# Oxygen Transport in the Leatherback Sea Turtle *Dermochelys coriacea*

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**Abstract**

*We have investigated aerobic metabolism and blood $O_2$ transport properties of the leatherback sea turtle (*Dermochelys coriacea*). During nesting, at a body temperature of 29° C, resting ventilation (9.2 ± 1.7 mL $min^{-1}$ $kg^{-1}$) and $O_2$ consumption (0.25 ± 0.04 mL $min^{-1}$ $kg^{-1}$; three turtles) were slightly below values given for other sea turtles. Tidal volume was considerably smaller than in other turtles (4.0 ± 1.06 mL $kg^{-1}$) suggesting that* Dermochelys *has small lungs. Blood (measured in four turtles) had an extremely high Hb concentration (15.6 ± 1.8 g $dL^{-1}$), hematocrit (39% ± 1.2%), and carried 21 ± 2.5 mL · $dL^{-1}$ blood, which exceeds the blood $O_2$ carrying capacity of other sea turtles and was similar to that of most mammals. Pectoral muscle myoglobin content, indicative of tissue $O_2$ stores, was 4.9 g $dL^{-1}$, twice that of other sea turtles. The $P_{50}$, however, was similar to that of the loggerhead sea turtle: 31 and 40 mmHg for blood equilibrated with 2.2% (pH 7.84) and 5% (pH 7.52) $CO_2$, respectively. We suggest that leatherback turtles rely on their enhanced blood and tissue $O_2$ stores rather than the lung $O_2$ store during deep dives.*

## Introduction

Sea turtles are among the deepest-diving vertebrates, reaching depths similar to those of mammalian divers such as elephant seals and sperm whales (Berkson 1967; Kooyman 1989). In diving mammals, natural dives in the range of 20–50 min appear to be made aerobically because of short surface times between dives and, in Weddell seals, the lack of any lactate accumulation in the blood during dives. These long aerobic dives are possible because of enhanced blood and tissue $O_2$ stores resulting from increased hematocrit and high myoglobin concentrations (Lenfant 1969; Kooyman,

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Castellini, and Davis 1981; Snyder 1983; Qvist et al. 1986). The lung $O_2$ store will be eliminated because of collapse at depth (Scholander 1940).

In contrast, the sea turtle's total blood and tissue $O_2$ stores are similar to those of its nondiving relatives (Berkson 1966; Lutz and Bentley 1985), and green and loggerhead turtles use their lung as the principal $O_2$ store during diving (Prange and Jackson 1976; Lapennas and Lutz 1982; Wood, Gatz, and Glass 1984). The depths to which turtles dive must be an important determinant of usable $O_2$ stores and aerobic diving limits because of the effects of hydrostatic pressure on gas in the lung. There is evidence to suggest that deep-diving turtles experience lung collapse because of their compliant respiratory system (Tenney et al. 1974; Lutcavage, Lutz, and Baier 1989). In green sea turtles, Berkson (1967) found that lung collapse would occur at pressures equivalent to depths ranging from 80–160 m.

Among sea turtle species, the deepest dives are consistently recorded in the leatherback sea turtle, *Dermochelys coriacea*. While most sea turtles are found in relatively shallow coastal waters, the leatherback turtle displays a preference for deep water (Hendrickson 1980), diving frequently to depths ranging from 100 to over 1,000 m (Eckert et al. 1986). If their lung compliance is assumed to be similar to that of other sea turtles, leatherback turtles must dive without access to a lung $O_2$ store, as the lungs will collapse at these depths. Consequently, we undertook a field study to measure aerobic metabolism along with the $O_2$ transport properties of blood with a view to obtaining a greater understanding of how these properties may affect their diving abilities.

## Material and Methods

Respiratory measurements and blood collection were performed on female leatherback turtles nesting on Sandy Point Beach, Saint Croix, U.S. Virgin Islands (May, 1989). Air and surf temperatures on the beach during measurement periods ranged from 21° to 24°C and from 25° to 26°C, respectively. In order to reduce the level of disturbance, body mass was not measured but estimated from a length-weight regression established from nesting records of leatherback turtles at Sandy Point (S. Basford, R. Boulon, R. Brandner, unpublished data).

