Chapter 1
A Decidedly Unique Creature

“Terrapin” is a term from the Native American language to describe edible turtles that live in fresh or brackish waters. One such species is *Malaclemys terrapin*, the diamondback terrapin, the only U.S. turtle known to inhabit estuaries, coastal rivers, and mangrove swamps. The diamondback terrapin is unique. It tolerates fresh water, salt water, and everything in between. Unlike other turtle species that are exclusively freshwater or marine, the diamondback terrapin actually prefers an environment with intermediate salinity. This medium-sized turtle is confined to the Atlantic and Gulf coasts of the continental United States and can be found from Cape Cod, Massachusetts, the northernmost range of the species, to Corpus Christi, Texas. Seven subspecies have been identified.

The diamondback terrapin gets its name from the raised concentric rings formed on the subsections of the shell or carapace. The resulting grooves give the shell a sculpted appearance and are reminiscent of the facets on a cut diamond. The origin of the genus name, *Malaclemys*, is a bit obscure. An initial attempt at etymology would suggest that this is a genus of “bad” turtles. However, the genus has had several names, one of which was *Malacoclemys*. This was apparently shortened to *Malaclemys* at the end of the nineteenth century. The Greek “malakos” means “soft,” and “klemmys” is a Greek word for turtle. In one of the initial descriptions of the genus by Gray in 1844, it was noted that the turtles had soft, spongy heads. However, “mala” apparently refers neither to their temperament nor their spongy heads. Ernst and Bury (1982) posited that “soft” may relate to their soft-bodied molluscan prey. Diamondback terrapins are therefore “mollusk-eating turtles” rather than “evil” turtles.

Turtles are unusual creatures. There are many characteristics of turtles that cause them to stand out from most animals and even from other reptiles.
Undoubtedly, the turtle shell is the most noticeable and most unique feature of these animals. Another important feature, less noticeable and less unique, is the fact that most turtles, including diamondback terrapins, are ectothermic animals. Similar to other reptiles, they do not have a physiological mechanism to maintain a constant body temperature and must rely heavily on their surroundings and behavioral adjustments to provide suitable temperatures to carry out physiological and cellular functions. Another interesting biological idiosyncrasy that sets turtles apart from many other familiar animals is a phenomenon called temperature-dependent sex determination (TSD). Most turtles lack sex-determining chromosomes such as the X and Y chromosomes of many species. A turtle is destined to become a male or a female depending on the temperature at which it develops inside its egg. It is interesting to learn about how these reptiles appeared and how they have managed to persist, despite, or perhaps because of, their peculiar characteristics.

**Evolution and Classification**

Shelled reptiles are known by several names. Historically, they have been called tortoises if they are land-dwelling, turtles if they are aquatic, or terrapins if they belong to certain edible species. They are collectively known by the proper scientific name, “Chelonians,” derived from another Greek word describing turtles. The Greeks also used the word to designate a battle formation in which soldiers marched against the enemy with interlocking shields. “Testudo” was also used to describe this type of formation. This “engine of war” would indeed physically and functionally resemble the upper shell or carapace of a turtle. Despite the diversity within the Chelonians, we commonly use the term "turtle" as an all-inclusive identifier. How did they originate, these strange creatures that carry their homes on their backs? We can trace the evolution of the turtle back about 200 million years, during the Triassic period, when *Proganochelys* made its appearance on the earth. There is a dearth of evidence to tell us the complete story of the transition of some of the early reptiles into turtles, but the oldest turtle fossils were found in modern-day Germany, Greenland, and Thailand. Evolutionary biologists believe that turtles evolved from small reptiles and may have retained many of the features present in their ancient predecessors. There is some speculation among scientists that turtles arose from the ooze: marshy areas or swampland between terra firma and fresh bodies of water. Based on several criteria, Reippel and Reisz (1999) postulated an aquatic origin for turtles. The type of respiration...
and locomotion exhibited by turtles could probably be achieved more easily in the water, where buoyancy could support the extra weight of the shell and limb muscles could assist with breathing. The presence of a bony plastron, the lower shell, makes sense for an aquatic organism that would need protection on its ventral, or lower, body surface. It could be argued that there is less exposure of the ventral surface of four-legged land-dwelling animals to possible predators.

The development of a boxlike shell undoubtedly gave turtles protection from sharp-toothed and/or strong-jawed predators. No matter how it occurred, the development of a shell was so successful that the basic components of the turtle body plan have changed very little over time. A major difference between the first turtle, Proganochelys, which was about 0.6 meters (2 feet) in length (Alderton, 1988), and the modern Chelonian is the modification of a jaw that originally contained teeth into a horny, beaklike jaw. During the Jurassic period, 210 to 144 million years ago, some turtles moved away from the swamps or their freshwater homes, into the oceans and onto the land. At the end of the Jurassic, turtles had developed a flexible neck and could retract their heads into their shells. During the Cretaceous period, 144 to 65 million years ago, a huge turtle named Archelon, 3.6 meters (12 feet) long, roamed the oceans. During the mass extinction at the end of the Cretaceous, Archelon went the way of the dinosaurs, but some of his smaller turtle relatives survived the catastrophic events that led to the demise of so many species. During the Eocene, approximately 55 to 35 million years ago, the emydid turtles emerged. This is the largest group of extant (contemporary) turtles and the group to which diamondback terrapins belong.

Chelonians, as well as other reptiles, birds, and mammals, are characterized by their ability to produce eggs that have protective coverings supported by extraembryonic membranes. The covering or shell inhibits the egg from drying out and is also supplied with the energy source for the developing embryo. Another important reptilian feature is dry skin or scales. Since these animals can live on land, the scales are an important adaptation to prevent desiccation. The reptile represents the completion of a full transition from water to land-dwelling animal. The ability to produce covered eggs and the ability to prevent desiccation allowed reptiles to break their dependence on the watery habitat utilized by their amphibian ancestors and thus to take advantage of a terrestrial way of life. Although some amphibians can live on land, they must return to the water to lay eggs. Paradoxically, some reptiles, including the aquatic turtles, live in water but must lay eggs on land.
The lack of fossil evidence that would link turtles to an evolutionary pre-cursor leads to much speculation about the evolutionary development of the basic turtle body plan. If we adhere to the classical definition of a reptile, which does not include birds, turtles are the only modern representatives without teeth and they are the only extant vertebrate with a shell. The turtle's shell is a one-of-a-kind evolutionary item. It represents a major anatomical contortion. The shell, which originated from an amalgam of ribs and spine, is fused to the skeleton in such a way that the pelvic and pectoral girdles (hips and shoulders) lie within the rib cage. This unique anatomy makes it difficult to easily propose morphologically based phylogenetic relationships between turtles and other reptiles. The true marvel of this body plan was described by the world-renowned turtle expert Archie Carr (1952):

The first of the innovations made by the stem reptiles was in a way the most extraordinary and ambitious of all—the most drastic departure from the basic reptile plan ever attempted before or since. By a cryptic series of changes, few of which are illustrated in the fossil record, there evolved a curious and improbable creature which, though it retained the old cotylosaur skull (with no openings in the temporal region), has a horny, toothless beak and a bent and twisted body encased in a bony box the likes of which had never been seen. And more than this, within the box the girdles connecting the legs and the rest of the skeleton had by some legerdemain been uprooted and hauled down to an awkward position underneath the ribs. (p.1)

The presence of a shell undoubtedly had an impact on the status of some turtles in the food web. With a coat of armor, land turtles no longer needed to be swift of foot; they could rely on a unique shielding mechanism for protection from predators. As an added bonus, land turtles no longer needed to be swift to capture their own prey. Although some had dietary preferences, others adopted a vegetarian or generalized omnivorous diet, munching on anything within reasonable reach. Turtle adaptations were apparently successful. With the protection of their shell, turtles could take life at a somewhat more relaxed pace than their evolutionary forebears. And thus they persisted and witnessed the decline of other reptile relatives. The first appearance of the diamondback terrapin from early turtle ancestors remains a mystery. The only known diamondback terrapin fossils, two tiny bones, a nuchal (from the neck region of the shell) and a costal (from the side or lateral portion of the shell) from different individuals, date back to the Pleistocene epoch (approximately
1.65 million to 10,000 years ago). They were found at Edisto Beach, along the coastal plain of South Carolina (Dobie and Jackson, 1979). This region lies within the current range of *Malaclemys terrapin*.

Who would think that turtles are the center of a major controversy among evolutionary biologists? Long considered a living fossil and one of the most primitive reptiles, an egg-laying precursor to snakes, lizards, alligators, and crocodiles, new evidence suggests that turtles may belong to a branch of the evolutionary tree that links them more closely with advanced reptiles and very closely to birds. Biologists have used skull type as one important criterion for determining evolutionary relationships and classification of reptiles. In the anapsid skull, bone completely covers the regions around the eye socket; the skull is solid. This is thought to be the most primitive type of skull, and indeed, turtles are anapsid reptiles. In the diapsid skull, characteristic of reptiles such as crocodiles and also seen in birds and in dinosaur fossils, there are two openings in the skull, posterior to the eye sockets. These openings are believed to be important for attachment of muscles that function in jaw movement. In the traditional evolutionary timeline, anapsid turtles are thought to predate diapsid reptiles.

