

CHAPTER 1

MAMMALIAN CHARACTERISTICS

A central question of this laboratory is, "what is a mammal?" However, we urge you to get beyond that simple, descriptive question immediately, to ask the more fundamental and interesting question, "why (in the evolutionary sense of "how come?") is a mammal?" What is the adaptive significance of the structures observed? Where did they come from? Under what "selective pressures"? We answer these questions best using the comparative method. Do not be content to observe only a few species. Look at as many as you can.

Our approach will necessarily be comparative. The structural and functional features of mammals each have an evolutionary antecedent. Mammals arose from mammal-like reptiles in the Triassic Period. Therefore, to understand mammals it is important to compare them with "reptiles."

Within the Mammalia, tremendous diversity of body form and ecology exists. Mammalian diversity--from tiny shrews to gigantic whales, from flying bats to burrowing badgers, from pronghorns to sloths, from opossums to artists and engineers and mammalogists--is a continual theme in this laboratory. Surely we appreciate diversity best when we actually see it, so a wide variety of material will be available for examination.

As you go through this lab it might be useful to think about some of the Synapomorphies of mammals:

1. **Mandible is made up of a pair of single bones- dentary / dentaries**
2. **Dentary/ squamosal articulation**
3. **Heterodont dentition**
4. **Diphyodont dentition**
5. **Formation of the incus and malleus inner ear bones from the articular and quadrate**
6. **Two occipital condyles**
7. **Secondary palate (crocodilians have this also)**
8. **Skin with muscles, hair and glands**

STATION 1 THE SKULL

Objectives.--The purpose of this first section is to encourage you to increase your familiarity with (and appreciation of) the mammalian skull as an adaptive complex. You will be expected to be able to define and/or identify on a specimen all **bold** terms, but make sure you also look at the structures that are underlined. Further, you will be expected to get beyond mere vocabulary to understand the importance of the skull in mammalian evolution.

Mammals are, in a broad sense, the epitome and the apogee of a general trend in animal evolution that commenced with the flatworms: cephalization. Cephalization is the tendency to concentrate structures and functions in a head. A head is that end of the organism that meets the environment. Heads are organized and adapted to deal with environmental resources and perils. In the head are the major organs of sensation: transducers for electromagnetic (light) and mechanical (sound) waves, and chemical (olfactory, gustatory) inputs; the skull houses the front end of the central nervous system, the body's "CPU"; it incorporates the front ends of the digestive and ventilatory ("respiratory") systems.

The head is the business end of a mammal; the skull is its bony infrastructure. Although the mammalian skull is a complicated affair, it is much simpler than its reptilian antecedent.

- Compare and contrast a reptile skull to a mammal skull.

Many reptilian bones have been lost or rearranged. Some principal differences are:

--On both sides of the skull are bars (the **zygomatic arches**) under which the jaw muscles reach from the lower jaw to the back of the head.

--A **secondary palate** separates the mouth from the nasal passages. In most reptiles the nostrils open directly into the front of the mouth; they therefore cannot breathe with their mouths full. The extensive palate also allows young mammals to suckle and breathe at the same time.

--The lower jaw (**mandible**) in mammals consists of a single bone (the **dentary**) on either side; in reptiles each half of the lower jaw is made up of as many as seven bones.

--The mammalian middle ear includes three bones, the **malleus, incus and stapes**, that of reptiles only one. The two additional bones in mammals (**incus** and **malleus**) are modified parts of the reptilian lower jaw. **what are these?*

-- Mammals have two **occipital condyles** versus the single condyle seen in reptiles.

-- Most mammals have **heterodont** dentition, whereas reptiles have homodont dentition.

-- Mammals have **thecodont** dentition, where the teeth fit into a socket or **alveolus** in the **dentary**.

Because of adaptations to vastly different lifestyles, mammalian skulls are very diverse. The skull can therefore be used effectively to classify and to identify orders, families, genera, and sometimes even individual species. Taxonomic keys rely heavily on knowledge of cranial and dental characters. In the following we will therefore discuss the visible anatomy of mammalian skull.

STATION 2 PARTS OF THE MAMMALIAN CRANIUM

For starters, obtain a skull of a coyote (*Canis latrans*) or other canid and identify the following bones and other features. As you identify a feature, label it on Figure 1-1. By the way, we use a canid because canids have a fairly "primitive" skull of a size large enough to observe readily. Once you have identified features on a canid skull, it should be fairly easy (or at least possible) to find them on any other mammal.

The cranium is the skull "proper"; it is commonly divided into two regions: **braincase** and **rostrum**. The braincase is the portion of the cranium containing the brain. Compared to other vertebrates, it is particularly well developed in mammals. The rostrum is the portion of the cranium which corresponds with the snout or muzzle of the intact animal.

Note the irregular margins of the bones of the skull and note how they are "stitched" together along their margins in immovable, fibrous joints, the sutures. With age, the sutures tend to ossify completely and eventually they are obliterated. The order of closure and degree of ossification of sutures may permit relative (or even absolute) aging within a mammalian species.

Dorsal aspect of the cranium.--The **nasal bones** are a pair of bones roofing over the nasal passages. The paired **premaxillary bones** are at the anterior upper jaw. They form the lower margin of the nasal openings (**nares**) and the anteriormost part of the **bony palate**. The upper incisor teeth reside on these bones.

The **maxillary bones** are a pair of relatively large bones that make up major parts of the rostrum and the bony palate. They bear all upper teeth except the incisors. They also form the anterior base of the **zygomatic arch** (see beyond).

The **frontal bones** are a pair of bones just posterior to the maxillary bones. They are the anteriormost bones to form the roof (or dorsal part) of the braincase. In many mammals, each frontal bone has a lateral projection, the postorbital process, which marks the posterior border of the **orbit**, or eye socket. Sometimes the postorbital process joins with the zygomatic arch to form a postorbital bar (as in the Perissodactyla) or even a postorbital plate (as in Old World monkeys).

The **parietal bones** are located posterior to the frontals and contribute much of the roof of the braincase. The interparietal bone is an unpaired bone located between the parietals at the posterior end of the braincase in some mammals--observe this on a pocket mouse or rabbit. **Squamosal bones** are located lateral and ventral to their corresponding parietal bone and form major portions of the lateral walls of the braincase, as well as the posterior root of the zygomatic arch. They also include the **mandibular fossae** which are the points of articulation between the **dentary** and **squamosal** bones.