Ventilation volume ($\dot{V}_E$) and respiratory gas exchange were measured during egg deposition in three turtles by placing a specially constructed helmet equipped with an expandable plastic sleeve over the turtle's head. The helmet fitted snugly (to reduce dead space), but did not restrict the movement of the head and jaws during ventilation. A 34-L (±3 L) gas collec-

tion bag (Douglas) was attached to the helmet by a low-resistance one-way respiratory valve (no. 2600, Hans Rudolph). Expired gas was collected and ventilation frequency ($f$) recorded until the bag was completely filled. Breathing frequency was also recorded before the gas collection apparatus was placed on the turtle's head. Expired gas samples were then sealed and analyzed (within 3 h of collection) for $CO_2$ and $O_2$. The partial pressures of gases in the sample were measured by first humidifying the sample and passing it into a Radiometer blood gas analyzer calibrated with precision mixed gases. Preliminary tests with known gas mixtures showed that samples could be stored at least 8 h without change in composition.

Oxygen uptake ($\dot{V}O_2$) was estimated by multiplying the volume of dry expired gas, corrected by the Haldane transformation for the fractional difference in nitrogen concentration of inspired and expired air (Prange and Jackson 1976), by the difference in fractional concentration of inspired and expired $O_2$. Carbon dioxide production was calculated from the product of corrected expired volume and the difference in fractional concentration of $CO_2$ in expired and inspired air. Tidal volume ($V_T$) was estimated by dividing the total gas volume collected by the number of breaths during the sampling period. All gas volumes were corrected to the turtle's body temperature, which was approximated by measuring the temperature of the eggs in the center of the egg mass during laying (Mrosovsky and Pritchard 1971) with a bead thermistor (8502-50, Cole Palmer).

### *Blood Sampling*

Blood samples were obtained from four leatherback turtles during egg deposition with a 16-gauge spinal needle attached to a 50-mL disposable syringe. The dead space of the needle and the syringe contained sodium heparin to prevent coagulation. Venous blood was withdrawn from the cervical sinus as described by Owens and Ruiz (1980). Depth of penetration varied from 7 to 14 cm, depending on the size of the turtle. Blood samples were stored on ice until they could be processed upon return to the lab, at which time a 2-mL sample was decanted and frozen for hemoglobin analysis and 50 mL was used for hematocrit determination. The remainder of the blood was refrigerated on ice and later used for construction of blood dissociation curves.

### *Blood $O_2$ Dissociation Curves*

Approximately 7-mL aliquots of blood were decanted into each of two round-bottom, temperature-controlled tonometer flasks (25°C). The re-

mainder of the blood sample was stored on ice. Each aliquot of blood was fully equilibrated with precision gas mixtures (Liquid Carbonic) of $CO_2$ (2.2% or 4.8%) balanced with air or $CO_2$ balanced with nitrogen. The partial pressure of $O_2$ and $CO_2$, as well as pH, were measured at 25°C with a digital blood gas analyzer (PHM73/Mk2, Radiometer, Copenhagen). Oxygen content was determined by the Tucker method (Tucker 1967) with a purpose-built chamber thermostated to 40°C and a Radiometer PHM 72/Mk2 blood gas analyzer and $P_{O_2}$ electrode.

A two-point calibration of the $P_{O_2}$, $P_{CO_2}$, and pH electrodes was performed at the beginning of the day. The $P_{O_2}$ electrode was calibrated with zero solution (1 mg $Na_2SO_3$/5 mL of 0.01 M $Na_2B_4O_7$) and air-saturated saline, the $P_{CO_2}$ electrode with the precision mixed gases, and the pH electrode with precision buffers (pH 7.00 and 8.00). The calibration of $P_{O_2}$ and pH was checked between blood sample readings, while the $P_{CO_2}$ calibration was checked at the beginning and end of every complete blood curve measurement.