Other morphological features can be brought into the evolutionary equation. Depending on the methods for comparing morphological characteristics, turtles can be moved up to the top branches or down to the trunk of the evolutionary reptilian tree. Rieppel and Reisz (1999) used powerful computer software to take a fresh look at the fossil evidence, combined with morphological characters seen in reptiles that roam the earth today. Their resulting

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**Fig. 1.1.** These diagrams depict two theories of turtle evolution.
analysis led them to hypothesize that turtles are nested within the diapsid clade. Perhaps they were originally diapsid and reverted to the anapsid condition in a later evolutionary transition.

Another method to examine evolutionary relationships employs molecular analysis. DNA sequence information allows scientists to examine evolutionary relationships based on DNA sequence similarities and differences. This technique also relies on powerful computer software to make the necessary analyses and comparisons in DNA sequence between the same genes in different organisms. In many cases, DNA sequence information and morphological comparisons lead to the same conclusions. Hedges and Poling (1999) compared DNA sequences in reptiles using nine genes found within cellular organelles known as mitochondria, and twenty-three genes found within the cell’s nucleus, and found strong evidence for a turtle–crocodilian relationship. Therefore, DNA sequence data support the hypothesis that turtles are not as “primitive” or genetically distinct as originally thought. The phylogenetic trees in fig. 1.1 summarize the two theories of turtle evolution.

Terrapins share features of the truly marine turtles as well as their freshwater relatives. But from which ancestor is the terrapin derived: a freshwater turtle or a marine ancestor?

Terrapins belong to the large family of turtles known as the Emydidae. Most members of the family, with the exception of most box turtles (Genus Terrapene), are aquatic. Included in this family are some familiar freshwater species such as painted turtles (Chysemys picta), spotted turtles (Clemmys guttata), wood turtles (Glyptemys insculpta), map turtles (Graptemys), Blanding’s turtles (Emydoidea blandingii), cooters (Pseudemys), and sliders (Trachemys). Among turtles, diamondback terrapins are unique in their habitat and adaptations. The closest turtle relative of the diamondback terrapin is the freshwater map turtle, Graptemys. Despite their morphological similarities, there are significant differences in their appearance. But more importantly, they differ physiologically since Graptemys is a strictly freshwater turtle while Malaclemys is the lone occupant of the brackish water niche. There have been several proposals to explain the evolutionary relationship between the two species, and from a theoretical viewpoint, one could look at current distribution, morphological characters, and physiological adaptations.

Dobie (1981) used detailed analysis of skull and shell features to compare current Graptemys with current Malaclemys. Osteological (bone structure) comparisons of skull, jaw, and neck and aspects of external morphology led Dobie to propose that Malaclemys may have arisen from Graptemys or that
both arose from a common Eocene precursor approximately 60 million years ago.

Other factors can also provide clues to the origin of *Malaclemys*. In a study of habitat utilization of sympatric reptiles, that is, those that occupy the same territory, in Florida Bay, Dunson and Mazzioti (1989) point to salinity as the limiting factor in the utilization of habitats rich in food and nutrients. Very few reptiles have been able to adapt to a euryhaline environment, i.e., one that has a wide range of salinity, for prolonged periods. They suggest a four-stage evolutionary adaptation to salinity which allows reptiles to regulate the salt content in their body fluids, a process known as osmoregulation, which includes:

1. Behavioral osmoregulation: By keeping the mouth closed except while feeding and drinking rainwater rather than salt water, some freshwater reptiles, such as snapping turtles, can use habitat that is temporarily salty.
2. Physiological specialization: a decrease in net salt uptake, net water loss, and incidental drinking of salt water while feeding.
3. Appearance of salt glands: an extrarenal (non-kidney-mediated) mechanism for elimination of excess salt.
4. Development of larger salt glands and external features suited for pelagic life (the open sea): These traits are seen in marine iguanas and sea turtles. Although the terrapin also has a salt gland, it is different from that of sea turtles and may have evolved independently.

According to this scheme, the diamondback terrapin is an estuarine reptile with an intermediate adaptation to a marine environment. Similar to Dobie’s conclusions (1981), this hypothesized evolutionary pathway also suggests that *Malaclemys* may have originated from *Graptemys* or a common freshwater ancestor.

In agreement with this interpretation, molecular evidence points to a fresh to brackish water evolutionary pathway for *Malaclemys*. Lamb and Osentoski (1997) used molecular data to propose an evolutionary relationship between *Malaclemys* and *Graptemys*. They focused on certain mitochondrial genes that are often used in evolutionary and phylogenetic analysis because of their tendency to be quite variable. The general assumption behind such an approach is that the more similar the DNA sequences of specific genes, the more similar the species that are being compared. When the variable mitochondrial control region and the more conserved cytochrome *b* gene were sequenced and compared, the genetic data point to a scenario in which both genera
evolved from a common ancestor some 7 to 11 million years ago during the late Miocene.

It is certain that diamondback terrapins have been around for a long time. As Wood (1977) stated:

In view of the fact that diamondbacks have no apparent competitors in the salt marshes to which they are uniquely adapted, that this habitat may be of considerable antiquity, that they are quite different from all the emydines except *Graptemys*, and that emydines are a fairly ancient group (being known from late Paleocene and early Eocene deposits of Western North America), *Malaclemys* may be a taxon that has persisted over a fairly great time span while undergoing little change. (p. 420)

**TAXONOMY**

Even without the evolutionary pieces falling into place, it is still possible to classify the diamondback terrapin based on morphological traits and current geographic distribution (Ernst and Bury, 1982). With a general turtle phylogeny in mind, the diamondback terrapin has been placed as follows:

**Kingdom:** Animalia (i.e., animals).
**Subkingdom:** Eumetazoa (animals having definite symmetry and tissues).
**Phylum:** Chordata (chordates have the following four characteristics: a hollow dorsal nerve cord, a notocord, pharyngeal slits, and a postanal tail, at some point in their development).
**Subphylum:** Vertebrata (vertebrates are basically chordates with a spine).
**Class:** Reptilia (from the Latin, creepy, crawly).
**Order:** Chelonia (from the Greek word suggesting interlocking shields or armor).
**Family:** Emydiiiae (a freshwater turtle, in Aristotle’s “History of Animals”).
**Genus:** *Malaclemys* (from the Greek, mollusk-eating turtle).
**Species:** *terrapin* (from Algonquian, edible turtle).
**Subspecies:** *terrapin; centrata* (from the Greek, kentron, center, refers to formation of growth rings on scutes); *tequesta* (after Tequesta, Native American tribe in eastern Florida); *rhizophorarum* (Greek for genus of mangrove in the habitat of this subspecies); *macrospliota* (from the Greek macron, large and spilados, spot; refers to the yellow spot at the center of each scute); *pileata* (from the Latin, capped; refers to black marking at top of the head); and *littoralis* (from the Latin, littoralis, seashore).
The morphological characteristics of the diamondback terrapin subspecies are outlined in table 1.1.

**Table 1.1 Morphological Comparison of Diamondback Terrapin Subspecies**

<table>
<thead>
<tr>
<th>Subspecies</th>
<th>Common name</th>
<th>Distinguishing morphological features</th>
<th>Range</th>
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<tbody>
<tr>
<td>terrapin</td>
<td>Northern diamondback</td>
<td>No knobs on median keel; carapace is black to light brown/olive with distinct concentric rings on scutes; plastron is light-colored, yellow, orange, or greenish gray; carapace is wider behind bridge</td>
<td>Cape Cod, Mass., to Cape Hatteras, N.C.</td>
</tr>
<tr>
<td>centrata</td>
<td>Carolina terrapin or Southern diamondback</td>
<td>No knobs on median keel; posterior margins curled upward</td>
<td>Cape Hatteras, N.C., to Northern Florida</td>
</tr>
<tr>
<td>tequesta</td>
<td>Florida East Coast terrapin</td>
<td>Median keel has posterior-facing knobs; carapace dark or sometimes tan with light centers on scutes; no pattern of light concentric circles</td>
<td>Florida’s east coast</td>
</tr>
<tr>
<td>rhizophorarum</td>
<td>Mangrove terrapin</td>
<td>Median keel has bulbous knobs; oblong shell; carapace is brown or black; plastral scutes are outlined in black; neck and forelimbs are uniform gray with no markings; black striations may be found on hindlimbs</td>
<td>Florida Keys</td>
</tr>
<tr>
<td>macropsikota</td>
<td>Ornate diamondback</td>
<td>Median keel has terminal knobs; carapace scutes have orange or yellow centers</td>
<td>Florida Bay to Florida Panhandle</td>
</tr>
<tr>
<td>pileata</td>
<td>Mississippi diamondback, Biloxi terrapin, Gulf terrapin</td>
<td>Median keel has terminal tuberculate knobs; plastron is yellow; upturned edges of marginals are yellow; dorsal surfaces of head, neck, and limbs are dark brown or black</td>
<td>Florida Panhandle to western Louisiana</td>
</tr>
<tr>
<td>littoralis</td>
<td>Texas diamondback</td>
<td>Deep carapace with terminal knobs on median keel; plastron is very pale; dorsal surface of head is white or light color</td>
<td>Western Louisiana to Western Texas</td>
</tr>
</tbody>
</table>

**Source:** Adapted from Carr (1952) and Ernst, Lovich and Barbour (1994).
Fig. 1.2. Diagram of the scute pattern on carapace (dorsal view) and plastron (ventral view).