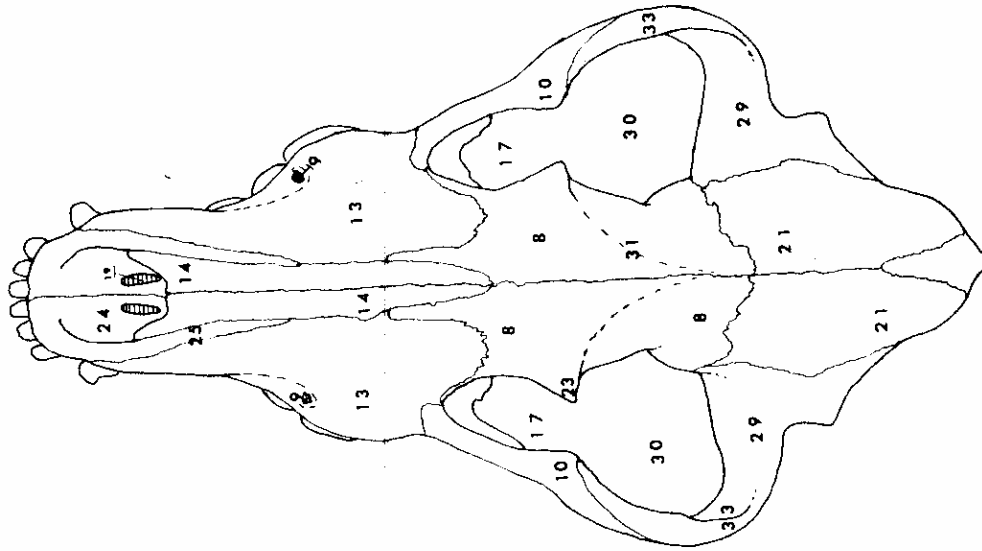


Figure 1-1A. *Dorsal aspect of cranium of coyote (Canis latrans) (after DeBlase and Martin, 1981).*

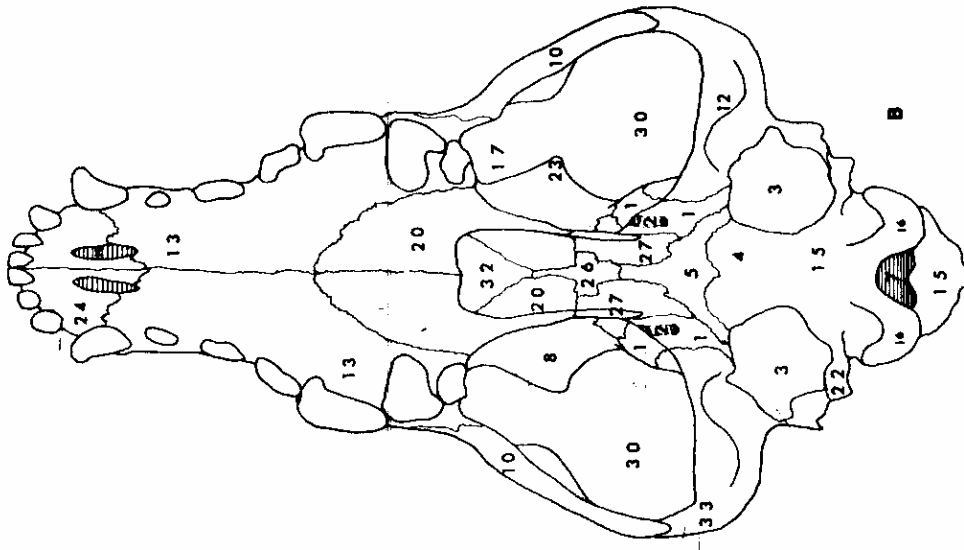


Figure 1-1B. *Ventral aspect of cranium of coyote (Canis latrans) (after DeBlase and Martin, 1981).*

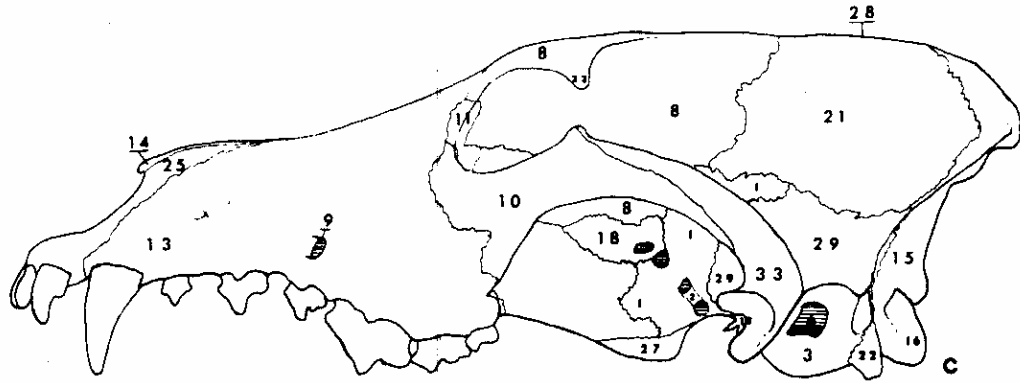


Figure 1-1C. *Lateral aspect of cranium of coyote (Canis latrans) (after DeBlase and Martin, 1981).*

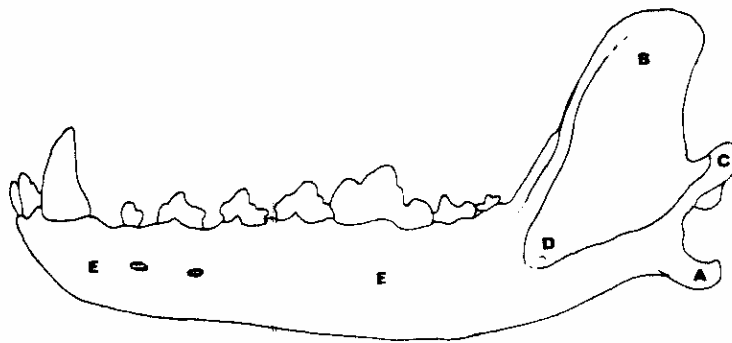


Figure 1-1D. *Lateral aspect of mandible of coyote (Canis latrans) (after DeBlase and Martin, 1981).*

Key to Figure 1-1

1. alisphenoid bone
2. alisphenoid canal
3. auditory bulla (tympanic bone)
4. basioccipital
5. basisphenoid
6. external auditory meatus
7. foramen magnum
8. frontal bone
9. infraorbital foramen
10. jugal bone

11. lacrimal bone
12. mandibular fossa
13. maxilla
14. nasal bone
15. occipital bone
16. occipital condyle
17. orbit
18. orbitosphenoid
19. palatal (= incisive) foramen
20. palatine
21. parietal
22. paraoccipital process
23. postorbital process of frontal
24. premaxilla—palatal branch
25. premaxilla—nasal branch
26. presphenoid
27. pterygoid
28. sagittal crest
29. squamosal bone
30. temporal fossa
31. temporal ridge
32. vomer
33. zygomatic process of squamosal bone
34. zygomatic process of maxilla
35. angular process
36. coronoid process
37. mandibular condyle
38. masseteric fossa
39. ramus

The **zygomatic arches** (sometimes appropriately called "cheekbones") are composite structures on the sides of the cranium. They form the lateral and ventral borders of the orbits and the **temporal fossae**. They are sometimes incomplete (as in some insectivores). The jugal bones form the central portion of the zygomatic arch. They are located between the zygomatic processes of the **maxillary** (anterior) and the **squamosal** (posterior). The temporal fossae (singular, fossa) are spaces bounded laterally by the zygomatic arch and lying posterior to the **orbit**, or eye socket.

Ventral aspect of the cranium.--Turn the skull on its dorsum and take a careful ventral view of the cranium. The **occipital bone** is the large bone forming the posterior part of the braincase. It is formed by the fusion of several bones: two lateral exoccipitals, a ventral basioccipital, and a dorsal supraoccipital. (If your specimen is an older individual, sutures between these bones may be strongly fused and it may be impossible to distinguish the components of the occipital.)

