VERTEBRATE AIR BREATHING AROSE IN FRESH WATERS
AND NOT IN THE OCEANS

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Packard (1974) recently suggested, in contrast to the consensus of opinion, that the evolution of air breathing in the early fishes most probably occurred in forms inhabiting seawater. He noted the much discussed occurrence of some Silurian gnathostome fossils in marine deposits (Romer, 1966, 1968; Thomson, 1969, 1971) and supported his argument with references to the known differences in O_2 solubility of fresh and salt water as well as to recent studies on the respiratory physiology of fishes. His argument was that conditions requisite for the evolution of air breathing existed in saltwater habitats, such as enclosed hypersaline estuaries and lagoons.

A review of his suggestions indicates that the evidence does not support them. While some marine fishes breathe air, the marine environment is and probably was an exceptional one for these adaptations. Consequently, we question the concept that air breathing (1) arose in salt water or (2) represents a response to the higher density and lower O_2 solubility of that medium. The several counter-arguments are summarized below.

DOES THE O_2 CONCENTRATION OF SEAWATER
IMPOSE A SEVERE PUMPING LOAD?

The solubility of O_2 is inversely proportional to the salinity of water; thus, and depending upon temperature, air-equilibrated fresh water contains about 25–30% more O_2 than water with a salinity of 35‰ (Randall, 1970). Packard used this observation to argue that marine fishes historically have had to deal with an environment which is relatively hypoxic compared to that of freshwater fishes. He concluded that a marine fish must expend 25–30% more energy for gill ventilation . . . (Packard, Table 3) in order to obtain the same amount of O_2 as a freshwater fish.

Is seawater sufficiently deoxygenated to impose energetically prohibitive limits on fish ventilation? Estimates of the metabolic cost of gill ventilation vary but using a value recently ob-

tained for freshwater fishes (10% of standard O_2 consumption; Hughes, 1973), we have charted the probable allocation of O_2 to gill ventilation and other oxidative processes in hypothetical salt- and freshwater fishes (Table 1; based on Packard's data). Assuming that the freshwater fish uses 10% of its metabolic rate for the acquisition of O_2 and that gill ventilation requires as much as 30% more energy on the part of the saltwater fish, then the latter would only be deficient by 3% in terms of supplying O_2 for its metabolic processes. In other words, it would have to increase its overall rate by that amount to maintain other functions. The ventilation efficiency might also decrease with the increase of ventilation forced by the lower O_2 content of seawater, and this could produce a disproportionately high caloric cost. However, even if the cost is doubled, the maximum reduction in the O_2 available to other tissues is only 11%.

The foregoing considerations indicate that only a slight adjustment of metabolic rate is needed to enable a fish to respire in seawater. Air-equilibrated seawater, although containing quantitatively less dissolved O_2 than fresh water, has the same partial pressure of O_2 (PO_2; about 150 torr at 1 atmosphere). The PO_2 of water directly affects diffusion rate and thus is a more important consideration, in terms of O_2 transfer at the gill surface, than is the O_2 content (Dejours, 1975). The estimated 3% to 11% deficiency in O_2 uptake that a marine fish might experience could be overcome by simply absorbing more O_2 from water passing over the gills.

Probably this deficiency is too small to establish a selective advantage sufficient to lead to the evolution of air breathing. Fishes such as eels and salmon migrate to and from salt water, apparently without encountering major limitations in their gill-ventilatory capability, although compensatory changes in hemoglobin-O_2 affinity do take place (Vanstone et al., 1964; Kaloustian and Poluhowich, 1976). There are a number of well-documented, long- and short-term respiratory adaptations of fishes (viz., changes in ventilation pattern, gill area or gill geometry; increased hemoglobin-O_2 affinity) that could be invoked to increase O_2 utilization by the required

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TABLE 1. *Comparison of the metabolic cost of gill ventilation and other oxidative processes in hypothetical fresh- and saltwater fishes. It is assumed that both fish have the same standard O_2 uptake rate and that branchial ventilation requires 10% of O_2 uptake for the freshwater fish but is 30% higher for the saltwater fish. Standard O_2 consumption rates are from Packard (1974); units are ml/g/h.*