In order to construct blood dissociation curves, the $P_{O_2}$ of mixed blood samples was determined at various increments of saturation. Approximate levels of $O_2$ saturation (0%, 10%, 20%, 30%, 40%, 50%, 65%, 90%, and 100%) were achieved by mixing deoxygenated blood (blood equilibrated with $N_2$ + $CO_2$) and oxygenated blood (equilibrated with air + $CO_2$) in appropriate proportions in glass syringes fitted with 19-gauge needle hubs. The exact volume of blood mixed was determined by weighing the syringes and hubs on an analytical balance (Mettler A300) before and after they were filled with blood. Once the proper weight ratio had been achieved, the two needle hubs were joined with a short length of PE 90 tubing and their contents mixed anaerobically by alternately expelling the blood from one syringe to the other. The $P_{O_2}$, $P_{CO_2}$ and pH of the mixed blood sample were then recorded.

Hematocrit (5 min centrifugation at 13,500 *g*) and $O_2$ content of deoxygenated ($[O_2]_{deoxy}$) and oxygenated ($[O_2]_{oxy}$) blood were measured, in triplicate, at the beginning and upon completion of blood curve determinations. Any blood remaining in the tonometers was discarded, the gas mixture to the tonometer changed to the other $CO_2$ level, and the tonometers refilled with a new aliquot of blood from the remaining sample.

Hemoglobin concentration ([Hb]) was determined in triplicate from thawed whole blood samples with a Sigma Total Hemoglobin diagnostic kit (no. 525-A). Absorbance was recorded at 540 nm with a recording spectrophotometer (SP8-400 UV/VIS, Pye Unicam, Cambridge, U.K.). Oxygen-carrying capacity of the blood was calculated by multiplying [Hb] by 1.34, the amount of $O_2$ (mL) bound to each gram of hemoglobin (Ganong 1983).

In order to determine the exact level of saturation of the mixed sample, the calculated $O_2$ content was divided by the total oxygen carrying capacity of the sample:

$$\frac{([O_2]_{deoxy} \times vol_{deoxy}) + ([O_2]_{oxy} \times vol_{oxy})}{(vol_{deoxy} + vol_{oxy}) \times O_2\text{-carrying capacity}},$$

where $vol_{deoxy}$ and $vol_{oxy}$ are the volumes (mL) of deoxygenated and oxygenated blood, respectively. The final curves presented in figure 1 were fitted by eye. Because of the small difference in pH between oxygenated and deoxygenated blood, no correction was applied when the curve was fitted.

Myoglobin content ([Mb]) was determined in frozen tissue samples obtained from an adult leatherback turtle (914 kg) that died shortly after capture in Wales in 1989 (J. Davenport, personal communication). Pectoral muscle sections weighing 0.5 g were thawed and processed for [Mb] according to the technique described by Reynafarje (1963). All values in the text, tables, and figures are given as mean ± SD.

## Results

At an estimated body temperature of 29°C, resting ventilation and metabolism of nesting leatherback turtles (table 1) were slightly below values given for other sea turtles. Mean $\dot{V}O_2$ and minute ventilation were 0.25 ± 0.04 and 9.2 ± 1.7 mL $min^{-1}$ $kg^{-1}$, respectively, for a mean air convection requirement ($\dot{V}_E/\dot{V}O_2$) of 37.1 ± 5.5 mL body temperature and pressure saturated (BTPS)/mL standard temperature and pressure, dry (STPD). Mean $CO_2$ production was 0.19 mL $min^{-1}$ $kg^{-1}$, resulting in a respiratory quotient (RQ) of 0.77 ± 0.19. While depositing eggs, turtles took an average of 2.3 ± 0.17 breaths $min^{-1}$ at fairly regular intervals before and during gas collection, with an estimated mean $V_T$ ranging from 0.82 to 1.7 L. Although we were unable to measure $\dot{V}_E$ after egg deposition, turtles became quite active while covering the nest and *f* increased severalfold.