Fig. 1.3. Arrangement of turtle internal bony structure; bones that would be visible if the scutes of the carapace and plastron were removed.
A DECIDEDLY UNIQUE CREATURE

Anatomy and Morphology

The Turtle

The turtle lives 'twixt plated decks
Which practically conceal its sex
I think it clever of the turtle
In such a fix to be so fertile
—Ogden Nash

THE SHELL

When we think about turtle anatomy, the first thing that comes to mind is the shell. The shell is made of bone. The upper shell is called the carapace, and during embryonic development it is formed by the fusion of the spine with bones that would normally form the rib cage in other animals. The ribs of other animals are present to protect vital organs, but in turtles the ribs serve as buttresses to support the carapace. Turtles do not have a breastbone or sternum. The plastron or bottom shell is composed of bone and has no equivalent structure in other reptiles: its embryological origin remains a mystery. An unconfirmed study suggests that the plastron may originate from an embryonic area known as the neural crest, a region that gives rise to muscles, blood vessels, and facial bones (Pennisi, 2004). The bridge is the bony segment that connects the two halves of the shell and serves as a brace or structural support that prevents the upper and lower shells from collapsing upon one another after a heavy impact. The plastron of the diamondback terrapin does not have a hinge and is thus immobile; the terrapin cannot completely hide within, as can some turtles. The shell is more than a protective structure that simply covers a reptilian body. It is an integrated, much modified part of the body. Fat, stored under the shell, imparts the characteristic flavor to turtle soup. Due to the development and placement of the shell, the turtle has a body plan that is inside-out. As mentioned earlier, its pectoral and pelvic girdles (shoulders and hips) are inside its ribs.

The shell of most turtles has a similar structure (see Carr, 1952; Alderton, 1988). A cross section of the turtle shell would reveal a two-layered structure. The inner, dermal layer is composed of fused bony plates, while the outer, epidermal layer is scaly tissue, filled with keratin, a connective-tissue protein found in the hair, nails, hooves, and horns of other animals. The epidermal layer of the carapace and plastron is divided into segments called “scutes” that form a mosaic over the bones. In diamondback terrapins the scutes do not overlap (fig. 1.2). Instead, they abut one another like closely spaced tiles. The
pattern of scutes does not correspond to the distribution and pattern of the underlying dermal bones (fig. 1.3). There are many more dermal bones than the scutes that cover them. In the diamondback terrapin carapace, we can observe vertebral scutes along the midline or center of the back, pleural or costal scutes along each side, one cervical or nuchal scute near the neck region, and an apron of marginal scutes. The plastron has scutes that are divided into gular, humeral, pectoral, abdominal, femoral, and anal sections (fig. 1.2). It is not unusual to find diamondback terrapins with minor scute variations. Some have extra, missing or sectored scutes (see fig. 1.4). These minor anomalies arise during shell development and do not compromise the viability of the terrapin.

The main ridge along the midline of the carapace is the keel. In the diamondback terrapin, it is sometimes smooth and barely noticeable, but it may also be prominent with protruding knobs, especially in younger animals and also among some of the subspecies (fig. 1.5). Anomalies are sometimes seen in the number and formation of ridges that make up the keel. Some ridges may be subdivided or slightly deformed. The major vertebrae that make up the turtle spine are fused to the carapace and are therefore very rigid. The smaller tail and neck vertebrae are covered by muscle and have great flexibility.

As turtles grow, so do their shells. Under each scute, within the epidermal layer, Malphigian cells produce keratin. Scutes grow outward in all directions from a central section known as the areolus. As the scute expands, keratin is added. Pigment is also deposited to produce spotting patterns or rays, unique to each scute. Diamondback terrapins are only active for part of the year, and growth is restricted to these periods. As a result, there will be a new margin of growth that will represent a season of eating and activity (fig. 1.6). Sometimes it is possible to estimate the age of diamondback terrapins by counting the growth rings, or anuli, on carapace or plastron, similar to counting the growth rings of tree cross-sections to estimate the age of a tree. As terrapins age, the growth rings may become worn, smooth and difficult to discern. After six to eight years, when growth occurs in smaller increments, it is very difficult to distinguish annuli at the margins of the scutes. Terrapins raised indoors, in captivity, do not have a hibernation period and often experience continuous growth, independent of the seasons. There may be more gradual, rather than distinct, deposition of keratin during enlargement of scutes.

Terrapins have been found with shell injuries resulting from boating accidents, dredging operations, and close encounters between nesting females and automobiles. If the injuries are not life-threatening, healing will occur and the
Fig. 1.4. Four anomalous scute patterns.
Fig. 1.5. The keel is particularly pronounced on hatchlings.

Fig. 1.6. Growth rings or annuli are easy to discern in young terrapins.
bone will gradually mend. Wildlife veterinarians have developed treatments for terrapins with more seriously injured shells. Temporary patching of the shell with fiberglasslike materials or special taping compounds makes it possible to preserve proper dermal bone alignment so that natural healing can take place. Healing is a slow process, and it may take over a year for the bones of the shell to mend.

Terrapin number 1195 presents a case study in shell healing. This 13-year-old female was found on the beach near Wellfleet Harbor on Cape Cod in mid October, 2001. Sediments were being removed from the shallow harbor, and it seems likely that number 1195 was a victim of heavy dredging equipment. Her carapace was cracked, but the underlying vital organs were not penetrated. In addition, her left bridge was broken. After she was brought to the attention of the Wellfleet Bay Wildlife Sanctuary, Don Lewis, terrapin researcher and Massachusetts Audubon Society volunteer, transported the bleeding terrapin to the Cape Wildlife Center in Barnstable, Massachusetts, where veterinarians Rachel Blackmer and Catherine Brown began treatment. The broken bridge was diagnosed as the more serious injury. The bridge bones were taped into place and the terrapin was kept in a heated tank over the winter so that her progress could be monitored. Lewis provided a daily clam and oyster feast for number 1195. By springtime, her bridge was completely healed. Her return to Wellfleet Harbor was a celebrated event that was covered by the local newspaper, *The Cape Codder*, on April 19, 2002.

At Cape May, along the southern New Jersey shore, approximately 500 female terrapins each year are struck by automobiles. Most of these are killed, but occasionally, an auto victim will survive. Such a survivor will have her shell fiberglassed and will spend the fall, winter, and spring at Richard Stockton College of New Jersey under the watchful eyes of Drs. Roger Wood and Roz Herlands. These females are returned to the Cape May salt marshes after sufficient healing has occurred (fig. 1.7).

Although life in a shell is a successful strategy for turtles, it is not without its disadvantages. Wherever a turtle goes, the heavy shell must go with it. This may be less of a problem for aquatic turtles than terrestrial species, but the female diamondback terrapin, as well as her hatchlings, must sometimes travel about on land. Their limb muscles operate very differently from those of nonshelled vertebrates. Terrapins can move relatively rapidly on land but are not often quick enough to elude a terrestrial predator or a determined researcher.
Internal Anatomy

Within the terrapin shell lie structures that are very similar to those of other turtles. Details of turtle internal anatomy have been reviewed by others (Pope, 1946; Carr, 1952; Alderton, 1988; Ferri, 2002). I describe the most significant aspects.

The cardiopulmonary system (heart, blood vessels, and lungs) of turtles is very specialized. Aquatic turtles are air breathers but can spend months submerged during hibernation. They have great tolerance to anoxia (lack of oxygen) and can undergo long periods without breathing. They also differ markedly from other vertebrates that are able to use chest movement via muscles of the thorax and a diaphragm to fill and empty their lungs. Aquatic turtles are thought to use muscles at the base of their limbs and beneath their vital internal organs to assist them in breathing. To inhale, these muscles contract, the body cavity or coelom enlarges, and pressure is reduced, thus allowing the lungs to fill. To exhale, the muscles relax and water pressure will do the
rest in order to push the organs against the lungs and allow air to be forced out (Carr, 1952). The volume of air in an aquatic turtle’s lungs will affect its buoyancy. Similar to other turtles, the terrapin has a three-chambered heart constructed of two atria and one ventricle. The hint of structural division in the ventricle provides a preview of the development of the four-chambered heart found in crocodilians, birds, and mammals (Carr, 1952; Ferri, 2002). The terrapin digestive and excretory systems resemble those of other freshwater emydid turtles (Carr, 1952; Ferri, 2002). Terrapins do not have a rectum; the cloaca (from the Greek word for “sewer”) serves as an all-inclusive excretory and genital area, collecting fecal matter from the gut and urine from the bladder and serving as the location for the genital organs. The bladder is often emptied when turtles are handled—a response that most researchers become wary of after their initial “christening.”

The turtle brain is well developed in those regions that process visual and olfactory signals. Turtles have well-developed eyes, protected by heavy lids, and they have a good sense of smell, but they may not be well equipped for hearing. Their tympanic membrane, behind their eyes, is covered with skin, lacks an external opening, and may only respond to low notes (Alderton, 1988). It is clear that terrapins can respond to some sounds. In the absence of any visual stimulus, farm-raised terrapins, kept in pens in the early 1900s, became extremely responsive in anticipation of feeding when they heard their food being chopped up (Coker, 1906).