	Freshwater fish	Saltwater fish
Standard O_2 consumption	0.169	0.169
O_2 used for gill ventilation (10%)	0.017	0.017
Additional O_2 used for gill ventilation in seawater (30%)	–	0.005
Total ventilatory cost	0.017	0.022
Net O_2 remaining for other processes	0.152	0.147
O_2 deficiency* of seawater (%)	–	3.3

$$* \ 100 - \left(\frac{0.147}{0.152} \times 100 \right)$$

or, increased O_2 uptake required to maintain other processes:

$$\left(\frac{0.174}{0.169} \times 100 \right) - 100 = 2.95 \cong 3\%.$$

amount (Hughes, 1960, 1973; Srivastava and Griffith, 1974). These would, in our opinion, supercede, both in selective advantage and efficacy, the evolution of air breathing in salt water through "an aberrant behavior pattern involving gulping at the surface" (Packard, 1974, p. 323).

But, under what circumstances would a marine fish encounter a situation in which some of its population started to gulp air? Ventilation cost is probably not monitored on the short time span and even an 11% increase should not be physiologically significant over a short time course. Blood PO_2 is monitored by fishes and, along with other properties, controls respiration; however, only large reductions in ambient PO_2 are likely to affect blood O_2 level sufficiently to cause compensation (Shelton, 1970). Observations show that low ambient PO_2 can drive fishes to the surface (Breder, 1941). This can easily be visualized as leading to early stages of bubble pickup (Gans, 1970). Air-breathing fishes, both freshwater and estuarine (Graham, 1976), breathe air in response to anoxia rather than to reduced O_2 solubility (see below).

CONDITIONS IN SILURIAN SEAS

Large and somewhat isolated bodies of seawater were common in the Silurian Period

(Moore, 1958, p. 178). Packard likened these to estuaries, the physical characteristics of which he used as a model in speculating about physical conditions. He postulated that elevated temperature and hypersalinity may have been common conditions in tropical and subtropical bodies of water that were cut off from the ocean. Both of these conditions reduce O_2 content and the former raises O_2 demand. Together with the ventilatory limitations initially imposed by salt water, these were, in Packard's opinion, a primary factor leading to the evolution of air breathing.

This hypothesis does not give adequate weight to the probability that early fishes could have adapted to elevated temperatures by adjusting their metabolic rate and thus reducing the temperature effect on ventilation requirements (as indicated in Packard's Table 1; Fry, 1971; Holeton, 1974). Other compensatory adjustments in O_2 utilization (e.g., changes in hemoglobin-O_2 affinity, and heart rate; Grigg, 1969; Randall, 1970) would also reduce this continuous effect. Packard emphasized the importance of low O_2 concentrations, resulting from changes in physical conditions affecting O_2 solubility; a major complication derives from the influence of anoxic conditions caused principally by biological oxygen demand. This lowers PO_2 and, if not balanced by diffusion from the atmosphere, may result in anoxia. Anoxia does occasionally occur in parts of some estuaries, but is far more commonly a phenomenon of tropical freshwater swamps, pools and streams. Anoxia, moreover, is a more frequent cause of fish kills in estuaries than are changes in O_2 solubility (Biggs, 1967; McHugh, 1967; Green, 1968). Recent fishes of tropical waters are generally thought to breathe air in order to enable them to endure such biologically caused anoxic conditions (Gans, 1970; Johansen, 1970).

Several additional reasons suggest it is unlikely that air breathing evolved in Silurian seas. First, salinity and temperature are significant environmental variables that directly affect aquatic species, with high temperature acting on factors such as metabolism, and hypersalinity acting on osmotic functions. The combined and probably synergistic effects would likely pose direct problems long before eliciting possible effects on respiration through a reduction of O_2 solubility. For example, the above-mentioned biotic respiration in a stagnant freshwater swamp can easily remove over 90% of the O_2 (Kramer and Graham, 1976), lowering the PO_2 to about 15 torr, while a 32 C increase in temperature combined with a 9‰ increase in salinity only changes the O_2 content of seawater by 50% (Sverdrup et al., 1964, p. 188), leaving the PO_2 near about 150 torr.

Such typically estuarine forms as cyprinodonts and mullet have physiological adaptations both for varying temperature and salinity (Green,

1968) but none known that permit aerial respiration. Also, the modern air-breathing species oppose rather than support the hypothesis for the estuarine-evolution of air breathing. The vast majority of air-breathing fishes occur in fresh waters (Gans, 1970; Roberts, 1975). The vast majority of marine air-breathing fishes occur in oxygenated intertidal zones and only breathe air while amphibious or when exposed during low tide. Only a few species are estuarine and, as indicated above, these breathe air primarily in response to low PO_2 (Graham, 1976).

