

Multiple Sites of Gas Exchange¹

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SYNOPSIS. For many years the general body surface has been recognized as the primitive site of respiratory gas exchange in the animal kingdom. Even in simple animals such as the sea anemones, however, some specialization has occurred. In epifaunal species the tentacular crown appears to be the major site of gas exchange while in one infaunal species dermal papillae are more important. In both, the columnar body wall remains an additional site of O₂ uptake.

In the polychaete annelids an evolutionary trend can be seen from the predominance of the general body surface over simple, metameric gills to the predominance of highly specialized and branched anterior gills over the general body surface. In the oligochaetes reversion to the general body surface was followed in at least one species to specialization of the tail region to form a "lung."

Multiple sites clearly exist in the molluscs, but their relative importance is poorly known. Several sites exist in the echinoderms, the best known being the approximately equal allocation of O₂ uptake between modified tube feet and respiratory trees in the holothurians. Multiple sites of gas exchange persist even in the crustaceans, in temporal as well as spatial dimensions. Water breathers revert to cutaneous O₂ uptake following a molt, and air breathers have evolved an array of gas exchangers adapted to their new medium. This array is so diverse that it does not provide a single selection pressure for hemocyanin O₂ binding properties which, when compared broadly, remain indistinguishable from those of water breathers found in similar thermal regimes.

INTRODUCTION

When I was asked to participate in this symposium, I was assigned the topic of multiple sites of gas exchange with the external medium rather than the water-air transition. Although I noted that the use of the term bimodal to describe this condition would be rather special, I agreed to it. Now I find myself among veritable experts on air vs. water breathing, to which only a portion of the present contribution is relevant.

Here I shall discuss the existence of more than one site of gas exchange in several highly selected examples. I made the selection on the basis of the availability of phys-

iological information, and I shall not attempt to cover the much larger body of literature on morphology alone. It is clear, however, that morphological findings have been and will continue to be the basis of physiological investigation of this subject.

CNIDARIANS

One of the oldest generalizations in respiratory physiology is that the original, primitive site of gas exchange was the unspecialized outer epidermis. Indeed, this condition persists in many lower metazoans, and little should be said about it because the generalization is such an obvious truism that it has been investigated almost not at all.

Nonetheless, a number of years ago several of my students and I did examine the somewhat more subtle specializations that have already occurred in the cnidarians. Despite the proliferation of tentacular sur-

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face in large scyphozoans such as *Cyanea capillata*, there is no hard evidence to suggest that an appreciable volume of the O_2 taken up at any particular site is transported to any other site, and the rate is fairly closely related to ambient P_{O_2} (Fig. 1). Specialization for gas exchange with the medium has been demonstrated in the anthozoans, however, where it is correlated with increasing departure from strict oxyconformity relative to the pattern in *Cyanea* (Fig. 1; also Mangum and Van Winkle, 1973). An epifaunal sea anemone such as *Metridium senile* has a crown of hollow, internally and externally ciliated, and thus perfused tentacles that are ventilated passively as well as actively when extended into the water column. Not only is the tentacular crown the largest gas exchange surface, it is also the thinnest. The diameter of a tentacle is estimated to average about half a mm along its length, so each of the two epithelia must be considerably less than half that. Although the columnar body wall is much thicker, it is still thin enough to permit appreciable O_2 permeation through it into the circulating gastrovascular fluid (Sassaman and Mangum, 1972; Shick, 1991).

Thanks to histological sections of the New Zealand species *Calliactis conchicola* and *Phellia aucklandica* kindly made available to me by Cadet Hand (see 1975a, b), more exact comparison is now possible. In *C. conchicola*, the minimum thickness of the tentacular epithelium was 11 μm . In the same individual the very thinnest region of the body wall, where the mesogleal sphincter was absent, was at least 88 μm thick; the figure for thicker regions containing the mesogleal sphincter rose to almost 0.5 mm. Although one might expect the diffusivity of O_2 to be lower in mesoglea (55 to 300 μm , depending on location) than in epidermal and gastrodermal tissue, it is not a stirred layer and thus must still serve as a barrier to free diffusion. Even the upper end of the range for the tentacles, which may represent a diagonal section rather than the true dimensions, was only 30 μm . In *P. aucklandica*, the thickness of the tentacular epithelium ranged from 18 to 33 μm , and that of the body wall from 187 to 200 μm . In life, both surfaces are usually translucent

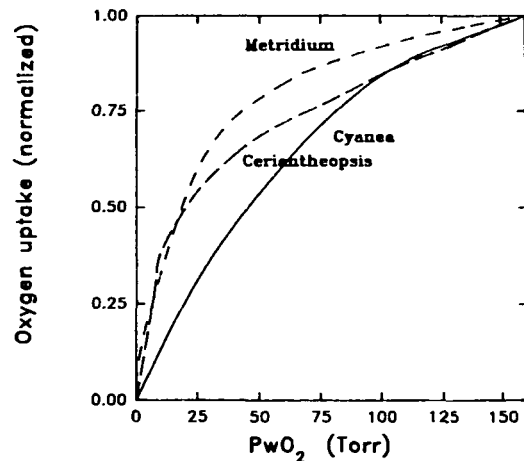


FIG. 1. The relationship between the normalized rate of O_2 uptake (V_{O_2}) and ambient P_{O_2} in the scyphozoan jellyfish *Cyanea capillata*, the epifaunal anthozoan *Metridium senile* and the tube-dwelling anthozoan *Ceriantheopsis americanus*.