### *Oxygen-carrying and Storage Capacity of Blood and Tissue*

Average hematocrit and hemoglobin concentrations were 39% ± 1.2% and 15.6 ± 1.8 g $dL^{-1}$, respectively, yielding a mean $O_2$-carrying capacity of nearly 21 mL · $dL^{-1}$ blood (table 2). Mean cellular hemoglobin concentration (MCHC) was 0.41 ± 0.04 g $dL^{-1}$. Myoglobin content of pectoral muscle obtained from salvaged tissue was 4.9 ± 0.33 mg $g^{-1}$.

TABLE 1

*Summary of respiratory variables in the leatherback sea turtle,* Dermochelys coriacea

| | Turtle Identification No. | | |
|---|---|---|---|
| | AAG854 | VI1266 | AAG270 |
| Mass[a] (kg) | 280 | 306 | 328 |
| $\dot{V}_E$ (BTPS) (mL $min^{-1}$ $kg^{-1}$) | 7.33 | 9.90 | 10.45 |
| $\dot{V}O_2$ (STPD) (mL $min^{-1}$ $kg^{-1}$) | .23 | .23 | .29 |
| $\dot{V}CO_2$ (STPD) (mL $min^{-1}$ $kg^{-1}$) | .14 | .23 | .21 |
| RQ | .62 | .98 | .72 |
| $V_T$ (mL $kg^{-1}$) | 2.9 | 4.2 | 5.0 |
| $\dot{V}_E/\dot{V}O_2$ (mL BTPS/mL STPD) | 32.4 | 43.2 | 35.9 |
| $f$ ($min^{-1}$) | 2.4 | 2.4 | 2.1 |
| Body temperature (°C) | 29.2 | 28.8 | 28.7 |

[a] Mass estimate based on length-weight regression of Sandy Point leatherback turtles (R. Boulon, R. Brandner, and S. Bassford, unpublished data).

*Oxygen Dissociation Curves*

The $O_2$ dissociation curves of *Dermochelys* were sigmoid in shape, with $P_{50}$ (50% saturation) values of 31 and 40 mmHg at $P_{CO_2}$ levels of 2.2% and 4.8%,

TABLE 2

*Blood $O_2$ transport in the leatherback sea turtle*

| Turtle Identification No. | Hematocrit (%) | Hemoglobin Content (g $dL^{-1}$) | $O_2$-carrying Capacity (mL · $dL^{-1}$) | MCHC (g $dL^{-1}$) |
|---|---|---|---|---|
| AAG861 | 36.5 | 13.3 | 17.8 | .37 |
| AAG854 | 38 | 17.8 | 23.8 | .46 |
| AAR907 | 39 | 15.7 | 21.0 | .41 |
| AAG270 | 39 | 15.7 | 21.1 | .41 |

Note. Values are means of three determinations on each animal.