Within the brain, turtles have a relatively large pineal body, an area that produces the hormone melatonin. In many animals, this section of the brain responds to an internal biological clock that governs daily (circadian) rhythms. The clock ticks in approximately twenty-four-hour cycles to respond to external cues such as daylight. Turtles also have other internal timepieces. A field study of a Long Island, New York, terrapin cluster suggests that *M. t. terrapin* has activity patterns that are regulated by tides. Swimming was correlated with high tides, while basking was correlated with high and low tides, depending on the brightest hours of the day. The idea that this was internally regulated and represented an innate tidal activity cycle stemmed from observations of laboratory-raised hatchlings that displayed the same types of approximately six-hour daily fluctuations in locomotor activities (Muehlbauer, 1987). It is highly probable that terrapins also have another clock that governs yearly (circannual) behaviors such as mating, winter dormancy (hibernation or brumation), and local movement. But very little is known about the internal mechanisms that drive these longer cycle periods.
<table>
<thead>
<tr>
<th>Geographic Location</th>
<th>Males</th>
<th>Females</th>
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<tbody>
<tr>
<td><strong>Wellfleet, Cape Cod, Massachusetts</strong>&lt;br&gt;M. t. terrapin (Wellfleet Bay Wildlife Sanctuary)</td>
<td>9.7 cm (3.8 in.); 263 g (0.58 lb.) average (largest = 400g [0.88 lb.]); Maturation: reach 8 cm (3.15 in.) by 5th year.</td>
<td>16.4 cm (6.46 in.); 1063 g (2.34 lbs.) average Maturation: 8–10 years; 14 cm (5.51 in.)</td>
</tr>
<tr>
<td><strong>Rhode Island</strong>&lt;br&gt;M. t. terrapin</td>
<td>—</td>
<td>20.0 cm (7.87 in.); range = 17.5–22.5 cm (6.9–8.9 in.)</td>
</tr>
<tr>
<td><strong>Little Beach Island, New Jersey</strong>&lt;br&gt;M. t. terrapin</td>
<td>—</td>
<td>15.4 cm (6 in.) average; range = 13.2–18.4 cm (5.2–7.24 in.)</td>
</tr>
<tr>
<td><strong>Patuxent River, Maryland</strong>: Maturation: 300 g (0.66 lbs.); 4–7 years.</td>
<td></td>
<td>Maturation: 1100 g (2.43 lbs.); 17.5 cm (6.9 in.); 8–13 years.</td>
</tr>
<tr>
<td><strong>North Carolina</strong>: Largest = 12 cm (4.72 in.)</td>
<td>Maturation: 8–9 cm (3.2–3.5 in.); 5 years.</td>
<td>Largest =18.5 cm (7.3 in.). Maturation: over 13.7 cm. (5.4 in.) Smallest = 11.97cm (4.7 in.), 7 years; (range = 4–8 years).</td>
</tr>
<tr>
<td><strong>South Carolina</strong>: Maturation: 9 cm (3.5 in.); 3–4 years.</td>
<td>10.26 cm (4 in.) average; 242 g (0.53 lb.)</td>
<td>14.42 cm (5.7 in.) average; 667 g (1.47 lbs.)</td>
</tr>
<tr>
<td><strong>Merritt Island, Florida</strong>: Maturation: over 9.5 cm (3.7 in.); 2–3 years.</td>
<td>10.4 cm (4 in.) average; 283 g (0.62 lb.)</td>
<td>15.4 cm (6 in.) average; 886 g (2 lbs.)</td>
</tr>
<tr>
<td><strong>Louisiana</strong>: Maturation: over 9.5 cm (3.7 in.); 2–3 years.</td>
<td>3 years</td>
<td>6 years</td>
</tr>
<tr>
<td><strong>Texas</strong>&lt;br&gt;M. litoralis</td>
<td>12.6 cm (5 in.); range = 11.1–15.3 cm (4.4–6.0 in.)</td>
<td>16.1 cm (6.3 in.); range = 10.1–22 cm (4.0–8.7 in.)</td>
</tr>
</tbody>
</table>

Table 1.2  Mean Adult Size: Size and Age at Maturity of Diamondback Terrapins

Linear Measurements in cm (in.) Correspond to Straight-Line Plastron Length
EXTERNAL MORPHOLOGY: SEXUAL DIMORPHISM

Males and females of many animal species can be readily distinguished from one another by observable differences in external morphology that are called secondary sexual characteristics. Sexual dimorphism in the diamondback terrapin can be seen in adults at the level of total body size. Carr (1952) observed that adult diamondback terrapins have greater size disparity between the males and females of the species than any other North American turtle. Although the size of terrapins generally varies and is normally distributed, similar to the different sizes and shapes of humans and other animals, adult females are always much larger than males. For example, on Cape Cod, females often attain plastron lengths (PL) (straight-line measurements with a caliper) of 16 centimeters (about 6 inches), while adult males average around 10 centimeters (about 4 inches) PL. Adult females may weigh 1000 grams (2.2 pounds) or more, while adult males top out at an average of approximately 275 grams (0.6 pounds). This size disparity exists among terrapins throughout their range (table 1.2).

Adult males and females are also distinguishable by head size and the size and shape of the tail. Mature females have larger heads than mature males; the neck muscles in both sexes are well developed to allow rapid retraction of the head into the shell when the terrapin is threatened.

The tail of the female is shorter and narrower than that of the male (plate 1). The tail of the diamondback terrapin, similar to that of other aquatic turtles, is muscular and flexible and can serve as a rudder for steering. For males, it is important in grasping and aligning with females during mating.

The cloacal opening of the male is posterior to the shell margin, while the opening of the female does not extend far beyond the apron of the shell. The carapace of the adult male is flatter than that of the female. Although sexual dimorphism is seen in adult terrapins, it is more difficult, if not impossible, to distinguish the gender of hatchlings and juveniles by external observation.

JAW AND APPENDAGES

Similar to other emydid turtles, the limbs of the diamondback terrapin have a structure that is intermediate between a true sea turtle, whose limbs are basically flattened and shaped like flippers, and the thick and columnar limbs of land-dwelling turtles. Terrapin limbs terminate with webbed toes and sharp nails; rear limbs are larger and more powerful than forelimbs. The webbing is a feature of most aquatic turtles and serves the terrapin well for life in the
water. Unlike sea turtles, which can glide very swiftly through the water using up-and-down, winglike movements of their front flippers, diamondback terrapins rely on swimming strokes similar to those of their freshwater emydid cousins, employing alternate diagonal movement of front and rear limbs. Nails on the webbed toes are employed for digging into sand, soil, or mud, as when females dig nests or when terrapins burrow into the muddy bottoms of creeks and marshes during the cold weather. Nails also assist terrapins in grasping food while they use their powerful jaws to tear food into bite-sized pieces. Diamondback terrapins are surprisingly good climbers. With the help of their nails, they have been known to climb vertical surfaces. During terrapin farming attempts in Beaufort, North Carolina, they were observed to scale several feet up the walls of their pens in attempts to escape (Coker, 1906).

The terrapin upper jaw is usually thick and white, giving the appearance of lips shaped into a comical smile (fig. 1.8). Males as well as females occasionally have a dark coloration to the upper jaw, resembling a moustache. The terrapin jaw is a hard bony hinge without teeth. It is capable of crushing shells of mollusks such as snails and crustaceans such as crabs. These jaws can draw blood from a researcher who is not vigilant. One unfortunate encounter with a terrapin demonstrates both their climbing ability and their strong jaws: Jack Rudloe was working as a specimen collector in Florida’s Panacea Channel. On one of his trips, many of the terrapin specimens climbed out of the buckets in which they were contained and were observed crawling over the boat’s deck. It wasn’t long before a large female clamped her jaws around Rudloe’s big toe and wouldn’t let go until he submerged his foot in a bucket of water (the same method used to induce blue crabs to release their grip). Rudloe’s toe remained bruised and swollen for days afterwards (Rudloe, 1979).

**Geographic Variation**

Even amateur herpetologists can identify a diamondback terrapin and pick it out from a lineup of similar turtles. Aside from habitat preferences, there are morphological characteristics that are unique to diamondback terrapins such as their distinctive shell patterns and the various designs of spots and stripes on their exposed integument. They also differ quite a bit from each other: no two are exactly alike. The grouping of diamondback terrapins into subspecies is based primarily on overall visible characteristics and geographic location.

Although all members of *Malaclemys terrapin* have similar morphology, experienced researchers have characterized seven subspecies. The shape of the
shell varies slightly, and there are also subtle variations in coloring and patterning (plate 2). These morphological differences among the subspecies were summarized in table 1.1. I have observed much overlap in these categories. For example, black striations on hind limbs, sometimes referred to as “striped pants,” are descriptive of the mangrove terrapin, but not all mangrove terrapins have black stripes on their limbs. Furthermore, I have seen these distinctive markings on New York terrapins.

There is also some size variation among the subspecies (table 1.2). The Chesapeake population has larger adult specimens than the more northern

Fig. 1.8. The upper jaw of the diamondback terrapin is thick and strong. When it is lightly colored it resembles clown lips. When it is darkly colored it resembles a moustache.
and southern populations. Rhode Island females are larger than Massachusetts and New Jersey counterparts. The _M. t. centrata_ females from South Carolina are the smallest.

Coloration is mediated by the pigment melanin, which is deposited in various amounts and in a variety of patterns, on both shell and skin. Carapace color varies from pale olive green to almost black, with many shades of greenish-gray and brownish-green in between. The plastron is lighter in color than the carapace and can be pale yellow to bright orange. Plastron coloration tends to become duller as terrapins age. Each hatching possesses distinctive plastron spotting patterns or markings that persist for several years but eventually become blurred as the terrapin grows. We have found these markings to be unique to each hatching and have used the plastron patterns as a convenient way to identify young terrapins (plate 3). In addition to shell color variation, skin color and skin markings differ among subspecies (table 1.1).