and, when fully extended into the water column, both may become almost transparent. Clearly, gas exchange with the medium is carried out at more than one site. In these epifaunal, solitary anemones whose gas exchangers are generally well ventilated with normoxic water, the PO_2 gradient driving O_2 into both sites is known to be large in the case of the body column and believed to be large in the case of the tentacles. Nonetheless, the very size of the tentacular surface area implicates some specialization for gas exchange (Sassaman and Mangum, 1972).

Shick (1991) has questioned the inference that the tentacles are the primary site of O_2 entry into the animal. His reason was that, because the tentacles must continually replace discharged nematocytes, tentacular tissue must be more metabolically active than other tissue and the O_2 entering into the circulation here may be consumed before it reaches the gastrovascular fluid. In addition, mitochondrial density is greater in tentacular than in other tissue. While the rate of oxygen uptake may be greater as well, it is highly unlikely that such a thin epithelium is O_2 impermeable. Moreover, the rate of O_2 consumption by tentacular tissue would have to be 1) an order of magnitude greater than that of columnar tissue to counteract

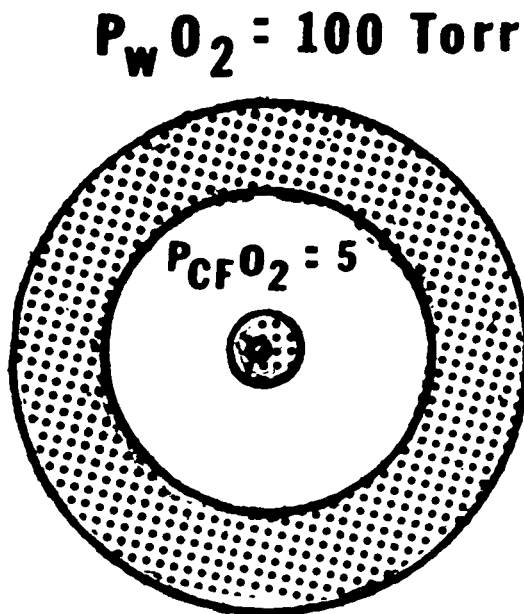


FIG. 2. Coelomic fluid and water P_{O_2} in the bloodworm *Glycera dibranchiata*.

the difference in diffusion distance, and 2) many times greater still to counteract the difference in surface area. Nonetheless, direct measurement of both O_2 permeability and consumption at the two sites is a feasible experiment that should certainly be performed, preferably in conjunction with dimensional analysis.

Burrowing or tube-building in severely hypoxic to truly anoxic sediments has occurred independently on several occasions in anthozoans, two of which were also investigated by Clay Sassaman and myself, with interestingly diverse results.

One was the burrowing anemone *Haloclava producta*, in which the tentacular surface is greatly reduced and active (ciliary) ventilation of it is abandoned in favor of the column, which is ventilated by peristaltic-like muscular contractions. The body wall is thinner in *Haloclava* than in an individual of *Metridium* of the same size, and additional thinning takes place in some 400–600 dermal papillae that are concentrated toward the upper end of the burrow, where water P_{O_2} should be maximal. Finally, gross tissue bulk is lower in *Haloclava* than in the more massive *Metridium*. In this burrowing species, the column is the more important

of the two sites of gas exchange (Sassaman and Mangum, 1972).

Ceriantheopsis americanus, commonly known as the tube anemone, diverged in the opposite direction. The allocation of surface area resembles that in *Metridium* more than *Haloclava*. In addition the species is infaunal and the column is now located within a tube, which is not ventilated; effectively, there is no driving P_{O_2} gradient into the columnar body wall. In addition, the column has no papillae. Diffusion distances across the tentacular epithelium are about $\frac{1}{6}$ of those across the columnar body wall. So, in this case, the column appears to be an insignificant site of gas exchange and multiplicity has essentially disappeared (Sassaman and Mangum, 1974).