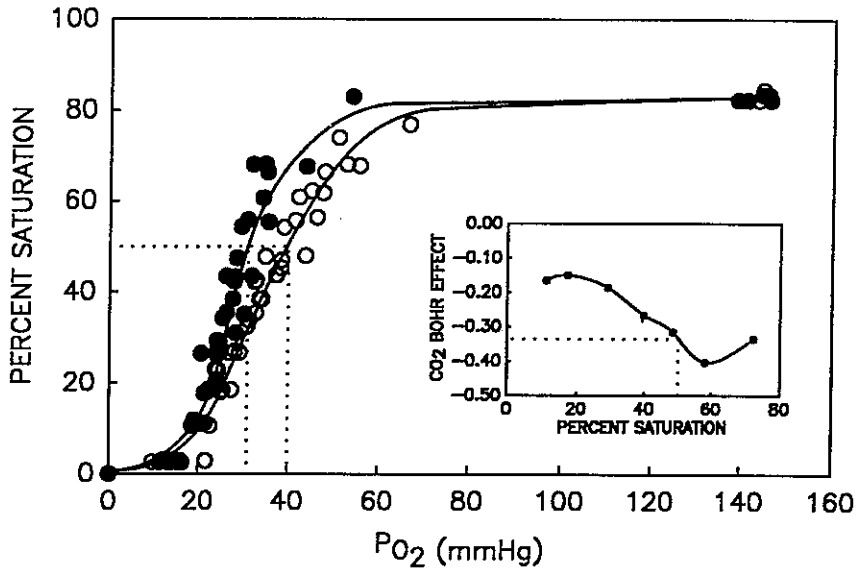


*Fig. 1. Blood $O_2$ dissociation curves and $CO_2$ Bohr values (inset) in* Dermochelys coriacea *at 25° C. ● = 2.2% $CO_2$, pH = 7.84; ○ = 4.8% $CO_2$, pH = 7.52. Curves were fitted by eye.*

respectively (fig. 1). The $CO_2$ Bohr value at the $P_{50}$ ($\Delta$ log $P_{O_2}/\Delta$pH) was −0.34 and varied as a function of $O_2$ tension, being less at lower $P_{O_2}$'s. The upper portions of the blood curves were flattened at $O_2$ tensions above 70 mmHg.

Hill plots calculated between 20% and 80% saturation (fig. 2) resulted in lines with statistically different ($P < 0.05$) slopes (n values) of 3.6 at 2.2% $CO_2$ and 2.7 at 4.8% $CO_2$ ($t = 2.2$, df = 52).

## Discussion

Deep dives by leatherback turtles may be supported by an increased $O_2$-carrying capacity of blood and tissue under conditions where increased hydrostatic pressure collapses the lung, eliminating its use as an $O_2$ store. The hematocrits and hemoglobin and myoglobin concentrations found in leatherback turtles were among the highest recorded in reptiles, and approached levels found in diving mammals (table 3). In contrast, sea turtles that are not deep divers appear to support aerobic diving patterns primarily on lung $O_2$ stores, having blood and tissue $O_2$ stores similar to those of their terrestrial relatives.

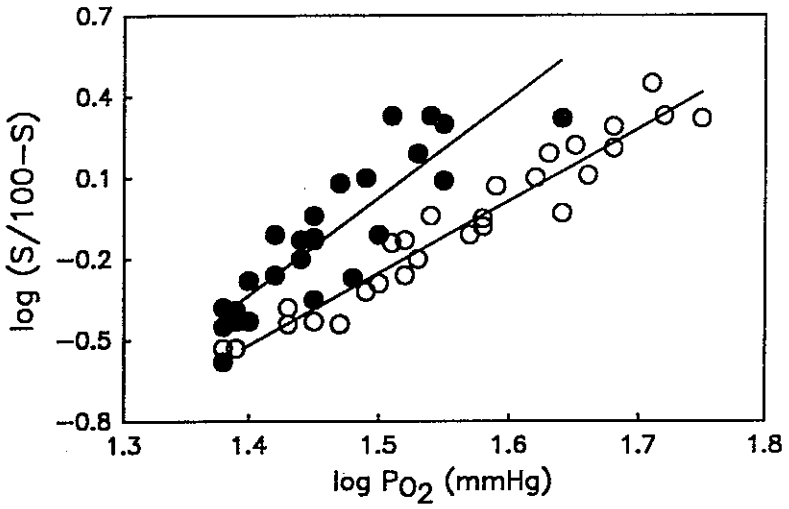


*Fig. 2. Hill plot for* Dermochelys coriacea *blood at 25° C. Linear regression is plotted for values from 20% to 80% saturation.* ● = *2.2% $CO_2$, pH = 7.84, Hill value = 3.6;* ○ = *4.8% $CO_2$, pH = 7.52, Hill value = 2.7.*