The **foramen magnum** is the large opening in the occiput through which pass the spinal cord and the vertebral arteries. The **occipital condyles** project from the occipital bone on either side of the foramen magnum and articulate with the first cervical

vertebra, the atlas (notice that they are paired). The **auditory bullae** are swollen capsules on each side of the anteriormost part of the occipital. They protect the middle-ear bones and facilitate efficient transmission of sound to the inner ear. The paroccipital processes are projections of the occipital extending laterally just posterior to the auditory bullae.

The **palatines** are a pair of bones forming the posterior part of the secondary palate. They are located between the cheekteeth and posterior to the ventral parts of the maxillaries. The palatines surround the posterior openings of the nasal passages and ventrally reach up to contact the frontals.

Mandible.--The mammalian mandible is a simple structure composed of only two bones: the left and right **dentary bones**. In species of most mammalian orders dentaries are firmly fused

anteriorly at the mandibular symphysis. The horizontal ramus is the tooth-bearing portion of the dentary. The coronoid process (occasionally called the ascending or vertical ramus) is the posterior, vertical part of the dentary. It fits into the temporal fossa of the cranium and provides the attachment sites for jaw muscles. The masseteric fossa is the shallow depression at the base of the coronoid process. (It may be more conspicuous in mammals other than canids and sometimes penetrates the dentary to form a masseteric canal.) The **mandibular condyle** articulates with the mandibular fossa of the cranium. It is the pivot around which the mandible moves. The angular process protrudes ventrally to the mandibular condyle and provides additional attachment sites for the jaw muscles.

Having identified the bones of the canid skull, you should be able to identify and name homologous structures of skulls of other mammalian groups. Labeled drawings of skulls of a number of species are provided in the Glossary in Hall (1946). Observe as many of the following as possible:

Rodentia: beaver, porcupine, marmot, rat, pocket gopher
Artiodactyla: cow, sheep, deer
Chiroptera: vespertilionid, pteropodid
Insectivora: shrew, mole
Carnivora: bear, weasel, cat
Primates: human, ape, monkey
Ondontoceti: dolphin

STATION 3 Teeth

General.--Mammalian teeth have three peculiarities, based on trends laid down by their therapsid ancestors: (1) the toothrow is differentiated front to rear (**heterodont**); (2) the teeth are set in sockets (**thecodont**); and (3) the teeth are present in two and only two sets (**diphyodont**), the **deciduous** (temporary) "milk teeth" and the **permanent teeth**. The milk teeth ("baby teeth") are lost as the **permanent teeth** move into place in the jaws. These conditions contrast with those in primitive vertebrates (including most living reptiles) where teeth are (1) all the same size and shape (**homodont**); (2) are perched atop the jaw bones (**acrodont**) or on the side (**pleurodont**), and (3) are mostly replaced as needed throughout life (**polyphyodont**).

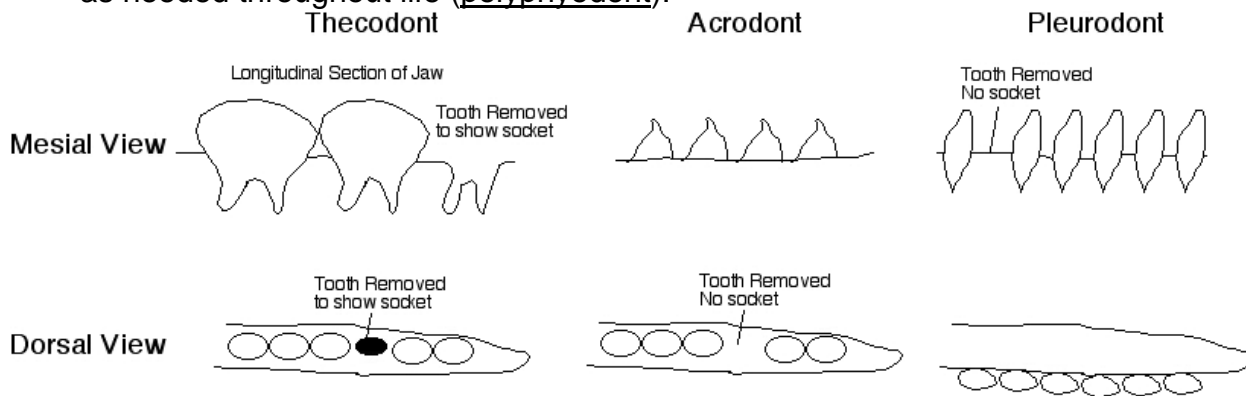


Figure 3.1 Tooth arrangement in vertebrates. From <http://www.auburn.edu/academic/classes/zy/0301/Topic13/>

The evolutionary plasticity of mammalian teeth has been remarkable. The typical deviation from the primitive condition has been to lose teeth. Herbivores, like rodents, rabbits, and most even-toed hoofed mammals have lost the canines and simplified the incisors. Carnivores have sacrificed grinding cheekteeth. Some whales and anteaters have given up on teeth altogether. The toothed whales, by contrast, have re-emphasized teeth; some have over 200 of them.

Not only have numbers of teeth changed over millions of years of evolutionary history, but form has been altered as well. Teeth give helpful clues as to the different lifestyles of mammals. In this laboratory we will see how dental form and function are related.

*A reminder: in this section, it will be wise to read directions and descriptions with appropriate specimens in hand, and it probably will pay to work with a colleague. **To preserve the quality of specimens, when pointing to particular structures, do not use a pen or pencil. Also, skulls and teeth are hard, but they are brittle and fragile. Handle with respect.***

□ Obtain the skull of a coyote or other canid. Identify all structures whose names are in **bold**. Note: in describing dental adaptations, the usual orientational terms are used: anterior, posterior, medial, etc. In addition, the term labial refers to the outside of the tooth, the side closer to the lips, and lingual refers to the inner border of the tooth, the side closer to the tongue.

The portion of the tooth exposed above the gumline is the **crown**. The portion fitting into the socket or **alveolus** is the **root**. The major portion of each tooth is made up of a bone-like substance called **dentine**. At the crown the dentine is covered with the harder **enamel**, the hardest substance in the vertebrate body. The root is covered with another bone-like substance, **cementum**. The central, living portion of the growing tooth, the pulp (which occupies the **pulp cavity**), is supplied with blood vessels and nerves through one or more openings in the endings of the tooth's roots. In most mammals, growth of the tooth ceases after some time and the blood supply is reduced. Teeth of this type are termed rooted. In some cases (e.g., the incisors of rodents and the cheekteeth of highly derived grazers of several orders like horses), the teeth grow throughout the animal's life. Such evergrowing teeth are said to be "rootless."

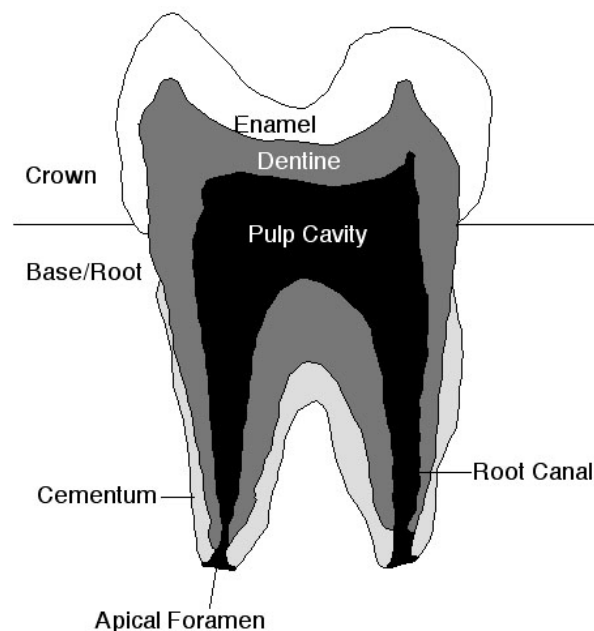


Figure 3.2 Parts of a tooth. From <http://www.auburn.edu/academic/classes/zy/0301/Topic13/>

- Examine the evergrowing ("rootless") incisors of a rodent, such as a beaver (*Castoridae*). Carefully extract the incisor and note the open pulp cavity.