ANNELIDS

The annelids represent a continuum between quite radical extremes from a respiratory and cardiovascular point of view. On several occasions I have suggested that the glycerid bloodworms represent a primitive condition in which O_2 is taken up through simple though thin walled gills, with physiological but no anatomical separation of afferent and efferent streams. O_2 is then transported throughout the open coelomic space by red blood cells (RBCs). The motive force is provided by a combination of coelomic cilia and the ventilatory movements of the muscular body wall which also change the shape of the coelomic cavity. The consequence is fluid movement of cyclical velocity and, so far as known, in not especially determinate pathways. The body wall is several mm thick, and thus O_2 uptake by the RBCs is restricted to the gills; the very geometry, however, suggests that O_2 permeation directly from the ventilatory stream into the outer body wall, driven by a large P_{O_2} gradient, is greater than O_2 permeation from the RBCs into the inner body wall and intestinal epithelium, driven by a much smaller P_{O_2} gradient. Although the O_2 carrying capacity of coelomic fluid is $7\times$ greater than that of the ventilation current, the driving P_{O_2} gradient is $1/20$ th of that moving O_2 into the outer body wall (Fig. 2). The RBCs are estimated to transport only about 20% of the total volume of O_2 con-

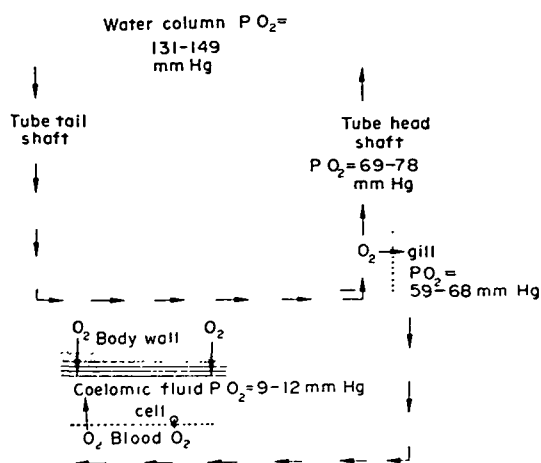


FIG. 3. Blood, coelomic fluid and water P_{O_2} in the terebellid *Amphitrite ornata*. The value for blood P_{O_2} is guesswork, based on the thickness of the branchial epithelium and the value for water P_{O_2} in the headshaft of the burrow; all others are measured values.

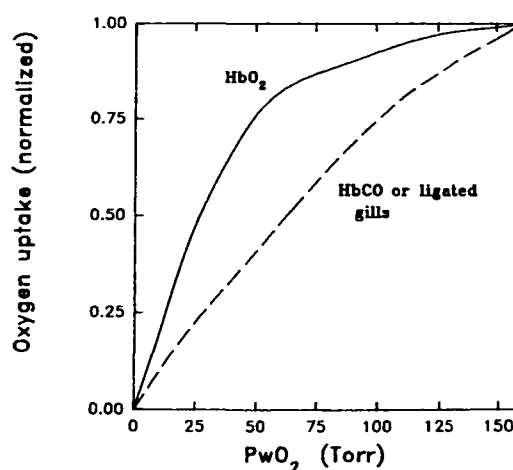


FIG. 4. The relationship between the normalized rate of O_2 uptake (\dot{V}_{O_2}) and ambient P_{O_2} in *Amphitrite ornata*.

sumed at all sites (Hoffman and Mangum, 1970; Mangum, 1977).

At the other end of the annelid spectrum lies a far more advanced group such as the terebellids. Branchial metamerism has all but disappeared and the gills are confined to a few anterior segments. This is correlated with an increasingly benthic, infaunal way of life, in which the animal spends much of its time positioned vertically with unvascularized feeding tentacles spread over the sand. One might suppose that the gills were moved anteriorly to facilitate ventilation. However terebellids ventilate backwards, tail to head, so the gills take up O_2 only after the water current has first been extracted by the body wall (Fig. 3). The anterior location simply keeps them in the fully extended position; these gills have only a low pressure hydrostatic skeleton and they would collapse against the head if the water were pumped tailwards. It is not clear whether the body wall is or is not too thick to permit O_2 permeation all the way through into the coelom; neither careful measurements of its thickness nor direct determination of O_2 permeation have been attempted. Nonetheless, a large fraction of direct O_2 uptake into unvascularized tissue is implicated by the decrease in P_{O_2} as the ventilation current moves through the burrow; the only ques-

tion is whether it is all consumed at the site of entry (Mangum *et al.*, 1975a).

In terebellids as in several other families the gills have now been partitioned within, to not only discrete afferent and efferent vessels but also to repeated shunts between them, which are more superficial than the arterial and venous vessels (see Wells *et al.*, 1980; Johnson, in Mangum, 1982a; Jouin and Toulmond, 1989). The major vessels lead to a complex, closed circulatory system, which in this family is equipped with a muscular pump but which has little or no microcirculation in deep tissue. The cardiovascular system contains a low O_2 affinity extracellular hemoglobin (Hb). In an O_2 transfer system analogous to the vertebrate maternal-fetal one, the large longitudinal blood vessels are bathed by coelomic fluid, which contains RBCs with a second Hb that has a high O_2 affinity (Mangum *et al.*, 1975a), and which I suggest is a relict of the ancestral condition. O_2 transport rises to a little more than half of the total at microenvironmental P_{O_2} (Mangum *et al.*, 1975a), and O_2 uptake assumes a far more regulatory pattern than in bloodworms, an evolutionary trend that can be reversed by either blocking the active site of the Hbs or by tying off the gills (Fig. 4).