*Ventilation and Metabolism*

The $\dot{V}_{O_2}$ in *Dermochelys* during egg deposition was approximately half the value reported for *Chelonia mydas* at rest (0.4 mL $min^{-1}$ $kg^{-1}$, mean body mass 128 kg; Jackson and Prange 1979) and less than 10% of the mean value reported for *Dermochelys* hatchlings swimming continuously (0.46 mL $min^{-1}$ $kg^{-1}$, mean body mass 0.053 kg; Lutcavage and Lutz 1986). Even when the present values are scaled for size according to the allometric exponent given for turtles (0.86; Bennett 1982), the predicted $\dot{V}_{O_2}$ of a 128-kg leatherback turtle is only 0.28 mL $min^{-1}$ $kg^{-1}$, considerably below values given for similarly sized green turtles. Hence, aerobic metabolic rate of adult leatherback turtles is low, at least during egg laying.

The *f* of leatherback turtles was approximately half that reported for active leatherback turtle hatchlings (Lutcavage and Lutz 1986) but 10 times higher than in resting green turtles (Prange and Jackson 1976). In contrast, estimated mean $V_T$ (4 mL $kg^{-1}$) was considerably smaller than in adult green turtles (e.g., 35 mL $kg^{-1}$; Jackson and Prange 1979) and subadult loggerhead turtles (35–45 mL $kg^{-1}$; Lutz and Bentley 1985). Allometric factors cannot account for a small $V_T$, if we assume that lung volume scales to $mass^{0.75}$ (Tenney and Tenney 1970). For example, if a 30-kg loggerhead turtle having a $V_T$ of 35 mL $kg^{-1}$ were scaled up to 300 kg (leatherback turtle size), its $V_T$ would be about 20 mL $kg^{-1}$, considerably larger than the 4 mL $kg^{-1}$ determined for the leatherback turtle. Hence, it appears that leatherback turtles

TABLE 3

*Blood $O_2$ affinity and transport properties of diving reptiles and mammals*

| | Sea Turtles | | | | | |
|---|---|---|---|---|---|---|
| | Leatherback[a] | Loggerhead[b] | Green[b] | Crocodile[c] | Killer Whale[d] | Weddell Seal[d] |
| Maximum dive depth (m) | >1,000 | <300 | <100 | <30 | 260 | 600 |
| Hematocrit (%) | 39 | 29 | 30 | 28 | 44 | 58 |
| Hemoglobin (g $dL^{-1}$) | 15.6 | 9.8 | 8.8 | 8.7 | 16.0 | 17–22 |
| Myoglobin (mg $g^{-1}$) | 4.9 | 2.9[e] | ... | ... | ... | 44.6[g] |
| $O_2$-carrying capacity (mL · $dL^{-1}$) | 21 | ... | 7.5–11.9<br>8.8[f] | 12.4 | 23.7 | 31.6 |
| $P_{50}$ (mmHg) | 40 | 47 | 29<br>18.2[f] | 22 | 31 | 29 |
| pH at $P_{50}$ | 7.52 | 7.45 | 7.45<br>7.6[f] | 7.5 | 7.4 | 7.4 |
| Bohr effect | −.34 | −.34 | −.30<br>−.59[f] | −.43 | −.74 | −.61 |
| Hill number | 2.7 | ... | 2.8<br>2.8[f] | 2.7 | 2.6 | ... |

Sources. [a]Present study; [b]Lapennas and Lutz 1982; [c]Grigg and Cairncross 1980; [d]Lenfant 1969; [e]Lutz and Bentley 1985; [f]Wood et al. 1984; [g]Castellini and Somero 1981.

have small lungs. This would make sense for a species diving repetitively on inspiration. By minimizing lung volume, turtles would reduce their buoyancy and, therefore, the work of diving. In addition, susceptibility to the bends, demonstrated to occur following rapid decompression in green turtles (Berkson 1967), would be decreased.