Some of the subspecies are found in wide geographic tracts that span two biogeographic regions (Fig. 1.9). _Malaclemys t. terrapin_ ranges from Cape Cod to North Carolina; _M. t. centrata_ is found from South Carolina to northern Florida. Florida has the highest number of subspecies; five of the seven subspecies can be found in the Sunshine State. In 1940, when Archie Carr summarized the fauna of Florida, only three subspecies were listed and described (Carr, 1940). Although a specimen of an apparently different subspecies, _M. t. rhizophorarum_, was discovered in 1904, the subspecies was not officially recognized until several years later (Carr, 1946, 1952). Roger Wood provided evidence for the spatial distinction of the two most southern Florida populations. _Malaclemys t. rhizophorarum_ is only found on small islands south of Marathon Key, most of which are located in the Key West National Wildlife Refuge. This population may be morphologically and geographically distinct from the group that occupies Florida Bay (Wood, 1992).

Recent genetic evidence questions whether the current subspecies classification is valid and accurately reflects the population distribution of terrapins. For example, molecular studies point to a very close genetic relationship between all subspecies of Florida terrapins. Furthermore, genetic analysis, based on mitochondrial genes, shows divergence between the mid-Atlantic (_centrata, terrapin_) and Gulf Coast (_rhizophorarum, macropilota, and pileata_) subspecies (Lamb and Osentoski, 1997). This divergence was originally noted by Carr on the basis of morphology (Carr, 1946). This type of phylogenetic
split between Atlantic and Gulf terrapins may have been caused by landmass expansion believed to have occurred approximately 15,000 years ago as a result of a massive sea-level drop. Along with other factors, changing sea level created an ecological and spatial barrier between the two populations. Finer scale genetic studies may lead to reevaluation of the subspecies designations. Population genetic studies and their implications are further described in chapter 6.

Occasionally, at the intersection of the range of two subspecies, terrapins are found crossing over to the range of another subspecies. If mating occurs, intergrades or hybrids will be produced. These intergrades have been observed on the west coast of Florida, where *M. t. rhizophorarum* has been found trespassing in the range of *M. t. macrospilota*, near Naples (Johnson, 1952). The subspecies can interbreed. Some attempts at increasing market value for terrapins at the beginning of the twentieth century included the production of hybrids: *terrapin x centrata*. Ecological differences among the subspecies are highlighted in chapter 2.

*Fig. 1.9. Geographic range and subspecies distribution for Malaclemys terrapin.*
Salt, in the form of sodium chloride (NaCl), is a compound that is necessary for life, but there are instances when there may be too little or too much of a good thing. Many small creatures that live in salt water, such as invertebrates, exist in a situation in which the salt concentration within their body fluids is exactly the same as the salt concentration in their environment. Turtles, on the other hand, belong to the group of animals that are able to regulate the salt concentration in their blood and body fluids. The salt concentration will be relatively constant despite the salt or lack of salt in their environment and will generally be about one-third that of seawater. This type of regulation is known as osmoregulation and is not always precise. Under certain circumstances, too much water may be lost and the internal salt concentration may rise to a higher than ideal level. This causes dehydration that may be serious if the condition persists.

Osmoregulation is a particular challenge for diamondback terrapins because the salinity of the diamondback terrapin habitat is quite variable. In some river estuaries where considerable mixing of fresh and salt water occurs, the salt concentration may be relatively low, less than 10 parts per thousand (ppt). Waters that flow across marshes and in tidal creeks may have an intermediate salinity that changes after rainfall and with tides (10 to 20 ppt). Further out into the larger embayments, salinity can increase to 20 to 30 ppt and can even approximate that found in marine environments of the open seas (30 to 35 ppt). Captive terrapins can survive and grow under a variety of salinity conditions and even in fresh water. The diamondback terrapin adjusts to these varied salinities and can spend considerable time in fresh water, brackish water, or water with marine salinity levels.

Most turtles cannot survive very long in 100 percent seawater. The diamondback terrapin is the only emydid turtle that can spend weeks at a time under such conditions. Freshwater emydid turtles that are kept in seawater become salt loaded and osmotically dehydrated. Some, like the snapping turtle, can tolerate brief excursions into brackish water but are not truly adapted to life in an estuary or tidal creek. Truly marine turtles have a special adaptation: a type of orbital or eye gland, called the lacrymal gland, which works with the kidneys to prevent sea turtles from dehydration. Sea turtles effectively desalinate the water in their environment. Salt is excreted and seawater is converted to fresh water. These marine turtles never drink fresh water. Unlike sea turtles, the diamondback terrapin is dependent on an external source of fresh water. Clues about the importance of fresh water to terrapin...
health were gleaned in the early 1900s during attempts to farm raise terrapins for the food trade (Coker, 1906). Trappers who impounded them for long periods of time while waiting for better market prices recognized the value of periodic hosing with fresh water to maintain the weight and viability of their captives. In its natural environment, the diamondback terrapin copes with salt in its surroundings in a number of physiological and behavioral ways.

Physiological adaptations to salinity include a pair of orbital glands, similar to those of sea turtles. While terrapin and sea turtle salt glands are similar, they may have evolved independently. Initial studies of the location and function of the terrapin salt gland produced some confusing results. Salty tears, collected from the orbital region of terrapins, were initially attributed to the secretions of the Hardarian gland. It was latter shown that the Hardarian gland was similar to that of freshwater turtles and had a function in the secretion of organic compounds (Cowan, 1971). Ultrastructural studies utilizing staining and electron microscopy allowed visualization of a postorbital (behind the eye) gland in terrapins (lacrymal gland) that is considerably different from that of freshwater turtles and has a structure that implicates its role in salt secretion (fig. 1.10) (Cowan, 1971, 1973; Dunson, 1976).

The lacrymal glands can work as an accessory kidney, enabling terrapins to produce tearlike secretions with high salt content. However, these glands may not be as efficient at eliminating excess salt as their counterparts in sea turtles. Terrapins kept in seawater always have measurably higher sodium levels and higher plasma osmotic pressure than terrapins kept in fresh water.
Dunson and colleagues performed a series of osmoregulation studies on diamondback terrapins in the 1970s (Dunson, 1970; Dunson and Dunson, 1975; Robinson and Dunson, 1976). Terrapins were maintained under various conditions: fresh water, salt water, and brackish water of varying salt concentrations. Immersion of terrapins in salt water was shown to activate the lacrymal gland, but the total secretory capacity is low compared to the salt glands of marine reptiles and the lacrymal glands of sea turtles (Dunson, 1970). Furthermore, the terrapin lacrymal gland may only be activated during prolonged dehydration. During laboratory tests, it was necessary to artificially salt load terrapins to observe a high level of activation of the enzymatic activity responsible for sodium efflux (Dunson and Dunson, 1975). Thus, it appears that the lacrymal gland activity of terrapins is modest and cannot operate alone to routinely prevent salt concentrations in blood and body fluids from increasing. The gland is not active enough to allow for complete osmoregulation in 100 percent seawater. To further complicate our understanding of osmoregulation, it appears that terrapins can inhabit seawater for many months without even utilizing the function of the lacrymal gland (Dunson and Mazzoti, 1989). Some studies suggest that severe dehydration must set in before the lacrymal gland is maximally active (Dunson and Dunson, 1975).

But there are additional mechanisms at work. The diamondback terrapin also has a relatively impermeable integument. This means that the turtle’s skin and tissues have a low permeability to salts. In addition, there is a low permeability to water, which helps to prevent diuresis (loss of water) and thus keeps the volume of water in terrapin tissues at a high level (Dunson, 1970; Robinson and Dunson, 1976). Terrapins kept in fresh water weigh up to twice as much as terrapins of the same plastron length that were kept in salt water (Robinson and Dunson, 1976). The weight difference can be attributed to water uptake. Diamondback terrapins that have been kept in seawater hydrate rapidly and dramatically when exposed to fresh or low saline water. A reduced urinary output via the cloaca may help to prevent dehydration when diamondback terrapins are in seawater. Another important physiological adjustment to a salty environment is the tolerance of the diamondback terrapin to functioning with concentrated body fluids. As mentioned earlier, there can be a considerably higher sodium concentration in blood and orbital fluid, depending on whether the terrapin is in fresh or salt water.

Gilles-Baillen (1970, 1973b, 1973c) proposed a mechanism for osmoregulation in which urea, retained in the bladder as a result of decreased urinary output, spills into the blood and contributes significantly to the increased
osmotic blood pressure of terrapins that remain in 100 percent seawater for long periods of time. Thus, one of the waste products of nitrogen metabolism can be harnessed to assist in osmoregulation.

When Robinson and Dunson (1976) studied the overall rate of sodium and water exchange in terrapins they determined that terrapin skin is impermeable to sodium and that almost 100 percent of sodium uptake was via an oral route. Terrapins are not able to hydrate when salinity is greater than 20.4 ppt. When fresh water is available, it is likely that terrapins have a system for rapid intake of fresh water and its expedited storage in subcutaneous tissues. The amount of water taken in by terrapins was shown to be dependent on the salinity of the water. Salt-loaded animals did not drink when salinity was 27.2 to 34 ppt; they drank slightly when salinity was in the range of 13.6 to 20 ppt, and they drank copiously at salinities between 0 and 10.2 ppt. These salt-loaded terrapins were able to completely hydrate within fifteen minutes of drinking fresh water (Davenport and Macedo, 1990).

When terrapins are reared in fresh water, some develop swellings at the base of their appendages, which disappear when they are exposed to salt water for extended periods. These “water bags” are storage compartments and reflect the ability of the terrapin to store interstitial water (water in a type of extracellular fluid compartment) (Robinson and Dunson, 1976). These swellings are also seen in terrapins in the wild, where they presumably have a similar water storage function. They allow terrapins to fill up with fresh water so that these stores can be tapped when conditions become more saline.