The annelids also exemplify the use of multiple sites of gas exchange separated in

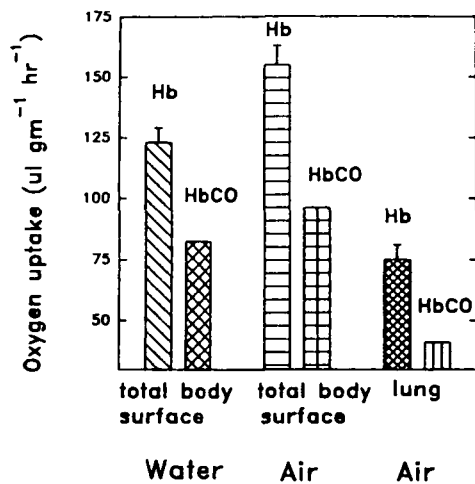


FIG. 5. The magnitude of O_2 uptake by different surfaces and in different media in the East African swampworm *Alma emini* with (Hb) and without (HbCO) functional hemoglobin.

time as well as space. The East African swampworm *Alma emini* spends the dry season burrowed in decomposing plant material, where it breathes moist air. During the rainy season the plant mats become water saturated and anoxic. The animal extends its richly vascularized tail out of the burrow and into the air, where it flattens and even becomes somewhat concave; it has been called a lung. Like many oligochaetes, these annelids do have a body wall microcirculation and, unlike many, in *Alma* it contains superficial components that are sites of O_2 uptake rather than delivery. Finally, the species is also found in fast flowing streams. So, under various conditions, it encounters not only air or water, but normoxic or hypoxic water.

Alma forms its lung in response not to hypoxia but to stagnation, a respiratory sensitivity which is common among aquatic animals. The lung, although not the only exchange surface, is disproportionately important in O_2 uptake. While the lung is only about 1.5% of total body surface, it alone is capable of taking up O_2 at a rate fully half that of the total body surface in air, and more than half that of the total body surface in water (Fig. 5). Like terebellid polychaetes, *Alma* has an extracellular Hb (in this case a high affinity molecule) that transports O_2 in a closed cardiovascular sys-

tem, although this species lacks both coelomic RBCs and Mb. The Hb carries at least 40% of the O_2 taken up by the total body surface, and more than 40% of that taken up by the lung (Mangum *et al.*, 1975b).

Beadle (1957) reported that the lung captures an air bubble and carries it back down into the hypoxic burrow. Our observations indicate that this is an infrequent event, however, and that the bubble is so small that it could supply the measured rate of aerobic metabolism for only a few minutes (Mangum *et al.*, 1975b).

MOLLUSCS

I would like to be able to discuss in quantitative detail the multiple sites of gas exchange in water-breathing molluscs, because they clearly exist. The mantle as well as the gill is highly vascularized. And in shelled groups the ventilatory current flushes the visceral mass as well as the gill and the mantle. Thus in mobile bivalves such as the mussel *Modiolus*, O_2 uptake into the blood occurs at a third site, a large sinus that can inflate the visceral mass (Booth and Mangum, 1978). While several investigators have presented evidence that O_2 uptake and transport in the blood is not especially important in bivalves that lack O_2 carriers (e.g., Booth and Mangum, 1978), there has been no serious attempt of which I am aware to quantitatively assess the allocation of gas exchange among the several sites. The exchange surface of the gill would seem to exceed that of the rest of the body. Nonetheless, we simply do not know what the contributions are.

For many years it has been known that the mantle becomes increasingly important in prosobranch gastropods with increasing exposure to air in the intertidal zone (reviewed by McMahon, 1988). The two sites appear to be equally effective in upper intertidal species, whereas subtidal species rely primarily on branchial gas exchange.

Finally, the distribution of gas exchange in aquatic pulmonates, true bimodal breathers, was also investigated in detail many years ago (Jones, 1961). Whereas cutaneous O_2 uptake is either somewhat more important than (57% of the total) or equally important as (50%) pulmonary O_2

uptake under normoxic conditions, the lung becomes increasingly important as water P_{O_2} drops, until it is responsible for 56–63% of the total in severely hypoxic water.

ECHINODERMS

Echinoderms have been repeatedly though not widely investigated. Most attention has been paid to the holothurians, a mind-blowing group if there ever was one. No less than three sites of gas exchange with the ambient medium and no less than three more or less separate circulatory systems have been described. The sites of gas exchange include: 1) the anteriorly located tentacles, and 2) the thin-walled dermal podia that run the length of the body, often in five clusters; both are modified tube feet that are components of the water vascular system (circulatory system No. 1). The remaining site of gas exchange with the medium is 3) the ventilated cloaca and its respiratory trees that both extend throughout the coelom (circulatory system No. 2) and, at least in some species, present an exchange surface to the hemal system (circulatory system No. 3). RBCs may be present in none to all three circulatory systems. Little is known of the properties of the Hbs in different compartments; a first step was taken by Baker (1988).