Small lung volumes are commonly found in other deep-diving vertebrates such as the Weddell seal and fin whale (Scholander 1940; Leith and Lowe 1972; Butler and Jones 1982), suggesting a common adaptation for deep diving. A consequence of small lung volume is that more time must be spent at the surface to restore blood and tissue $O_2$ stores. This is compatible with the observation that, on the basis of field tracking studies (see, e.g., Standora et al. 1984; Byles 1988), *Dermochelys* has greater surface-to-submergence ratios than other sea turtles.

*Oxygen Transport*

The $O_2$ binding properties of leatherback turtle blood are similar to those of other sea turtles in having low-$O_2$-affinity hemoglobins, a low Hill coefficient, and relative insensitivity to $CO_2$ and pH at low saturation (table 3). Leatherback turtles are larger and have higher body temperatures than other species (Mrosovsky and Pritchard 1971), yet the $P_{50}$ at 25°C is midway between values reported for green and loggerhead turtles (27 and 49 mmHg, respectively), and the $CO_2$ Bohr value is identical to that of loggerhead turtles (Lapennas and Lutz 1982). At the lowest $P_{O_2}$ generally found at the end of voluntary dives in other sea turtles (23 mmHg; Lutcavage and Lutz 1987), leatherback turtle blood would be approximately 20% saturated. The high $P_{50}$ we obtained for *Dermochelys* does not conform to the trend of increased blood $O_2$ affinity with size reported for reptiles including the green sea turtle (Wood et al. 1984) and lizards (Bennett 1973).

The shape of the $O_2$ dissociation curve and the reduced Bohr effect at low saturation may be important in the case of lung collapse, where blood-tissue unloading would be crucial for an animal relying on a circulating blood $O_2$ store. In fact, Friedman, Simon, and Scott (1985) report that structural properties indicate that sea turtle hemoglobins are better adapted for release of $O_2$ to tissues than for uptake of $O_2$ by the blood. The shallowness of the curve at low $P_{O_2}$ should maintain a steep gradient for release of oxygen to the tissues.

It has been suggested that, in marine reptiles (Lapennas and Lutz 1982; Seymour 1982; Wood et al. 1984) and in diving mammals (Snyder 1983), blood $O_2$ affinity curves reflect adaptations for deep or shallow diving pat-

terns, or short versus long dives, depending on whether lung or blood $O_2$ stores are used. However, in comparison with other diving reptiles and mammals, *Dermochelys* appears to be somewhat of a hybrid (table 3). Blood $O_2$ transport values are similar to those of diving mammals utilizing blood and tissue stores (high [Hb], [Mb], and hematocrit), but in blood $O_2$ affinity, Hill coefficient, and Bohr effect, *Dermochelys* resembles other sea turtles thought to rely on lung stores during diving.

Reptiles that experience rapid changes in body temperature appear to have hemoglobins that are insensitive to temperature (Wood and Lenfant 1976; Grigg and Cairncross 1980). Temperature characteristics of the blood are of special interest in leatherback turtles as they have a large countercurrent heat exchange rete in the limbs (Greer, Lazell, and Wright 1973) and body-core-to-surface temperature differences that may be as great as 18°C (Mrosovsky and Pritchard 1971). In a study of structure and ligand binding kinetics of purified hemoglobin from *Chelonia mydas,* Friedman et al. (1985) reported strongly endothermal $O_2$ binding, or a reverse temperature effect on $P_{50}$. Although we were unable to complete our study of temperature effects on the blood affinity curve, a single determination of $P_{50}$ at 15°C demonstrated a normal (left) temperature shift compared with 25°C blood.

The enhanced blood and tissue $O_2$ stores may seem anomalous in light of behavioral studies that indicate leatherback turtles typically make short and relatively shallow dives (Duron 1978; Standora et al. 1984; Eckert et al. 1986). However, other deep divers such as the Weddell seal have large blood and tissue $O_2$ stores, but deep exploratory dives make up only a small percentage of their total number of dives (Kooyman 1989). Even when deep dives are a rare event, lung collapse is an unavoidable outcome that would seriously compromise $O_2$ transport in animals lacking blood and tissue stores.

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