STATION 4 Kinds of Teeth.

--Mammalian teeth are **heterodont**. That is, they are differentiated from front to rear in the toothrow. This contrasts with the **homodont** condition of most toothed vertebrates. In mammals, there are four basic kinds of teeth: **incisors**, **canines**, **premolars**, and **molars**. Usually, at least two of these kinds of teeth show morphological differences. The numbers of teeth are given per quadrant, (upper versus lower, right versus left) that means one half of the lower jaw or one premaxilla/maxilla of the upper jaw.

Incisors are the anteriormost teeth in the jaws of most mammals. The upper incisors are rooted wholly in the **premaxillae**. They are mostly simple in structure but in various

groups have been modified for grooming, cutting, gnawing, and other functions. Placental mammals never have more than three incisors in each jaw quadrant. Marsupials, however, may have up to five in each half of the upper jaw and up to four in each half of the lower jaw.

Canines are the anteriormost teeth in the maxillae (located right next to the suture between **premaxillae** and **maxillae**) and the corresponding teeth in the lower jaw. They are frequently used for holding and piercing prey. No known mammal has more than one canine per quadrant.

Because cheekteeth (**premolars** and **molars**) do the major job of masticating food, they have undergone major structural changes as mammals have diversified and exploited new nutritional resources. For this reason, the structure of cheekteeth is one of the most important clues to mammalian relationships and is therefore used as a principal criterion in mammalian classification. Further, cheekteeth provide strong clues to mammalian diets.

It is not always easy to distinguish **premolars** and **molars**, by the way. Premolars may be smaller than molars, but the fundamental distinction is that premolars are present in both the deciduous and permanent dentitions, whereas molars are present only in the permanent dentition. In modern mammals the shapes of the cheekteeth vary greatly in response to the demands of different diets. The most ancient known mammals (from the late Triassic) were insectivores, and their cheekteeth were adapted to crushing arthropod exoskeletons. These teeth had four main cusps arranged in a longitudinal or slightly triangular row and sheared together in a scissor-like action.

Examine a skull of a coyote or other canid. Identify the incisors, canines, premolars, and molars. Note which teeth arise from which bones. How do you know which teeth are premolars and which are molars? Note the possible function of each type of tooth. Observe the shearing action of the sectorial teeth (the so called carnassials, P4/m1).

Examine the skull of a few other mammals at this station. Compare and contrast with the coyote. Identify incisors, canines, premolars, and molars. Note which teeth arise from which bones. How do you know which teeth are premolars and which are molars? Note the possible function of each type of tooth.

STATION 5 FEEDING ADAPTATIONS IN THE DENTITION

Examine the skull of an omnivore, the hog, *Sus scrofa* (Artiodactyla: Suidae). Compare the cheekteeth with those of a bear and those of a human.

The situation often is different in specialized herbivores. Responding to the abrasive qualities of their food, they have evolved protective strategies against the quick erosion of their teeth. One convergent adaptation in several groups is a hypsodont

(high-crowned) dentition. The higher the crown, the longer the tooth will last. Grass contains large amounts of silica, and therefore some herbivores, especially grazers, evolved rootless, ever-growing teeth.

- Examine the dentition of a series of herbivorous mammals
- Examine the dentition of a series of carnivores. Again, notice the Carnassials.

STATION 6 DENTAL FORMULAE

--The dental formula is a shorthand method to indicate the number and variety of teeth in a particular mammal. Dental formulae frequently appear in keys. There is no need to memorize dental formulae. Rather, note Table 1-1 for future reference.

Dental formulae are expressed in a variety of ways, most of them fairly common-sensical. Here is a typical dental formula, for the genus *Canis*: $I = 3/3$, $C = 1/1$, $P = 4/4$, $M = 2/3$, Total = 42.

The number above each "slash" mark (solidus) represents the number of teeth in one quadrant of the upper jaw; the lower numeral represents the teeth of one quadrant of the lower jaw. I stands for incisors, C for canines, P for premolars, and M for molars. The total number of teeth is shown, calculated by adding together all the numbers given in the dental formula and multiplying them by two, for the two sides of the jaw.

The dental formula can be abbreviated further by deleting the initials for the tooth types: $3/3, 1/1, 4/4, 2/3 = 42$. A zero indicates that a particular kind of tooth is absent in a species. For example, many rodents lack canines and premolars. The dental formula for the deermouse (*Peromyscus maniculatus*) is therefore: $1/1 0/0 0/0 3/3 = 16$.

Recall that the distinction between molars and premolars is that molars are present only in the permanent dentition. It sometimes is impossible to distinguish premolars and molars in an adult animal. However, it is often possible to deduce the dental formula through the use of simple logic. If a mammal has the maximal number of cheekteeth (four premolars and three molars in placentals), a complete and accurate formula is no problem. Further, consider the carnivores. No matter how incomplete their set of postcanine teeth seems to be, the shearing pair of carnassial teeth can almost always be identified and the carnassials are always $P4/m1$. With that knowledge as a starting point, one can determine the complete dental formula.

Notation for Single Teeth.--A single tooth is often identified by giving the tooth type (I, C, P, or M) with a superscript (for the upper toothrow) or subscript (for the lower toothrow) numeral. Thus P^4 denotes the fourth upper premolar, whereas M_1 denotes the first lower molar. This form of notation is not always easy to type in a paper-, tree-, dollar-saving, single-spaced format. Therefore, we sometimes find the upper teeth abbreviated with upper case letters--I, C, P, M--and the lower teeth abbreviated with lower case letters--i, c, p, m. $P4 =$ the fourth upper premolar, $i1$ the first lower incisor.

The latter convention is generally used in this guide. Note, by the way, that premolars are lost from front to rear, whereas molars are lost from rear to front. Therefore, if a mammal has a single upper premolar it is P4; if it has a single lower molar it is m1.

In this guide, all references are to the permanent dentition. In other contexts, you may find that deciduous teeth are indicated by the letter d. Hence, dP4 = the last upper premolar (which is, by definition the last upper cheektooth) in the milk dentition. Minimally, the simple notation "dc" could indicate the deciduous lower canine, because there is never more than a single canine tooth above and below, on each side of the jaw.

- Examine the skulls of various mammals in the lab. Try to decipher the dental formula.