I once tried to determine the overall role of the Hbs in O_2 consumption of *Sclerodactyla briareus*, with no success at all because I was unable to block the active site with CO (Mangum, unpublished failure); later I learned that its affinity for CO is only $4\times$ higher than that for O_2 (L. J. Parkhurst, personal communication), as opposed to two orders of magnitude higher for mammalian Hb and three orders of magnitude higher for bloodworm Hb. We did conclude that the podia are unlikely to play an appreciable role in O_2 uptake in *Sclerodactyla*, on the grounds that the species is infaunal, ventilation of the burrow could not be detected, and the outer body wall is always covered by a thick black flocc (Mangum and Van Winkle, 1973); these observations were made on Woods Hole animals. During sublethal hypoxia, however, *Sclerodactyla* emerges from its burrow as much as half-way, and the podia become much more important (Brown and Shick, 1979). More-

over, in seaside waters of Virginia, individuals which are designated as the same species are epifaunal and the black flocc is absent; in these animals the podia could serve as sites of gas exchange under normoxic conditions (C. P. Mangum, unpublished observation).

Lawrence (1987) has questioned the respiratory significance of the hemal system on the grounds that it often lacks a lumen, occasionally it is not even continuous, and flow within it is tidal and weak, all of which are powerful arguments. If this proves to be the case, one wonders about the function of the RBC Hb sometimes present in this system. Even more baffling is the hemal system of *Isostichopus* (Herreid *et al.*, 1976), in which the microcirculation is so extensive that it is known as a *rete mirabile*. However, this *rete mirabile* is totally devoid of Hb, so it cannot possibly function as a counter-current multiplier of O_2 ! The answer may lie in its association with the digestive tract, for extensive gut plexi are common in the animal kingdom, though none has been so elegantly characterized as that in *Isostichopus*.

Brown and Shick (1979) made a strong case that O_2 uptake in epifaunal holothurians is about equally distributed between the respiratory trees and the other two sites of gas exchange. This seems to be true in species with and without Hbs, and with and without *rete mirabile* (Shick, 1983), which is quite remarkable.

O_2 uptake is also about equally divided between two sites in asteroids (Cole and Burggren, 1981). One is the aboral surface with its dermal branchiae, which lead to coelomic fluid, and the other the oral surface with its tube feet, which lead to the water vascular system. How much O_2 enters into each of the two fluid compartments is unknown; clearly the branchial epithelia are thinner than the walls of the tube feet.

CRUSTACEANS

More than one site of gas exchange is present in even large decapod crustaceans. For one dramatic and possibly ubiquitous example I refer the reader to the proceedings of a symposium held last year at this meeting: *viz.* the transient reversion to cutaneous

TABLE 1. Hemocyanin oxygen affinity in water and air-breathing brachyurans from similar latitudes.

Species	Medium	Gas exchanger	P_{50} (Torr) 2.5°C, pH 7.5	Source
<i>Calappa philargius</i>	water	gill	17	Mangum (1982b)
<i>Callinectes arcuatus</i>	water	gill	14	Reese and Mangum (1994)
<i>C. bellicosus</i>	water	gill	9	Reese and Mangum (1994)
<i>C. toxotes</i>	water	gill	11	Reese and Mangum (1994)
<i>Cataleptodius floridanus</i>	water	gill	15	Reese and Mangum (1994)
<i>Charybdis riversandersonii</i>	water	gill	10	Mangum (1982b)
<i>Lambrus validus</i>	water	gill	13	Mangum (1982b)
<i>Menippe adina</i>	water	gill	16	Reese and Mangum (1994)
<i>M. adina-mercenaria</i> hybrid	water	gill	20	Reese and Mangum (1994)
<i>Naxioides manillata</i>	water	gill	19	Mangum (1982b)
<i>Panopeus lacustris</i>	water	gill	5	Reese and Mangum (1994)
<i>Portunus pelagicus</i>	water	gill	18	Mangum (1982b)
<i>Scylla serrata</i>	water	gill	8	Mangum (1982b)
<i>Cardisoma carnifex</i>	bimodal	branchiostegal epithelium and gills	13	Burggren and McMahon (1981)
<i>C. guanhumi</i>	bimodal	branchiostegal epithelium and gills	3	Redmond (1968)
<i>Goniopsis cruentata</i>	bimodal	?	20	Young (1972)
<i>Uca crenulata coloradensis</i>	bimodal	tufted branchiostegal epithelium and gills	10	Reese and Mangum (1994)
<i>U. princeps monilifera</i>	bimodal	tufted branchiostegal epithelium and gills	14	Reese and Mangum (1994)
<i>Aratus pisoni</i>	air	?	8	Young (1972)
<i>Birgus latro</i>	air	tufted branchiostegal epithelium and gills	11	Morris <i>et al.</i> (1988)
<i>Coenobita clypeatus</i>	air	tufted branchiostegal epithelium and gills	10	Morris and Bridges (1986)
<i>C. brevimanus</i>	air	tufted branchiostegal epithelium and gills	15	Burggren and McMahon (1981)
<i>Gecarcinus lateralis</i>	air	tufted branchiostegal epithelium and gills	17	Taylor and Davies (1981)
<i>Gecarcoidea lalandii</i>	air	tufted branchiostegal epithelium and gills	11	Mangum (1982b)
<i>Ocypode saratan</i>	air	tufted branchiostegal epithelium and gills	21	Morris and Bridges (1985)
<i>Varuna litterata</i>	air	?	8	Mangum (1982b)
<i>Pseudothelphusa garmani</i>	air	invaginated lung	26–28*	Innes and Taylor (1986)