In addition to physiological adjustments to a saline environment, researchers have documented several behavioral responses that contribute to the overall salt tolerance of the terrapin. Diamondback terrapins take advantage of any occurrence of fresh water in their surroundings. The infusion of fresh water provided by rainfall causes them to drink copiously and hydrate rapidly. In a laboratory setting, simulated rainfall, produced by a watering can, caused diamondback terrapins to come to the surface to drink. The rapid response to the simulated rain appeared to be triggered by vibrational or visual cues or a combination of both types of stimuli (Davenport and Macedo, 1990).

Terrapins kept in 100 percent seawater were shown to drink fresh water from the transient films that form on the water surface before mixing occurs. These films can be as thin as 1.6 millimeters (0.06 inches). When the films are thin, terrapins assume a characteristic drinking posture in which they arch their necks in order to bring their mouths to the same level as the films. Some terrapins drank from water pockets found in the upturned marginal scutes or
limb pockets of other terrapins or even their own front limb pockets (Bels, Davenport and Renous, 1995). Some enterprising terrapins simply opened their mouths at the water’s surface to catch the simulated rain. This is an important survival technique that allows terrapins to rapidly hydrate in habitats in which fresh water may be a scarce resource.

The osmoregulatory studies just described suggest that in their natural habitats terrapins will drink significant amounts of fresh water when it is available and that they are able to take advantage of rainfall at the surface of water and on mudflats. Diamondback terrapins may also utilize additional behavioral approaches to osmoregulation. Terrapins have been shown to alter their food intake and basking behavior if fresh water is in short supply. The diet of adult terrapins is expected to have the same salt content, that is, be isosmotic, with the terrapin’s environment. Since the terrapin can only eat underwater, some seawater will also be taken in during ingestion of food. Davenport and Ward (1993) showed that food intake amounted to an average of 7.2 percent of body weight when terrapins were fed in fresh water. In contrast, food intake decreased significantly in salt water. Thus, terrapins appear to exhibit hyperphagia (eating of large quantities of food) in fresh water to maximize energy intake, while at the same time minimizing incidental salt intake during ingestion of food.
A DECIDEDLY UNIQUE CREATURE

Since reptiles are ectothermic (commonly referred to as cold-blooded), they often resort to regulating their body temperature by basking. In sunlight, basking, technically known as emersion, functions in thermoregulation. Basking can increase body temperature to maximize physiological processes such as digestion, but it is not without a down side. Basking exposes turtles and increases the likelihood of their detection by a predator. However, Davenport and Magill (1996) presented evidence suggesting that basking may be another behavioral aspect of the osmoregulatory mechanism in terrapins. They observed a progressive increase in basking frequency as a function of the length of time of deprivation of fresh water. When fresh water became available, there was a rapid decline in basking frequency. The first impression one would have about the observed increase in basking behavior with freshwater deprivation is that terrapins will lose even more water and undergo dehydration. Indeed, a significant water loss occurs. But concomitant with water loss, basking results in a decreased salt influx while salt efflux continues. This prevents further concentration of body fluids. Consequently, for terrapins, basking may function not only in thermoregulation; it may also have a role in osmoregulation. Thus, for diamondback terrapins, adjustment to life in a salty environment is a complex issue of osmoregulation involving a suite of physiological and behavioral mechanisms.

Although juvenile and adult terrapins have apparently mastered osmoregulation in an environment that experiences fluctuating levels of salinity, younger terrapins, including hatchlings and yearlings, may have a more difficult time coping with higher salinities. A number of tests performed under laboratory conditions indicate that hatchlings have a lower salt tolerance than adults. This may seem surprising when we consider that many terrapin nesting sites are adjacent to areas in which the nearest water body has a salinity approaching or equaling that of seawater. How do the hatchlings survive in this seemingly hostile osmotic environment?

Dunson (1985) completed a physiological study of sodium and water influx and efflux in adults and hatchlings. He found that hatchlings do not grow well in 100 percent seawater until they have achieved a weight of approximately 50 grams (0.11 pounds). Optimal growth was observed in 25 percent seawater (approximately 8 ppt), with slower growth at higher and lower salinities. In the laboratory, headstarted hatchlings can be pumped up to 50 grams (0.11 pounds) in a matter of months. But for most hatchlings in their natural habitat, this weight will not be achieved until the terrapin is from one to three years old. Dunson also found that hatchlings have a fully functional salt gland.
but they still have difficulty adjusting to a salty environment. For all terrapins, the rate of sodium influx was related to the salt content of the feeding water, not to the amount of food eaten. This suggests that one of the major sources of sodium influx in hatchlings, as for adults, is incidental water intake during feeding, rather than the food itself. Dunson observed that hatchlings could grow to some extent, but not optimally, in 100 percent seawater if they were offered fresh water every two weeks.

With these studies and also observation of hatchlings in the field, it is possible to propose a possible mechanism for the survival and growth of hatchlings during their first one or two years in a saline environment. The combination of a fully functional salt gland and the periodic access to fresh water, via rainfall, may be important in the overall viability of hatchling terrapins. A behavioral mechanism may also be at work: Hatchlings may not spend much time in the water. There is mounting evidence that the smallest terrapins spend most of their time hiding in the salt-marsh grasses or buried in the mud and are often out of the water except when flood tides inundate the marsh.

Although the mechanisms that allow diamondback terrapins to inhabit brackish environments are complex, they have provided this turtle with a unique advantage in comparison to other turtles. The diamondback terrapin has the marsh all to itself. It does not have to compete with other turtles or even with other reptiles for the nutrients and resources in the coastal habitats where it is found today.

**Temperature, Behavior, and Activity Cycles**

In ectothermic reptiles such as terrapins, daily, seasonal, and geographically related temperatures have a profound effect on activity. Ectotherms cannot internally adjust body temperature. Their body temperatures are dictated by the environment. Terrapins do not have fatty insulation, fur, or feathers to help maintain heat, so they are also poikilothermic. This means that they cannot maintain a set body temperature via metabolic activity; their body temperature fluctuates and they can quickly gain or lose heat. Temperature is regulated more by behavioral, rather than physiological mechanisms. For aquatic turtles such as terrapins, basking is an important mechanism to increase body temperature. Terrapins are considered to be heliothermic; that is, they use solar heat to achieve optimum temperatures for physiological processes. Terrapins are sometimes seen basking on land, especially in the
early spring, when water temperatures are still cool, but more often they are observed floating on the surface of the water, limbs splayed to expose as much skin as possible to the solar rays. From the terrapin’s perspective, water temperature is more stable than air temperature. Basking in water allows body temperature to increase, even on windy days when basking on land can limit increases in body temperature and cause dehydration. Basking also allows terrapins to synthesize vitamin D, which is needed for metabolic regulation of calcium and phosphorus metabolism and thus for bone and shell health. Deficiency of vitamin D can cause soft shell disease, a condition sometimes seen when turtles are maintained in captivity without an ultraviolet light source. Basking is also important in decreasing the incidence of shell parasites such as algae and fungi, which can penetrate between the scutes and cause shell damage. Basking also facilitates the shedding of old keratin when growth of the shell occurs. As the keratinized scute material dries out, it peels back from the carapace and is readily sloughed from the shell (fig. 1.1).

The annual activity cycle of terrapins is dictated by water temperature and may be divided into several phases: spring emergence and breeding, summer dispersal, fall retrenchment into smaller creeks, and winter dormancy. In the north, warming of waters to approximately 13°C (55°F) awakens terrapins from their winter slumber. The timing and extent of terrapin activity phases vary somewhat among the subspecies. On Cape Cod, the northernmost subspecies has an extensive dormancy period, with almost half the year, late October to late April, spent in hibernation. While exploring Cape Cod’s frozen Pleasant Bay during the winter, Elizabeth Hogan, photographer and naturalist, discovered a terrapin hibernation aberration. Contrary to the idea that Cape Cod terrapins are soundly locked into hibernation during the winter, Hogan found active terrapins while peering through a naturally formed hole in the ice. Apparently, an aquifer seep or a relatively warm spring was feeding fresh water into a section of the bay and allowing terrapins to maintain some winter activity in a very limited area.

A little farther south, on Cape May, New Jersey, terrapins are active for slightly longer periods. The winter habits of terrapins in the salt marshes of Cape May were studied by Yearicks, Wood, and Johnson (1981). By mid to late November, water drops from summer temperatures of 22 to 24°C (72 to 75°F) to 6 to 10°C (43 to 50°F). By late December, all signs of terrapins disappear from the larger bodies of water and the population hibernates in small creeks, 2 to 5 meters (approximately 6 to 16 ft.) wide. The terrapins do not emerge until April or May, and are not active even on relatively warm winter days. To
find out where and how the terrapins were spending the winter, creek bottoms and creek banks were probed with rods and hard objects were excavated. In this manner, 311 terrapins were unearthed. All were alive. Cape May terrapins utilized different hibernating locations. Some were found in natural depressions on the bottom of creeks where they were covered by a thin layer of mud and 1.5 to 2.5 meters (5 to 8 feet) of water at low tide. Others buried themselves 0.15 to 0.5 meters (0.5 to 1.6 feet) deep into the sides of creek banks in areas free of vegetation and underground roots. Beneath undercut banks in the intertidal zone, group burials were found. In the latter cases, hibernating clusters were always covered by a thin layer of mud.