Table 1-1. *Dental formulae of genera of mammals of Colorado.*

I 5/4, C 1/1, P 3/3, M 4/4 = 50	<i>Didelphis</i>
I 3/3, C 1/1, P 4/4, M 2/3 = 42	<i>Ursus*</i> , <i>Canis</i> , <i>Vulpes</i> , <i>Urocyon</i>
I 3/3, C 1/1, P 4/4, M 2/2 = 40	<i>Procyon</i> , <i>Bassariscus</i>
I 2/3, C 1/1, P 3/3, M 3/3 = 38	<i>Myotis</i>
I 3/3, C 1/1, P 4/4, M 1/2 = 38	<i>Martes</i> , <i>Gulo</i>
I 2/3, C 1/1, P 2/3, M 3/3 = 36	<i>Lasionycteris</i> , <i>Plecotus</i>
I 3/2, C 1/0, P 3/3, M 3/3 = 36	<i>Scalopus</i>
I 3/3, C 1/1, P 4/3, M 1/2 = 36	<i>Lutra</i>
I 2/3, C 1/1, P 2/2, M 3/3 = 34	<i>Pipistrellus</i>
I 3/3, C 1/1, P 3/3, M 1/2 = 34	<i>Mustela</i> , <i>Mephitis</i> , <i>Taxidea</i> , <i>Spilogale</i>
I 0/3, C 1/1, P 3/3, M 3/3 = 34	<i>Cervus</i>
I 2/2, C 1/1, P 2/2, M 3/3 = 32	<i>Homo</i>
I 3/3, C 1/1, P 2/3, M 1/2 = 32	<i>Conepatus</i>
I 2/3, C 1/1, P 1/2, M 3/3 = 32	<i>Eptesicus</i>
I 3/1, C 1/1, P 3/1, M 3/3 = 32	<i>Sorex</i>

I 1/3, C 1/1, P 2/2, M 3/3 = 32	<i>Lasiurus</i>
I 4/2, C 1/0, P 2/1, M 3/3 = 32	<i>Blarina</i>
I 0/3, C 0/1, P 3/3, M 3/3 = 32	<i>Odocoileus, Alces, Bison, Antilocapra, Ovis, Oreamnos</i>
I 1/2-3, C 1/1, P 2/2, M 3/3 = 30 or 32	<i>Tadarida</i>
I 3/3, C 1/1, P 2-3/2, M 1/1 = 28 or 30	<i>Felis</i>
I 3/2, C 1/0, P 2/1, M 3/3 = 30	<i>Cryptotis</i>

Table 1-1, continued. *Dental formulae of genera of mammals of Colorado.*

I 3/2, C 1/0, P 1/1, M 3/3 = 28	<i>Notiosorex</i>
I 1/2, C 1/1, P 1/2, M 3/3 = 28	<i>Antrozous</i>
I 2/1, C 0/0, P 3/2, M 3/3 = 28	<i>Lepus, Sylvilagus</i>
I 2/1, C 0/0, P 2/2, M 3/3 = 26	<i>Ochotona</i>
I 1/1, C 0/0, P 2/1, M 3/3 = 22	<i>Marmota, Spermophilus, Tamias, Tamiasciurus, Cynomys, Sciurus*</i>
I 1/1, C 0/0, P 1/1, M 3/3 = 20	<i>Castor, Erethizon, Thomomys, Cratogeomys, Perognathus, Dipodomys</i>
I 1/1, C 0/0, P 1/0, M 3/3 = 18	<i>Zapus</i>
I 1/1, C 0/0, P 0/0, M 3/3 = 16	<i>Onychomys, Phenacomys, Reithrodontomys, Neotoma, Clethrionomys, Microtus, Peromyscus, Lemmings, Ondatra, Sigmodon, Rattus, Mus</i>

*May have one upper premolar missing.

PART B. POSTCRANIAL SKELETON AND LOCOMOTOR ADAPTATIONS

This section is meant to facilitate an appreciation of the structural and functional diversity of mammalian locomotor patterns, through an examination of the postcranial skeleton. You should be able to (1) recognize the individual major bones of any articulated mammalian skeleton, (2) know and apply accurately all terms in **bold**, (3) name the stance or identify the mode of locomotion of a mammal from examination of any articulated limb. Figure B.1 will be a useful guide.

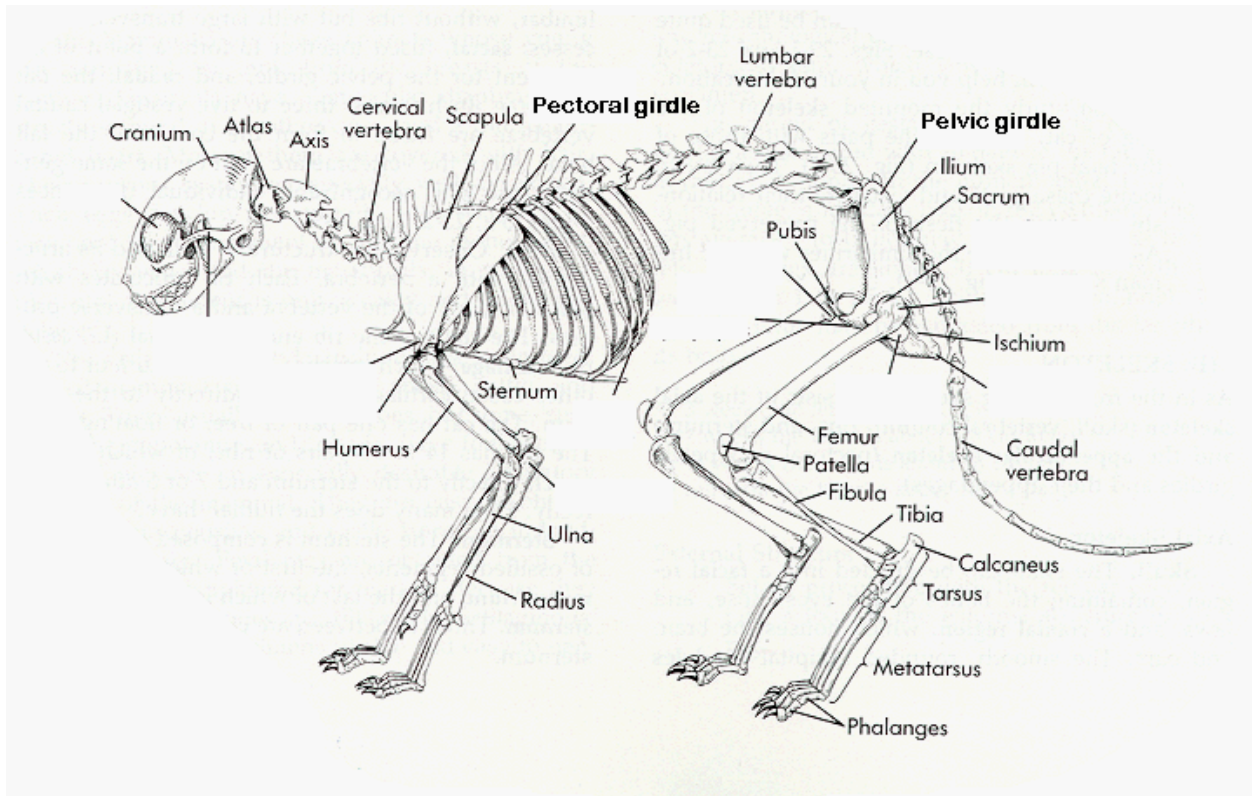


Figure B.1. *Skeleton of a domestic cat (Felis catus)*. From Hickman, *Laboratory Studies in Integrated Principles of Zoology*, 1992, 8th ed.

Most of the terminology in this section may be a matter of review. However, you may know best the anatomy of a rather peculiar bipedal primate, *Homo sapiens*. Don't take anything for granted!