* pH not specified.

O₂ uptake in postmolt animals (Mangum, 1992).

Multiple sites of gas exchange were also used on an evolutionary timescale as land crabs progressively underwent the transition from facultative to obligatory air-

breathing. One remarkable organ found in the ocypodid *Scopimera* was described by Maitland (1986). Some 60% of total O₂ uptake appears to occur through "high windows," thinned areas of the cuticle and epidermis overlying sinuses in the meral seg-

ments of the walking legs; the other adaptations for terrestrial gas exchange described below are not found in this species.

An evolutionary succession of gas exchangers in the transition from water to air has been formulated by Innes and Taylor (1986), as follows: 1) a conventional brachyuran gill, 2) a gill in conjunction with a "cutaneous lung," which is actually the roof of the branchial cavity or the branchiostegal epithelium, and 3) the branchiostegal epithelium in conjunction with an invagination of it, also called a "lung." Although Innes and Taylor (1986) do not make the distinction (possibly due to scarcity of information), category 2) should probably be further divided because, in some species, this epithelium has acquired a tuft or arborization, which enhances its surface area, and in some it has not.

On the basis of a rise in postbranchial blood P_{O_2} , Innes and Taylor (1986) suggested that the transition from 1) to 3) is also an evolution from a diffusion-limited to a perfusion-limited gas exchanger. Ventilation appears to decrease and, not surprisingly, blood P_{CO_2} increases, which is offset by a concomitant rise in HCO_3^- . These crabs are said to have reached the "lungfish stage of evolution" because they take up O_2 primarily at the branchiostegal membrane but they excrete CO_2 primarily by periodically flushing their gills with water.

Innes and Taylor's (1986) sample, which was probably constrained to include only reports that contained blood gas data, suggests that hemocyanin (Hc) O_2 affinity decreases with emergence onto land. But, if the database is expanded to include investigations made with alternative goals in mind, this generalization does not hold up. Table 1 is an update of a comparison of Hc O_2 affinity values in air and water breathers that I published 10 years ago (Mangum, 1982b). Like the earlier compilation, it includes only species found at similar depths and latitudes, thus eliminating the confounding and, I suggest, overriding effect of temperature. I chose tropical and subtropical latitudes rather than the temperate zone to maintain similar sample sizes; fewer land crabs are found in the temperate zone while

the number of reports on temperate zone water breathers is almost prohibitively large. My earlier comparison of necessity included a large taxonomic variety of crustaceans because so few data for tropical water breathers were available at the time. Sufficient progress has now been made that it can be restricted to brachyuran crabs. Nonetheless, when the comparison is made this broadly, there is no difference in Hc O_2 affinity between 13 water breathers and 14 bimodal and air breathers (Fig. 6). If air and bimodal breathers are treated separately, there is still no discernible difference (Fig. 6).

McMahon and Burggren (1988) correctly pointed out that inferences based on old data may include as well the effects of organic cofactors, which were unknown at the time, as well as intrinsic molecular properties. In the present comparison, however, obfuscation of the trend is unlikely; organic cofactors should *exaggerate* the trend inferred by Innes and Taylor (1986) if it exists. The known organic co-factors *raise* O_2 affinity, which may be artificially high in the water-breathers, but they would be unlikely to have appreciable effects in the air-breathers, the Hcs of which are often either insensitive or poorly sensitive to them. So the intrinsic affinity would be essentially the same as shown in the air breathers and possibly even lower in the water breathers (In fact, the data I reported in 1982 were collected on samples taken quickly from animals held overnight in their respective media; it is unlikely that appreciable levels of lactate and/or urate were present). Nonetheless, if one uses only recent data for purified Hcs, there is still no difference (Fig. 6).