In Beaufort, North Carolina, hibernation was observed beginning October 22 and ending on March 8. A little farther north, in Crisfield, Maryland, terrapins emerged from hibernation on April 1 (Coker, 1906). The terrapins in these locations were occasionally observed to move in and out of hibernation, depending on the temperature, until mid-December when they remained dormant until spring. Although mating may occur within a restricted time-frame, Florida terrapins, especially the mangrove terrapins that inhabit the Keys, may be active year-round (Wood, 1992).

Terrapins are found at latitudes from about 26°N to 40°N. In the northern latitudes, they inhabit waters with extreme seasonal temperature variation. In contrast, relatively little temperature variation occurs in southern latitudes. From New Jersey to Massachusetts, surface waters may be frozen for extended periods (plate 4).

Hibernation, or brumation as it is sometimes called with reference to reptiles, is a type of dormancy exhibited by many turtles in temperate climates. Turtle hibernation is not a true hibernation, typical of endotherms. In winter, when food sources become scarce and growth and reproduction are not possible, endotherms hibernate to conserve energy. In preparation for hibernation, these animals often store fat. When they hibernate, physiological adjustments in their metabolism compensate for lack of food input. This mechanism lowers body temperatures and maintains the lowered temperature, producing a seasonal state of torpor, the inactive state associated with dormancy.

In contrast to true hibernation, the physiological mechanisms responsible for hibernation in turtles are less clear. It is not known whether they anticipate or respond to declining temperature by storing fat. Declining water temperatures rather than a shortage of food may be a more significant trigger for entering dormancy. Because turtles cannot maintain body temperature, they must avoid freezing, which can damage tissues.
For terrapins, hibernation is the response to plummeting temperatures. Almost all metabolic activity comes to a halt. At the onset of hibernation, terrapins take a breath of air and then initiate their last dive of the season. They then become dormant to survive periods of physiological challenge presented by decreasing water temperatures. There is no danger of starvation because even when active, terrapins can survive for months without food. Moreover, there is much less food available as water temperatures decrease. Under the muddy layers in tidal creeks, terrapins protect themselves from freezing. It was once observed that, for short periods of time, terrapins can withstand “cold severe enough to leave them encased in ice” (Coker, 1920). Somehow, they do not suffocate. Their need for oxygen declines as their metabolism plummets. Although there might be enough oxygen dissolved in the cold water to support the terrapin during this period of torpor, it is not clear how they survive in the anoxic mud into which they burrow.

During hibernation, physiological activity declines and the diamondback terrapin is not able to use behavioral mechanisms to osmoregulate. How does the ability of the terrapin to regulate salt balance and osmotic pressure change during hibernation? Gilles-Bailléen (1973a) studied terrapins before, during, and after hibernation in either freshwater or seawater, and measured their osmotic pressure. As in other studies, higher osmotic pressures were measured throughout the year for seawater-maintained terrapins. The osmotic pressure of seawater terrapins increased throughout hibernation and did not decrease until after mid-April emergence from dormancy. The highest osmotic pressure correlated with passive entry of salt water at the time of emergence. The transient influx of sodium, seen during emergence and most likely due to incidental drinking, may actually serve an important function in reactivating the salt gland, which does not appear to function during hibernation. It seems that when terrapins are active, physiological mechanisms can maintain osmotic pressure of body fluids at a constant level, but during hibernation these mechanisms may be less effective. Nonetheless, hibernation has a successful outcome whether terrapins remain dormant in fresh water or salt water.

Dormancy in hibernating reptiles occurs in four stages. These stages, as they apply to diamondback terrapins, can be described as follows:

1. Fasting: Terrapins do not eat when temperatures dip below $15^\circ\text{C}$ ($59^\circ\text{F}$) (Davenport and Ward, 1993). When Yearicks et al. (1981) examined the gastrointestinal (GI) system of a subset of hibernating terrapins, they found their GI tracts to be empty. This observation agrees with findings from other hibernating turtle species. There is speculation that if food
were retained in the gut, it might lead to bacterial growth that could possibly produce internal damage.

2. Retreat to refugia or hibernacula: It is commonly observed that terrapins disappear from open waters as the temperature drops. They make their way into smaller creeks and burrow under the mud, where there will be less fluctuation in temperature than in the surrounding water.

3. Attainment of the dormant state: For northern diamondback terrapins, this may be a prominent feature of their annual activity (or lack of activity) cycle.

4. Metabolic depression: As food and air become inaccessible and as underwater temperatures further decline, metabolism slows down to conserve energy. Some dissolved oxygen can by obtained by gaseous exchange in the cloaca. If metabolism occurs without oxygen (anaerobic metabolism), lactic acid may accumulate and can be harmful if not eliminated. The extent of anaerobic metabolism that occurs in dormant terrapins is not known.

Turtles display another type of dormancy, called estivation, which serves as a behavioral response to dry heat. Terrapins in some areas will undergo estivation to survive heat and drought. The upper limit or critical thermal maximum for turtles is thought to be 41°C (105.8°F) (Alderton, 1988). During very hot weather, turtles will burrow, become dormant and exist in a state of torpor until the temperature cools enough for the turtles to emerge. In the Florida Keys, terrapins burrow in the marl (the clay and limestone muck typical of mangrove islands) in the dry season. For terrapins that populate other latitudes, the thermal stability of their aquatic habitat usually prevents large swings in environmental temperature within each season.

Feeding and Nutrition

Terrapins are carnivores. In captivity, they are usually fed commercial turtle food, but their gusto for fish, crustaceans, and mollusks, if offered, is readily observed. Terrapins can be voracious eaters. When they are fed a satiation meal, they may eat up to 7 percent of their body weight but are ready to eat again after six hours (Davenport and Ward, 1993). There are several ways to study the dietary preferences of terrapins. Cafeteria-type feeding experiments can be conducted under laboratory conditions. Terrapins are offered several food choices and their preferences are observed. In the field, observers can
take note of the food choices of feeding terrapins. If dead terrapins are found, dissections of their digestive tract may reveal a recent meal. Stomach flushing of live animals has been employed to identify dietary items. Lastly, fecal analysis can sometimes reveal the less digestible remains of terrapin prey. If captured and held for a short period of time (usually 24 hours is sufficient), terrapins will “donate” feces, commonly referred to as scat, to the researcher. Some investigators have described the construction of a device to sieve dried terrapin feces so that contents can be separated on the basis of size and identified (Bauer and Sadlier, 1992; Tucker and FitzSimmons, 1992). Using a combination of these methods for dietary analysis, we have some idea about the food preferences of terrapins.

A listing of the diet of terrapins reads like the menu of a seafood restaurant: crabs, snails, shrimp, fish, mussels, clams, and perhaps oysters. This list can be extended to include worms, insects, and carrion (Pope, 1946; Carr, 1952; Cook, 1989). Gastrointestinal dissection, stomach pumping, and fecal sampling sometimes reveal barnacles, algae, pieces of grass, and mud. The latter items are most likely incidentally swallowed with the more delectable food items.

Terrapins have no teeth; their strong horny jaws act as “seizers and choppers” (Pope, 1946). Terrapins have only been observed to eat under water. Claws help to tear the food apart, and muscular tongues manipulate food to the back of the mouth. Digestion is slow and temperature dependent.

In Beaufort, North Carolina, stomach contents of terrapins captured from their natural environment revealed that the major food item was the gastropod, *Littorina irrorata*, the periwinkle snail. In *Time of the Turtle*, Jack Rudloe’s colorful account of encounters with turtles while collecting marine specimens in Florida, an elderly terrapin fisherman described his technique for finding terrapins in the thick marsh grass by “listening for the loud pops that came when they shattered a periwinkle snail between their powerful jaws” (Rudloe, 1979). The remains of *Melampus lineatus* (saltmarsh snail), small crabs such as the fiddler crab (*Uca*) and bits and pieces of annelid worms were also found in terrapin stomachs from Beaufort (Coker, 1906). A somewhat different diet may be typical of terrapins that live in northwestern Florida. Fecal analysis of 46 samples revealed a preference for dwarf surf clams (*Mulina lateralis*), crabs, and periwinkles, with crabs as the most frequently occurring food item, while surf clams were the major dietary constituent, comprising 83.1 percent of total fecal mass (Butler, 2000). In some areas of Chesapeake Bay, the main food items are soft-shelled clams (*Mya arenaria*),
D I A M O N D S  I N  T H E  M A R S H

razor clams (Tagelus spp.), and smaller clams such as Macoma and Gemma (Roosenburg, 1994, Roosenburg et al., 1999).

Terrapins are not “sit-and-wait” feeders. After all, it is not often that a tasty periwinkle will saunter past a hungry terrapin. Eating only occurs in the water. High tides are thus prime meal times, contributing to the terrapin’s daily activity cycle. Terrapins will be most active when the marsh is flooded by the tide and they can have access to submerged food sources. Bels, Davenport, and Renous (1998) studied how terrapins behave as mobile predators, stalking fast-moving and elusive prey such as shrimp, crabs, and fish. They described these activities as “strikes” and documented the modification of normal swimming activity when a strike occurs. Instead of using alternate limb strokes, like a dog paddle, the terrapin will transition to simultaneous action of the forelimbs, similar to the breast stroke, to provide a propulsive force. The change in stroke is accompanied by a rapid and large neck extension to decrease the distance to the swimming prey. The researchers describe the terrapin as a “ram feeder,” rather than a suction feeder. It opens its jaws and overtakes its prey, rather than siphoning the food into its mouth like some of the jellyfish-eating sea turtles.