You probably have discussed the skeleton as being of two pieces: the **axial skeleton**--consisting of the skull and vertebral column, neck to tail, and the **appendicular skeleton**--the skeleton of the limbs and their girdles, pelvic and pectoral. When we use the term "postcranial" skeleton we are making a slightly different distinction. We have discussed the skull and we reviewed the fact that it is adapted to meeting the

environment and its opportunities and dangers. The post-cranium--the skeleton behind the skull--is concerned with locomotion.

In this section we continue to use the comparative method as a means to understand "why is a mammal?" Comparison will be between mammals and their reptilian progenitors and also among diverse groups of mammals. The mammal-like therapsid reptiles of the later Permian and Triassic not only exhibited some mammalian cranial and dental features, but also advances in postcranial structure. The most obvious change is that their bodies stood more erect than typical reptiles, the elbows pointed backward and the knees forward.

From this beginning in reptile-like mammals there has been a broad adaptive radiation in locomotion. The basic mammalian stock was four-footed (**quadrupedal**) and each of those feet had five toes (**pentadactyl**). (We humans retain this ancestral arrangement--although it has been modified in detail, of course, to accommodate our peculiar bipedal gait). Mammals have pushed the basic plan in myriad ways. A purpose of this laboratory is to develop an appreciation for this diversity.

Throughout the narrative that follows, a distinction is being made between two phenomena: stance and locomotion. Mammals show diverse adaptations in both. **Stance** describes the way an animal stands. **Locomotion** describes how an animal moves. Confusion is easy because some species change their stance as they change their mode of locomotion. For example, a human runner stands and walks on the soles of her feet (a stance we will describe as **plantigrade**). Leaving the starting blocks, she runs on her toes--that is, she becomes **digitigrade**. Loping along in full stride, she may again become essentially **plantigrade**. Again, stance and locomotion (gait) are easy to confuse but they are different, so make the distinction. Stance is about standing; gait about moving.

Elements of the Forelimb.--The shoulder or **pectoral girdle** of most mammals is composed of two elements. The **scapula** is a large, typically flat bone located dorsal to the ribs. It is embedded in back muscles and does not articulate directly to the axial skeleton. A **clavicle** (collar bone) is present in most mammals. It is a rod-like bone that extends from the scapula to the sternum, providing a firm support for the front limbs. Mammals that run on hard ground often have a reduced clavicle or none at all, missing the bony connection between the pectoral and the axial parts of their skeletons. The shock of the running body striking the ground is absorbed by the soft tissues surrounding the scapula.

The pectoral limb itself consists of three major parts. The proximal (situated nearest the body) **humerus** has a large head which is articulated to the scapula by a ball-and-socket joint. This allows great mobility. Distally (away from the base or point of attachment) the humerus meets the **ulna** and the **radius**. The ulna has a proximal extension, the olecranon process, which serves as the short arm of the lever for the muscles extending the forearm. Generally, ulna and radius are able to rotate around each other, enhancing the mobility of the forefoot. The forefoot or hand (**manus**)

includes three different sets of bones. The first, proximal group form the **carpus**, or wrist. Hence, the individual elements are called the **carpals**. They are followed by the **metacarpals**, one for every digit. The most distal series of bones is called the **phalanges** (singular, **phalanx**). In the primitive pattern, the first digit of the forelimb, or **pollex**, has two phalanges. The rest of the digits contain three. Hence, the ancestral mammalian phalangeal formula is 2-3-3-3-3. (This is a simplification of the general reptilian formula, 2-3-4-5-3.)

- On skeletons of several species, identify the bones of the forelimb.

Elements of the Hindlimb.--The hip or **pelvic girdle** is composed of two symmetrical halves, the **innominate bones** or **os coxae**, each of which was formed by the fusion of three bones. The **ilia** (singular, **ilium**) extend anterodorsally and articulate with the lower vertebral column. The **ischia** (singular, **ischium**) extend posteriorly and form the bony part of the rump. The **pubic bones** project anteroventrally and are joined at their distal ends. These three pairs of bones, together with their articulated vertebrae, form a ring through which the reproductive, urinary, and digestive tracts leave the body.

The pelvic limb is similar to the front limb. The proximal bone (corresponding to the pectoral humerus) is the **femur**. The middle segment of the hindlimb includes the larger **tibia** and narrower **fibula**. These two bones are often partly fused. Many mammals have a **patella** or knee-cap. This bone is formed independently from the other leg bones; it protects the knee joint. The hindfoot, or **pes**, consists of three series of bony elements. The most proximal are the **tarsals**. The largest of the **tarsals**, the **calcaneum** or heel bone, has a posterior process which serves as an attachment site for the tendon of the extensor muscle of the hind foot. The **tarsals** are followed by the **metatarsals** and, as in the manus, the distal **phalanges**. The number of the phalanges is the same as in the corresponding digits of the forefoot. The first digit (the "big toe") is the **hallux**. Carpals and tarsals are often referred to collectively as **podials**, metacarpals and metatarsals together are called **metapodials**.

- On skeletons of several species of mammals, identify the elements of the hind limb.

Adaptations to Distinctive Habitats

Terrestrial adaptations.--Early mammals were small, terrestrial, **pentadactyl** quadrupeds. They had the ancestral limb structure discussed above, which results in a **stance** (foot posture) where the sole (plantar surface) of the whole foot contacts the ground as the animal walks. This **plantigrade** stance persists or has developed secondarily in many mammals, from opossums to great apes (including humans). However, when forced to run, many **plantigrade** mammals tend to increase the effective length of the leg by lifting the heel off the ground. This is called **cursorial** (running) locomotion. Some carnivores that rely on running speed and endurance to

catch their prey became permanently cursorial, and always stand on their toes. This is called a **digitigrade** stance.

- Examine the limb skeleton of a cat. Compare the lengths and relative positions of the various limb elements with those of a plantigrade mammal. Compare the placement of the pads on the feet of cat with those of a raccoon.

Some of their prey further elaborated this principle, rising to stand only on the longest, medial digits. The side toes were reduced, and the remaining digits strengthened and elongated. The claws increased in size to support the toes and ended up surrounding the entire tips. These hooves were finally the only parts of the feet to have contact with the ground. Members of two living orders show this **unguligrade** stance--most artiodactyls and the horse (family Equidae, order Perissodactyla). Most artiodactyls are left with two principal digits of equal size on each foot. To reinforce the legs' stability the pairs of metacarpals and metatarsals are often fused to form a single so-called cannon bone. The horses (Equidae--order Perissodactyla) have only the medial digit in each foot. In addition to the modifications of the bones of the feet, many artiodactyls and the horses have reduced and fused the ulna to the radius and the fibula to the tibia. This results in only a single bone in the middle segment of the limbs. The trend towards long limbs specialized for high speed is generally accompanied by reduced lateral mobility.

A foot with an even number of toes is called **paraxonic**; the toes are situated beside (*para-*) the axis of symmetry of the foot. A foot with an odd number of toes is **mesaxonic**; the axis of symmetry passes through the middle (*meso-*) of the foot.

- Examine mounted limbs of **unguligrade** mammals. Compare lengths and arrangement of elements with those of **digitigrade** mammals. What causes the restriction of lateral movement in the unguligrade limb?