I make this point not to register a minor disagreement but rather to suggest that the diversity of O_2 affinity values in air-breathers reflects a comparable diversity of gas exchange systems, and that this diversity may vastly exceed that portrayed by the information presently available. In support of this inference are the very recent results reported in this volume by Steve Morris: when the comparison is made at the congeneric level, presumably narrowly constraining or perhaps even eliminating the systemic diversity, differences in intrinsic

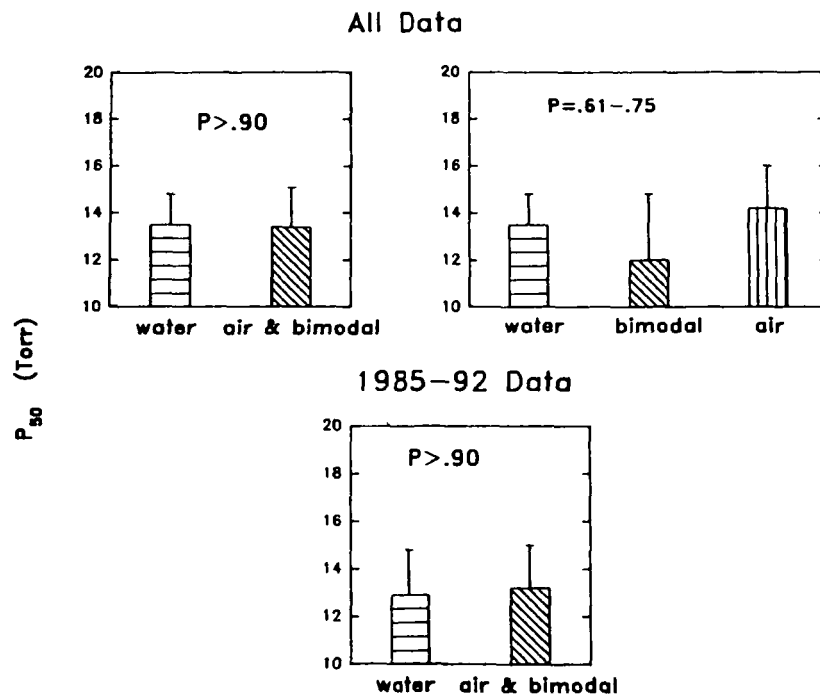


FIG. 6. Hemocyanin O_2 affinity (25°C, pH 7.5, physiological saline) in water- and air-breathing brachyuran crustaceans. The two panels at the top show all data available to the author at the time of writing (Table 1), whereas the bottom panel shows recent data for intrinsic O_2 affinity (i.e., stripped of organic co-factors); none show the recent findings made by Morris and Bridges (1994). The vertical bars represent SEM.

O_2 affinity can be related to the water-air transition.

Crustaceans are sometimes regarded as the laboratory rats of comparative respiratory physiology, and it is certainly true that they have received far more attention than all other groups combined. Nonetheless, we need to know a lot more about different kinds of air-breathing among crustaceans as well as the rest of the animal kingdom.

REFERENCES

- Baker, S. M. 1988. Hemoglobin function in a burrowing sea cucumber, *Paracaudina chilensis*. Master's Thesis, University of Oregon, Eugene.
- Beadle, L. C. 1957. Respiration in the African swampworm *alma emini*. *J. Exp. Biol.* 34:1-10.
- Booth, C. E. and C. P. Mangum. 1978. Oxygen uptake and transport in the lamellibranch mollusc *Modiolus demissus*. *Physiol. Zool.* 51:17-38.
- Brown, W. I. and J. M. Shick. 1979. Bimodal gas exchange and the regulation of oxygen uptake in holothurians. *Biol. Bull.* 156:272-288.
- Burggren, W. W. and B. R. McMahon. 1981. Hemolymph oxygen transport, acid-base status, and biomineral regulation during dehydration and rehydration in three terrestrial crabs, *Cardisoma*, *Birgus*, and *Coenobita*. *J. Exp. Zool.* 218:53-64.
- Cole, R. N. and W. W. Burggren. 1981. The contribution of respiratory papillae and tube feet to oxygen uptake in the sea star *Asteria forbesi* (Desor). *Mar. Biol. Lettr.* 2:279-288.
- Hand, C. 1975a. Descriptions of two New Zealand sea anemones (Actinaria: Hormathiidae). *New Zeal. J. Mar. Freshw. Res.* 9:493-507.
- Hand, C. 1975b. Redescription of the sea anemone *Phellia aucklandica* (Actinaria: Sagartiidae) from New Zealand. *New Zeal. J. Mar. Freshw. Res.* 9:529-538.
- Herreid, C. F., V. F. LaRussa, and C. R. DeFesi. 1976. Blood vascular system of the sea cucumber *Stichopus moebii*. *J. Morph.* 150:423-451.
- Hoffmann, R. J. and C. P. Mangum. 1970. The function of coelomic cell hemoglobin in the polychaete *Glycera dibranchiata*. *Comp. Biochem. Physiol.* 36:211-228.
- Innes, A. and E. W. Taylor. 1986. The evolution of air-breathing in crustaceans: A functional analysis of branchial, cutaneous and pulmonary gas exchange. *Comp. Biochem. Physiol.* 85A:621-637.
- Jones, J. D. 1961. Aspects of respiration in *Planorbis corneus* L. and *Lymnaea stagnalis* L. (Gastropoda: Pulmonata). *Comp. Biochem. Physiol.* 4:1-29.
- Jouin, C. and A. Toulmond. 1989. The ultrastructure of the gill of the lugworm *Arenicola marina* (L.) (Annelida, Polychaeta). *Acta Zool.* 70:121-129.