It is also worth noting that not all Silurian coastal waters were hypersaline, but that they varied in salinity with some being brackish (Cocks and McKerrow, 1973). A number of characteristic Silurian evaporite deposits contain either a low diversity or no fossils (Moore, 1958). This implies that hypersaline conditions were localized, irregular, and in some regions became progressively more severe, leading to ecological instability, low species diversity, and, ultimately, to extinctions; none of these conditions would seem to favor successful adaptatons for air breathing. By contrast, the "freshwater evolution" of air breathing is thought to have occurred as an adaptation for conditions such as the regular tropical dry seasons which have a widespread effect and result in variable drying, but generalized seasonal stagnation, and anoxia in the shaded, wind-protected, freshwater streambeds and swamps (Carter and Beadle, 1931; Gans, 1970; Johansen, 1970).

METABOLIC SCOPE

An additional aspect of Packard's hypothesis is the increased metabolic scope associated with air breathing. Several air-breathing fishes have higher rates of O_2 consumption when respiring bimodally (simultaneously in air and water) than when breathing in water only (Grigg, 1965; Hughes and Singh, 1970, 1971). Packard suggested that air breathing allowed ancient fishes competitive superiority by expanding their metabolic scope above that of non-air breathers. Although this suggestion is attractive, it is not supported by the evidence. Packard stated (p. 322) "oxygen requirements of resting (airbreathing) fishes generally can be satisfied by aquatic respiration, but they make regular visits to the surface while foraging or swimming actively." This, although accurate for a few species (Grigg, 1965; Johansen, 1970), does not apply to most. For example, facultative air breathers only use their capability when water is an unsuitable respiratory medium and obligate air breathers must continually breathe air, regardless of activity level or water conditions (Carter, 1957). Both activity and physical factors (PO_2, PCO_2, pH, and temperature) influence the rate

of air breathing (Grigg, 1965; Johansen, 1970; Horn and Riggs, 1973 and references).

If the initial stages of air breathing provided an effective increase of metabolic scope under other than near-anoxic conditions, we might expect to find it to be widespread among fishes. However, except for *Neoceratodus* and marine intertidal species, which breathe air only when they are out of water, air-breathing fishes experience hypoxic stress periodically, or at some stage in their life histories. *Neoceratodus* is really exceptional. Air breathing enables it to increase its metabolic rate (Grigg, 1965). However, as Grigg has cogently argued, this is not the factor that influenced the initial evolution of the lung. Many air-breathing fishes have reduced gill area and use gills mainly for CO_2 discharge (see review by Packard, 1976). Air breathing may enable these forms to maintain a high level of O_2 consumption without adding gill area which would elevate the energetic cost (of ventilation) (Grigg, 1965).

CONCLUSIONS

Packard has succinctly reviewed the arguments in favor of a freshwater origin of air breathing in early fishes. He has not attempted to negate this widely-held concept but has instead attempted to provide a viable alternative hypothesis not requiring a freshwater sojourn and to argue that it represents a more probable scenario for this set of events. However, the supporting arguments at best plead a special case for the evolution of air breathing in a marine or estuarine environment. We suggest that there is not sufficient basis for arguing that the lower solubility of O_2 in seawater imposed important ventilatory limitations on marine fishes and, therefore, was a driving force in the evolution of air breathing. Similarly, the extreme salinity and temperature conditions required in the marine origin hypothesis to reduce water-O_2 solubility in estuaries sufficiently to cause respiratory stress and result in the evolution of air breathing, would have probably been lethal to most populations living in such environments before respiratory patterns were modified. The suggestion that increased metabolic scope was an important factor in the development of air breathing, while feasible, is not consistent with the manner in which most extant air-breathing species utilize this capability. The majority of Recent air-breathing species occupy habitats that become hypoxic, and there are none that appear to have developed air breathing solely to increase metabolic scope apart from the presence of a hypoxic stress. The key point is that air breathers are able to endure hypoxic conditions, and thus can live in waters subject to extreme fluctuations in O_2 level. The capacity to survive critical times, rather than a

minor but continuous energy cost, is much more likely to have driven the transition to air breathing.

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