Terrapins eat crabs (Uca, Callinectus, Carcinus) but crabs can be dangerous prey. Davenport et al. (1992) observed that terrapins first make a visual assessment of the crabs: They are evaluating them for size. They then approach crabs with a maximum gape. If the crab is large, the terrapin will endeavor to crop off a limb and beat a hasty retreat.

In terms of less mobile prey, Tucker, Yeomans, and Gibbons (1997) wondered why terrapins prefer Littorina irrorata, which clings to the Spartina in the upper intertidal zone, when Ilyanassa obsoleta, the common mud snail, is so abundant and more accessible. What determines the preference for periwinkle in South Carolina marshes, where it can constitute 76 to 79 percent of the terrapin diet? It does not seem to be an issue of gape size. The answer seems to be the strength of the gastropod shell. When the compressive force required to crush the shells of the gastropods is compared, it becomes apparent that it requires 2 to 3 times more force to crush Ilyanassa. The researchers concluded that even though the energy cost in searching for Ilyanassa is less, the processing cost to consume the mud snail may deter terrapins.

It seems logical to predict that terrapins will cluster in areas with high food density, but this is not always the case. In a study of prey availability in several different creeks within a Connecticut salt marsh, Whitelaw and Zajac (2002) found that terrapin distribution in the marsh did not correlate with
A DECIDEDLY UNIQUE CREATURE

resource availability. It seems that other habitat factors such as tidal amplitudes of creeks and plant density may affect the distribution of terrapins within marsh systems.

There are no studies relating learned behaviors to feeding in adult terrapins but anecdotal reports point to a link. As mentioned previously, the sound of food being chopped up alerted farmed terrapins to a forthcoming meal. In addition to sound, other food-related stimuli may affect behavior. On some occasions when the feeding schedule of farm-raised terrapins was switched to evening hours, the appearance of a light source such as a flashlight brought terrapins “out in full force” (Coker, 1920).

Swiftly swimming fish are more difficult to catch than snails, but terrapins will catch fish if the opportunity arises. They have been observed feeding on Atlantic silversides (Menidia menidia) during spawning runs in the North Edisto River estuary in South Carolina (Middaugh, 1981).

Sexual dimorphism has an impact on the foraging ecology of adult diamondback terrapins. Because adult females are larger than juvenile females and males, it might be expected that they consume larger prey. In an effort to examine dietary preferences among different size classes of terrapins, Tucker, FitzSimmons, and Gibbons (1995) analyzed fecal samples from terrapins in the Kiawah Island marsh system in South Carolina. Data from captured terrapins were grouped according to gender, size, and age of the turtles. To achieve consistency, age was estimated by counting annuli on the right humeral scute of the plastron. Evidence for prey species was analyzed for occurrence, percent mass, and, in the case of Littorina, the number of opercula (covering of the shell opening) per terrapin. Undigested opercula, recovered from fecal samples, were used to calculate overall snail size. As expected, larger terrapins consumed larger snails. When consumption of Littorina was examined in female terrapins, size selection was apparent. Head size, and thus gape size and jaw strength, directly correlated with the size of the snails consumed. Small crab species, such as U. pugnax and S. reticulatum, were consumed by all terrapins, but only the medium and large terrapins ingested blue crab (C. sapidus), primarily by cropping their rear legs. Blue crabs were only a minor part of the total diet of the Kiawah Island terrapins. In this study, dietary diversity was found to be slightly higher in the largest size class of terrapins. Therefore, in female terrapins, resource acquisition can be expected to be related to body size. Small females consume fewer types of prey than larger females. The largest females are dietary generalists, consuming a wide variety of prey species. The fecal sieving technique does not allow researchers to accu-
rately determine how soft-bodied prey, such as annelid worms, are represented in the diet. Since they did not find evidence of remains of annelids, such as indigestible setae or mandibular cuticles, Tucker et al. (1995) concluded that during their study period soft-bodied invertebrates were not a significant component of the terrapin diet. The researchers encourage ecologists to take more notice of the role of diamondback terrapins as macroconsumers in the salt-marsh food web. In marshes where terrapins are numerous, they may have significant impacts, particularly on *Littorina*.

### Growth, Development, and Life Span

Diamondback terrapins inhabit a large swath, approximately 1300 miles, of north to south coastal areas that experience dramatic seasonal differences in temperature. Therefore, it is not surprising to learn that the growth rates and age at maturity for terrapins vary with the subpopulation. The terrapins that have longer annual activity periods are expected to grow faster and mature at an earlier age. However, differences in growth rates and onset of maturity may even be seen within local populations.

It has been virtually impossible to assess the growth rates of wild terrapins during the first year or two after hatching. A laboratory study by Roosenburg and Kelley (1996), using hatchlings from eggs incubated at constant temperatures, points to increased growth rates in female hatchlings after a few months. Growth in both sexes will slow down as terrapins reach sexual maturity but this will occur in males at a much younger age than in females. After maturity, growth will occur at a low rate, less than 5 percent per year.

There have been several studies of growth rates in terrapins from different local populations. When Cagle (1952) plotted the growth rate of Louisiana terrapins and compared growth to the North Carolina population studied by Hildebrand (1932), he found that the growth rate was similar for the first two years, but after that, Louisiana terrapins grew faster than the North Carolina animals. In studying a population of Florida East Coast terrapins at the Merritt Island National Wildlife Refuge, Siegel (1984) measured greater growth rates than those of either the Louisiana or North Carolina terrapins. It should be noted that the North Carolina population consisted of captive animals that were fed by caretakers. Taken together, these trends would suggest that Northern terrapins grow more slowly than Southern subspecies, commensurate with the shorter growing season for Northern turtles. Other potential contributions to growth rate differences, such as local feeding habits, food
availability, food quantity, and hatchling size, have not been fully compared across all the subspecies. Paradoxically, Northern female terrapins may grow more slowly than Southern ones, but they may achieve larger adult sizes.

Terrapins are assessed as “mature” by several criteria. For males and females, the appearance of secondary sexual characteristics is the hallmark of sexual maturity. When examining females, eggs can be detected by x-ray or palpitation of the inguinal pocket. Nesting activity by females is also an indicator of sexual maturity. In young animals that have been sacrificed or found dead, one can dissect the specimens and perform histological staining to observe seminiferous tubules (vas deferens) in males and oocytes in females.

In looking at the north to south gradient, a noteworthy trend emerges with respect to maturation (table 1.2). In northern populations, the average size at maturity for females is 16.4 centimeters (6.5 inches) PL and 1063 grams (2.3 pounds), while their southern female cousins are slightly shorter and may weigh considerably less: 705 grams (1.6 pounds) for South Carolina females, 886 grams (2 pounds) for Florida Indian River females (Siegel, 1984). These North/South differences are less pronounced or may not exist for males. The increased size of some Northern females may have an impact on clutch size or egg size, an aspect of reproductive strategy that is explored in chapter 3.

The trend is for earlier age at maturation in terrapins as we move south along the eastern seaboard (table 1.2). From the Cape Cod, Massachusetts, subpopulation, south to Chesapeake Bay in Maryland, a female *M.t.terrapin* may be almost a decade old before she matures, while her precocious Southern cousins may mature in as little as four years. Northern males mature when they are five to eight years old, while Southern terrapin males are contributing to the gene pool when they are three years old. Rather than age, the primary determinant of sexual maturity is size, as can been seen when mean plastron length is compared. Females usually achieve about 14 centimeters (5.5 inches) PL; males must reach 8 to 9 centimeters (3 to 3.5 inches) PL before maturation is complete.

It appears that terrapin growth and maturation conform to what is seen in other aquatic turtles. The common trends are that: (1) Males mature earlier and at smaller sizes than females. (2) Growth is more rapid before maturity. (3) In temperate regions, Southern populations mature before Northern populations. (4) Sexual maturity relates more to size than age (summarized in Siegel, 1984).

Scientists and naturalists have always wondered about the longevity of turtles. These slow-growing, late-maturing creatures live long and potentially
productive lives. There have been many stories, anecdotes, and even some documentation of terrestrial turtles that can be considered ancient by human standards. Aquatic turtles do not live as long as their land-dwelling relatives, but mark–recapture data have documented life spans of at least twenty years (Siegel, 1984; Wellfleet Bay Wildlife Sanctuary, unpublished records) for diamondback terrapins, and some researchers believe that they may live more than forty years. In populations that were studied in the early 1980s, marked individuals who were already mature at the time of capture can still be found, none the worse for wear. They do not seem to suffer from anatomical or physiological senility. Longevity may compensate for large variations in the success of reproduction from year to year (Gibbons, 1987). Certainly, older females continue to lay eggs and most likely do so throughout their life span. Since there is very high hatchling mortality in most species of turtles, it is the older, mature females that are lynchpins for the survival of the population. Unfortunately, these were the very specimens that were commercially valuable during the heyday of the commercial terrapin fishing industry.

Although much is known about the diamondback terrapin, there are considerable gaps in our understanding of how this turtle copes with stressful environmental conditions. The many studies on osmoregulation point to a suite of physiological and behavioral adaptations, but it is not clear how these mechanisms work in concert. The physiological aspects of hibernation and estivation are partially understood, and much of what we know is based on work with other turtles. The significance of the size differential between terrapins of the various subspecies is without explanation. Further research may help to answer these aspects of terrapin anatomy, physiology, and growth.