LOCOMOTOR ADAPTATIONS

Saltatory and Ricochetal adaptations. - - When a running squirrel or rabbit jumps forward, the stronger and longer hind legs leave the ground last, and the front legs touch it first when the animal lands. The hind limbs provide the major part of the thrust. Several mammals, including lagomorphs (other than pikas) and many rodents, use this so-called **saltatorial** locomotion. In contrast, kangaroo rats and kangaroos are completely bipedal. Their front feet are not used for locomotion. The hind feet are elongated and the usually strong, long tails provide support and counterbalance. Locomotion of animals like the kangaroo is termed **ricochetal**.

- Compare postcranial skeletons of saltatory and ricochetal mammals, noting especially the relative lengths of elements in the fore- and hind limbs.

Fossorial adaptations.--Many mammals are capable of digging. Some do it on a rather sporadic basis, like the coyote digging up lunch or enlarging a burrow to shelter the young. Other mammals dig elaborate burrows and use them as a permanent home.

Badgers, armadillos, prairie dogs, or marmots spend large amounts of time excavating and maintaining burrows, but they gather food outside their retreats. Some adaptations for this **semifossorial** way of life are increasingly small ears and stronger limbs and claws. But **semifossorial** prey species tend to retain keen senses of sight and hearing and rapid mobility above ground.

- Compare the limb structure and general body shape of a badger with that of a raccoon. What modifications for **semifossorial** life are present in the badger?

The seemingly small step from a **semifossorial** animal to one living and foraging permanently underground often comes about with great anatomical change. Truly **fossorial** mammals generally have sturdy, compact bodies, the length of neck and tail is reduced, tactile and olfactory senses are improved, the pinnae are small or absent, the eyes are small and sometimes non-functional, and the fur has no direction of lay. Highly specialized digging limbs have evolved. **Fossorial** insectivores (the moles) and marsupials (the marsupial mole, *Notoryctes*) have front limbs with large hands, strong claws, and powerful muscles. The palms of the hands point backwards. **Fossorial** rodents (like pocket gophers and mole rats) tend to use powerful, procumbent incisors for digging. The limbs are robust, but generally are used only to move the loosened soil backwards.

- Examine a mole skeleton. Compare the structures of the hind limbs and the forelimbs.

Arboreal adaptations.--Even mammals without obvious adaptations for climbing are often seen to take to the trees, either to reach food or to find elevated places to rest or escape. Many smaller rodents and insectivores with unspecialized hands are excellent climbers and forage in trees and shrubs. Cats, martens, raccoons, bears, and even goats and some foxes spend time in trees.

Tree squirrels have an essentially terrestrial structure. Their arboreal specializations are limited to very sharp claws and long bushy tails that aid in balance. They tend to live in the trees, where they have their nests, but they also forage on the ground. Tree squirrels are considered **scansorial** ("scampering") animals.

Mammals specialized for a more exclusive life in the trees are called **arboreal**. They often have opposable digits or prehensile tails, or both. Monkeys and most apes are essentially arboreal animals. Animals like the orangutan that essentially have a "hand" on every limb are termed quadrumanal. Gibbons employ one form of locomotion above all others: they hang by their hands and move forward by swinging from branch to branch. This brachiation is often compared to an up-side-down bipedal walk. Brachiating mammals have especially long fingers and short thumbs. Tree sloths hang from hook-like claws on manus and pes. Their arboreal locomotion resembles a slow up-side-down quadrupedal walk. Sloths are bradypodal ("slow-footed") animals. On the ground they walk on the sides of their feet.

- Examine a series of skulls of arboreal mammals. Which have the orbits directed anteriorly to provide overlapping visual ranges and, therefore, binocular vision? What is the selective advantage of depth perception in these forms?

Aerial adaptations: flight.--Bats (order Chiroptera) are the only mammals exhibiting true flight. These **volant** mammals are enormously successful and represent the second largest mammalian order after the Rodentia. A bat is closely adapted to its unique lifestyle. The bones of the forelimbs are long, slender, and often tubular. Greatly elongate finger bones support the flight surface (patagium). The whole skeleton is very light. The patagium is membranous, and usually mostly naked. The hind legs are rotated 180 degrees at the hip joint, so that the knees are directed posteriorly. The part of the patagium between the hind legs (the uropatagium) is often supported by a spur on the ankles, the calcar.

- Examine a bat skeleton, contrast it with a generalized terrestrial mammal like a rat, and note modifications for flight. How does the structure of the bat wing differ from those of the wings of the other flying vertebrates, the birds and pterosaurs? Identify homologous elements.

Aquatic adaptations.--When forced, virtually any mammal can swim, but some kinds are more specialized to swimming (**natatorial** locomotion) than are others. Amphibious mammals like the water shrew, muskrat, and beaver show adaptations for a **semiaquatic** life style. They may have webbed feet or strong hairs growing at the edges of their toes. The tail may be flattened. Generally the whole body is more streamlined than that of a terrestrial mammal. However, all amphibious mammals are well equipped to travel the land.

- Examine a platypus, water shrew, beaver, muskrat, river otter, and sea otter for modifications for amphibious life. In what way are they similar in structure? How are the feet of each modified to increase the surface area for propulsion in swimming?

Pinniped carnivores (seals, sea lions, walruses--once placed in a distinct order, the Pinnipedia, and still frequently discussed collectively) are strongly adapted for an aquatic life. They spend a large part of their lives in the water, coming ashore only to rest and to bear the young. The limbs have developed into flippers that are of only limited use on land. The hind flippers of sea lions and walruses (families Otariidae and Obobenidae, respectively) can be turned forward and used for locomotion when the animals come ashore. Seals (family Phocidae) have hind limbs that are permanently extended posteriorly.

Members of the order Sirenia, the dugongs and manatees, are strictly aquatic and never come onto land. Extant kinds occur in tropical coastal waters, including estuaries. They are the only completely aquatic mammals that are herbivorous. Their external features are similar in many ways to the whales, but they are believed to have a common ancestor with the elephants. The forelimbs are modified into flippers, and hindlimbs are absent. The tail forms a horizontal fluke.

Cetaceans or whales (orders Mysticeti and Odontoceti) are adapted for an exclusively **aquatic** lifestyle. When accidentally stranded whales often die because the body cannot support itself on land and individuals of larger species are crushed by their own weight. Whales are fusiform (torpedo-shaped), adapted to offering minimal hydrodynamic resistance. The forelimbs are modified into streamlined flippers, often with more than the ancestral number of phalanges. Hindlimbs are absent, though remnants of the pelvic girdles generally are present. The tail is horizontally flattened into flukes. The animals propel themselves almost completely by vertical movements of the tail. A dorsal fin is often present. What are its homologies with structures in other mammals?

C. INTEGUMENTARY SYSTEM

The skin and associated structures make up the **integumentary system**. No feature of a mammal is more obvious than its integument. In fact, the skin is such a readily apparent functional complex that we mostly take it for granted, forgetting that it is, in fact, both functional and complex.

The outer covering of land-dwelling organisms must protect from desiccation as well as other perils. In terrestrial organisms, skin reaches its highest development. Hence mammalian skin is about the fanciest integument there is. The skin is an individual mammal's largest organ. Its functions are prodigiously diverse: it protects the body against physical, chemical, and biological attacks, it helps to regulate body temperature, it is used in many ways to communicate to other individuals, and it even provides nourishment for the young.

As a consequence of working through this section of laboratory, you should have a deeper appreciation for the structure and function of the mammalian integument (the skin and its derivatives) and its role in homeostasis. Be sure that you know and can apply correctly all **bold** terms.

