patterns and mechanisms shown by the variety of living forms as a series of envelopes of possibility with respect to how the mid- to late Devonian sarcopterygian fishes that are considered to have been the probable ancestors of all tetrapods might themselves have dealt with the problems of transition from aquatic to terrestrial environments.

It is important to note, however, that studying these fishes can also have substantial practical significance as well. They are sensitive to changes in environmental conditions (Thaker, Chhaya, Nuzhat, Mittal, Mansuri & Kundu 1996; Chhaya, Thaker, Mittal, Nuzhat, Mansuri & Kundu 1997). Changes in their numbers and changes in their behaviours can be useful indicators of the ecological health of coastal habitats (Etim, Brey & Arntz 1996). They are important members of intertidal and coastal food webs, both as predators and prey (Colombini, Berti, Nocita & Chelazzi 1996). Thus changes in their populations are likely to reflect changes in abundances of other species, as well as having ripple effects on other spe-

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cies. They are much easier to observe than most fishes (since the most amphibious forms are out of the water almost continuously), so they can readily be used as indicators of developing environmental problems.

Living African mudskippers and rockskippers

Physiologists and behaviourists who study wild animals are not always aware of, or sufficiently concerned about, the proper scientific names for their study organisms. In many cases the forms they study belong to groups that are not well understood from the systematic biological point of view. This has been particularly the case for students (like me) of amphibious fishes, most notably for the mudskippers. Murdy (1989) has done the most recent and authoritative study of the classification of that group. He demonstrated that most of the names used in the physiological and behavioural literature on these fishes were incorrect. This situation continues up to the present. In what follows I use the names given in the papers cited. Murdy (1989) should be consulted to work out the proper synonymies. Table 2.4 (pp. 50–51) in Graham (1997) is an attempt at doing this.

Up to the present the entire ecophysiological and behavioural literature on African amphibious fishes has been based on two species: (i) the east African mudskipper *Periophthalmus sobrinus* [= *P. argentilineatus* of Murdy (1989)]; and (ii) the east and north-east African rockskipper *Alticus (Lophalticus) kirki*. The terms mudskipper and rockskipper refer from here on to these two fishes.

Mudskippers occur primarily in protected sandy to muddy intertidal habitats, usually in mangrove forests or near them. They are diurnally active carnivores. They spend over 90% of their time, both day and night and at most tidal stages, out of water (Gordon, Boetius, Evans & Oglesby 1968; Gordon, Boetius, Evans, McCarthy & Oglesby 1969; Colombini, Berti, Nocita & Chelazzi 1996). They feed, fight (about territories, status, mates, food, etc.), court potential mates, and build elaborate burrows — all out of water (Brillet 1975, 1976, 1984, 1986; Colombini, Berti, Ercolini, Nocita & Chelazzi 1995; Colombini, *et al.* 1996). While doing all these things, as well as avoiding predators, they know where they are on their mud- or sand-flats, and know the locations of the nearest safety exits (burrows, of their own or other mudskippers; Berti, Chelazzi, Colombini & Ercolini 1992; Berti, Colombini, Chelazzi & Ercolini 1994; Colombini, *et al.* 1995).

These behavioural capacities are based upon a suite of physiological resistance and capacity adaptations (Gordon, Boetius, Boetius, Evans, McCarthy & Oglesby 1965; Teal & Carey 1967; Gordon, *et al.* 1969). They are strongly euryhaline and good osmoregulators. They tolerate for extended periods salinities from somewhat above the salinity of the adjacent sea (they encounter higher salinities occasionally, for short periods, in evaporating puddles of water left behind on their flats by falling tides) down to about 10% seawater (they are frequently exposed to heavy rainfalls). Their body fluids rapidly become diluted and they will die fairly rapidly if confined to fresh water.

If kept in shade and protected from air movements they will survive out of water for at least 2–3 days under normal ambient temperature conditions. Under these conditions they lose water evaporatively more slowly than anuran amphibians of comparable size. If exposed to wind and bright sun, and given no behavioural options for avoiding these stresses, they lose water by evaporation much more rapidly and will succumb after losing about 1/3 of their body weight.

In their normal habitats they cope with both temperature and evaporative water loss stresses by varying behaviour. They are out of water and actively moving about right through the middle of bright sunny days, with breezes blowing over them. Under these conditions they frequently visit nearby bodies of water and briefly immerse themselves, or at least moisten their body surfaces by rolling onto their sides. They often leave with mouths partly full of water. They carry this water with them until they encounter a food item, at which time they lose the water as they open their mouths. They show no signs of behavioural thermoregulation.