- Lawrence, J. M. 1987. *A functional biology of echinoderms*. Johns Hopkins Univ. Press, Baltimore.
- Maitland, D. P. 1986. Crabs that breathe air with their legs. *Nature* 319:494-495.
- Mangum, C. P. 1977. The annelid hemoglobins: A dichotomy in structure and function. In D. J. Reish and K. Fauchald (eds.), *Essays in memory of Dr. Olga Hartman*, pp. 407-428. Allan Hancock Foundation Spec. Publ., Univ. So. Calif., Los Angeles.
- Mangum, C. P. 1982a. Structure and function of invertebrate gills. In D. Houlihan and T. Shuttleworth (eds.), *Gills*. Symp. Soc. Exp. Biol., pp. 77-98. Cambridge Univ. Press, Cambridge.
- Mangum, C. P. 1982b. On the relationship between P_{50} and the mode of gas exchange in tropical crustaceans. *Pacif. Sci.* 36:403-410.
- Mangum, C. P. 1992. Physiological aspects of a molt in the blue crab *Callinectes sapidus*. *Amer. Zool.* 32:459-469.
- Mangum, C. P. and W. Van Winkle. 1973. Responses of aquatic invertebrates to declining oxygen conditions. *Amer. Zool.* 13:529-541.
- Mangum, C. P., G. Lykkeboe, and K. Johansen. 1975b. Oxygen uptake and the role of hemoglobin in the East African swampworm *Alma emini*. *Comp. Biochem. Physiol.* 52A:477-482.
- Mangum, C. P., B. L. Woodin, C. Bonaventura, B. Sullivan, and J. Bonaventura. 1975a. The role of coelomic and vascular hemoglobins in the annelid family Terebellidae. *Comp. Biochem. Physiol.* 51A:281-294.
- McMahon, R. F. 1988. Respiratory response to periodic emergence in intertidal molluscs. *Amer. Zool.* 28:97-114.
- McMahon, B. R. and W. W. Burggren. 1988. Respiratory gas exchange and transport. In W. W. Burggren and B. R. McMahon, *Biology of land crabs*, pp. 249-297. Cambridge Univ. Press, New York.
- Morris, S. and C. R. Bridges. 1985. An investigation of haemocyanin oxygen affinity in the semi-terrestrial crab *Ocypode saratan* Forsk. *J. Exp. Biol.* 117:119-132.
- Morris, S. and C. R. Bridges. 1986. Oxygen binding by the hemocyanin of the terrestrial hermit crab *Coenobita clypeatus* (Herbst)-The effect of physiological parameters *in vitro*. *Physiol. Zool.* 59:606-615.
- Morris, S. and C. R. Bridges. 1994. Properties of respiratory pigments in bimodal breathing animals: Air and water breathing by fish and crustaceans. *Amer. Zool.* 34:216-228.
- Morris, S., P. Greenaway, and B. R. McMahon. 1988. Adaptations to a terrestrial existence by the robber crab *Birgus latro*. *J. Exp. Biol.* 140:477-491.
- Redmond, J. R. 1968. Oxygen-hemocyanin relationships in the land crab *Cardisoma guanhumi*. *Biol. Bull.* 122:252-262.
- Reese, J. E. and C. P. Mangum. 1994. Subunit composition and O_2 binding of the crustacean hemocyanins: Interspecific relationships. (in review)
- Sassaman, C. and C. P. Mangum. 1972. Adaptations to environmental oxygen levels in infaunal and epifaunal sea anemones. *Biol. Bull.* 143:657-678.
- Sassaman, C. and C. P. Mangum. 1974. Gas exchange in a cerianthid. *J. Exp. Zool.* 188:297-305.
- Shick, J. M. 1983. Respiratory gas exchange in echinoderms. In M. Jangoux and J. M. Lawrence (eds.), *Echinoderm studies*, Vol. 1, pp. 67-110. A. A. Balkema, Rotterdam.
- Shick, J. M. 1991. *A functional biology of sea anemones*. Chapman & Hall, London.
- Taylor, A. C. and P. S. Davies. 1981. Respiration in the land crab, *Gecarcinus lateralis*. *J. Exp. Biol.* 93:197-208.
- Wells, R. M. G., P. J. Jarvis, and S. E. Shumway. 1980. Oxygen uptake, the circulatory system, and haemoglobin function in the intertidal polychaete *Terebella haplochaeta* (Ehlers). *J. Exp. Mar. Biol. Ecol.* 46:255-277.
- Young, R. E. 1972. The physiological ecology of haemocyanin in some selected crabs. II. The characteristics of haemocyanin in relation to terrestriality. *J. Exp. Mar. Biol. Ecol.* 10:193-206.