Skin

Like the integuments of other vertebrates, mammalian skin is composed of two layers, the dermis and the epidermis. In your text (Pough et al., 1996:641, Figure 21-2) is a cross-section through "typical" mammalian skin. On a model of mammalian skin (and/or microscopic thin sections) identify all the structures in **bold** in the following account.

Epidermis--The epidermis consists of several layers, representing successive stages of development. The oldest part of the skin is an expendable outer layer of tough, protective, dead cells, continually worn off at the surface and continually replaced from below. As the cells age and mature, they eventually lose their nuclei and convert most of their cell contents to keratin, a protein that makes not only the protective layer of skin, but such structures as nails, hooves, hair, and horns--evolutionary and developmental derivatives of skin.

The outermost layer of epidermis is the **stratum corneum**, the "horny layer." The epidermis on the soles of walking feet and the palms of working hands is thick. Elsewhere on the body, the epidermis may be quite thin. Thickened portions of the epidermis form the pads on the feet of most mammals and the friction ridges on the digits and palm of primates. Fingerprints are the impression of these ridges. Calluses are also products of the epidermis. Hair, horn, claws, and epidermal scales are all made of modified keratinized cells of epidermal origin.

Dermis.--The dermis lies below the epidermis. It is a thick layer of connective tissue with associated muscles, nerves, and blood vessels. The connective tissue consists to a great degree of collagen. Collagen and the other fibers in the dermis become toughened and hardened during the process of tanning when a skin is transformed into leather. Unlike the epidermis, the dermis is well-supplied with blood vessels and nerves for sensation of touch, pressure, temperature, and pain. Beneath the dermis is a layer of fatty tissue, variably thick, that provides insulation and energy storage. In many species, the extent of subcutaneous fat varies dramatically with season.

Skin Glands.--Associated with the skin are two kinds of glands, sweat glands and sebaceous glands. The epidermal sebaceous glands lubricate the hair and are described below. Sweat glands (**sudoriferous glands**) are coiled tubes in the dermis connected with the surface by narrow ducts. They are well supplied with blood vessels, secrete mostly water and salts, and function largely in thermoregulation. In humans and some ungulates, sweat glands are distributed over much of the body, but in most other mammals they are found only in restricted regions of the surface.

Sweat glands in mammals have undergone some fundamentally important evolutionary modifications. Surely the most fundamental of these was the reorganization of some sweat glands to secrete a complex, energy-rich substance called milk. **Mammary glands** characterize the mammals and give the class its name. The importance of the mammary glands to the mammalian condition cannot be overstated. They are central to the mammalian success story. Milk provides neonatal mammals with a nutritional head start. Milk is a highly refined concoction of water, carbohydrates, fats, proteins, and salts, closely tuned to a particular species' developmental needs. But milk provides more than just a head start. Nursing makes neonates a captive audience and forces a period of interaction with the mother and (in most cases) with siblings that allows training and socialization.

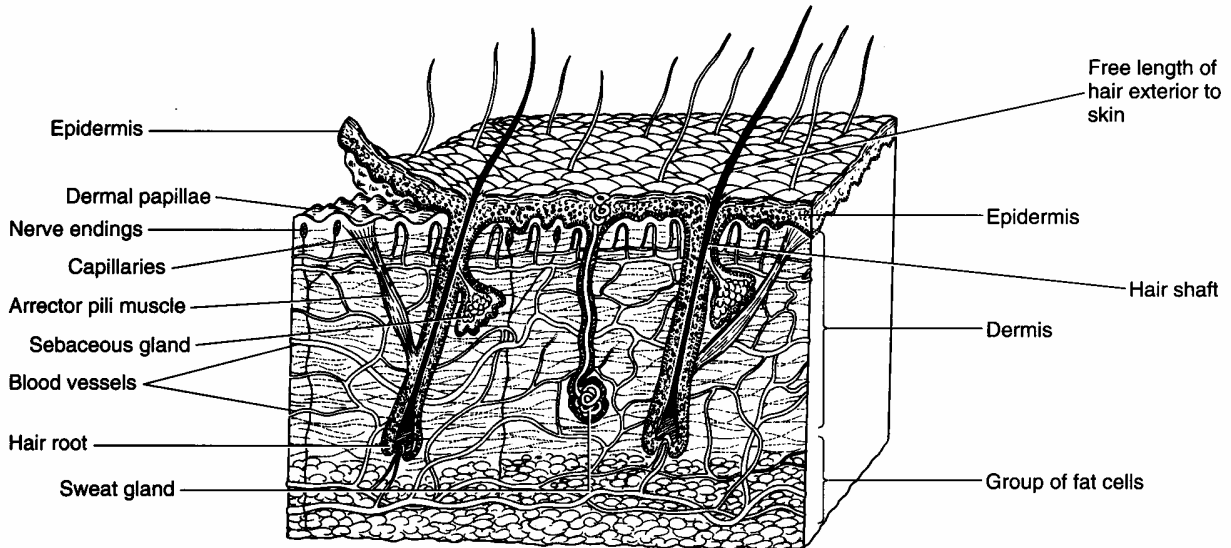


Figure 5-1. Diagrammatic cross-section through "typical" mammalian skin (from Vaughan et al., 2000).

Sebaceous glands open into each hair follicle. They secrete oily substances (**sebum**) that continually lubricate and condition skin and hair. Cells inside these glands gradually fill with grease and then break away, becoming part of the secretion themselves. Glands that secrete cellular debris as well as molecular products are termed apocrine glands. Sebum makes beavers waterproof and prevents undue drying of the pelage of terrestrial mammals.

Hair

General.--Hair is a uniquely mammalian feature. It can be considered an epidermal "secretion." The developing epidermis invaginates into the dermis to form a **follicle**. At the deepest point of the follicle, the dermis pushes back and forms a small structure called the **papilla**. The papilla is well supplied with blood vessels. Epidermal cells on top of the papilla multiply and are pushed towards the surface by those growing beneath them, keratinizing and forming the hair.

Each hair consists of three parts. The center is the **medulla** (Latin, "marrow"). This is surrounded by a denser **cortex** (Latin, "bark") containing most of the pigment granules that give each hair its characteristic color. The cortex is covered by a thin layer called the **cuticle** (Latin, "little skin"). Its cells often overlap like the shingles or tiles on a roof. Cuticular scales are often characteristic of particular genera or even species of mammal. They are never pigmented.

There are numerous instances in which skin glands have moved beyond their roles in lubrication to serve communicative functions. In some instances--skunks come to mind immediately-- protective and communicative functions are mixed. Some shrews have glands on their sides that advertise reproductive readiness. Some bats have

odor-producing glands on their throats that allow dominant individuals to mark subordinates as such. A variety of species use glandular scents to mark individual territories.

Hair musculature.--Hair does not grow vertically from the skin but emerges at an angle, which can be altered to regulate the depth of the pelage. A small **arrector pili** (plural, **arrectores pilorum**) muscle is attached to each follicle. As that muscle contracts, it increases the thickness (and hence the R-value) of the insulating layer of hair. Hair "standing on end" not only increases the insulative value (by increasing the dead air space). It can increase the apparent size of an individual, and thus protect it from attack. You may have seen such a reaction in the neck fur of a defensive dog, or the tail of a cat. Obviously, hair--a derivative of skin--is here serving a protective function at the level of behavioral interaction.

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