They respire at comparable rates in both water and air, using both their gills and skin. While normally active in air they show no signs of the 'diving syndrome'. They do not accumulate lactic acid in their bodies unless they carry out burst levels of activity (e.g. avoiding capture by a predator). A still unresolved aspect of their respiratory physiology centres on what happens when they are in their, usually water filled and probably almost anoxic, burrows. They hide from aerial or terrestrial predators in these burrows (though there are some, like some snakes, that enter the burrows) and they mate and lay their eggs in the burrows. The eggs also develop and hatch inside the burrows.

They appear to be capable of producing both ammonia and urea as end-products of nitrogen metabolism. Some shifting toward greater ureotelism occurs if they are kept out of contact with liquid water for extended periods. In nature behavioural adjustments probably obviate such shifts.

Rockskippers are dramatically different from mudskippers in many ways. They occur primarily on relatively exposed rocky shorelines. They are also diurnal, but are herbivores, grazing on algal growths on rocks, barnacle shells, etc. They spend over 90% of their time, both day and night, out of water, but move up and down the intertidal zone with tidally changing sea levels. Only infrequently and for short periods of time, will they move altogether out of the splash zone of breaking waves. Therefore they are frequently wet with spray, if not actually washed over by waves (Magnus 1966; Zander 1967, 1972a, b, 1974). They are usually very social, often feeding and resting in closely packed groups; aggressive interactions between them are rare. They take advantage of the physical complexities of their environments (e.g. exposed sunny surfaces, dark holes and crevices, tidepools, etc.) by making a wide variety of behavioural choices (Magnus 1966; Zander 1967; Brillet 1986; Brown, Gordon & Chin 1991). At least occasionally they will mate and lay their eggs in rock crevices and holes that are dry much of the time (Abel 1973).

Given these habitat and behavioural characteristics, it is apparent that the environmental physiological demands on rockskippers are in many respects more moderate than those on mudskippers. They frequently encounter high water salinities in small evaporating tidepools, but they leave such places almost immediately. The coastal regions where they live are often adjacent to extremely dry deserts, so they almost never encounter low salinity waters. Therefore their osmoregulatory capacities are rarely, if ever, tested. One result of this is that, in choice experiments, they behave as if they do not recognize fresh water when they encounter it.

They also can survive out of water for several days under moderate conditions. However, since evaporative water loss and thermal stresses are almost absent in their lives, their tolerance limits in these respects are not ecologically relevant. They also show no indications of behavioural thermoregulation.

Rockskippers carry on both aquatic and aerial respiration equally well (Martin & Lighton 1989; Brown, Gordon & Martin 1992; Martin 1993). Their gill filaments have thin cartilaginous reinforcing rods within them that help keep the entire gill surface area functional while they are out of water. They do not develop respiratory acidosis while in air. Chances are good that they lack the features of the diving syndrome.

They also produce both ammonia and urea, and shift toward ureotelism after extended periods out of contact with water (Rozemeijer & Plaut 1993). This is a laboratory phenomenon that probably never occurs in nature.

The origins of tetrapods

Detailed studies of other amphibious fish species from other parts of the world, belonging to several phylogenetically, mophologically, geographically, environmentally, and behaviourally diverse groups, further reinforce the evolutionary take-home lessons that are demonstrated so well by these African fishes (Gordon & Olson 1995; Graham 1997; Gordon 1998). As I see them, these lessons include the following.

(i) Living amphibious fishes are highly successful. Many are abundant and widely distributed. They show that it is possible to live both in and out of water, even to spend almost all of their time out of water, and still have the morphology of an unmodified fish.

(ii) It is not necessary to have jointed limbs, or lungs, or other specialized accessory respiratory organs, to be able to survive and be active on land.

(iii) It is possible to carry on successful amphibious lives with widely varied morphologies, in diverse habitats, and in diverse climates. There are no restrictions of such lifestyles to the humid tropics, or to freshwater environments. There are also no restrictions as to which developmental stages of fish life histories can show amphibious capacities.

(iv) If one makes the uniformitarian assumption that the present is a key to the past, the various scenarios that have been proposed by paleontologists and others concerning the evolutionary events and processes that may have been involved in the origins of the tetrapods (during the mid- to late Devonian period) remain plausible and possible. However, they do not begin to exhaust the full range of possible scenarios. The earliest known tetrapods were already highly evolved and diversified. They have been found in geographically far-flung localities. Combining what we know about the living amphibious fishes with what we know about the fossils leads me to believe it is probable that the tetrapods had multiple origins (from more than one species, or genera, or families, of sarcopterygian fishes) in several to many different places. In other words, the tetrapods were polyphyletic in origin.

This paper is not the proper locale for a detailed discussion of this topic. I have provided such a discussion in Gordon (1998). For those wishing to learn more about the state of present knowledge of tetrapod origins, based upon the fossil record and molecular biological evidence, recent reviews include Long (1995) and Carroll (1997).

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