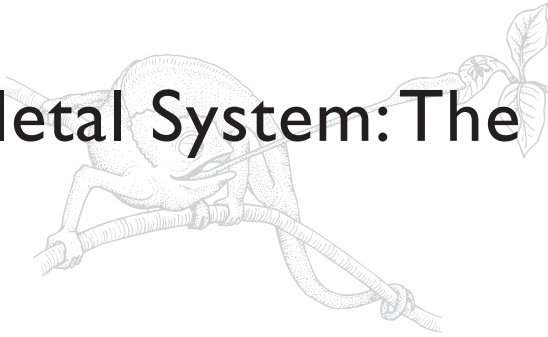


CHAPTER 7

Skeletal System: The Skull



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The skeleton gives the vertebrate body shape, supports its weight, offers a system of levers that together with muscles produces movement, and protects soft parts such as nerves, blood vessels, and other viscera. Because it is hard, bits of the skeleton often survive fossilization better than does soft tissue anatomy; so our most direct contact with long-extinct animals is often through their skeletons. The story of vertebrate function and evolution is written in the architecture of the skeleton.

The skeletal system is composed of an exoskeleton and an endoskeleton (figure 7.1a). The **exoskeleton** is formed from or within the integument, the dermis giving rise to bone and the epidermis to keratin. The **endoskeleton** forms deep within the body from mesoderm and other sources, not

directly from the integument. Tissues contributing to the endoskeleton include fibrous connective tissue, bone, and cartilage.

During the course of vertebrate evolution, most bones of the exoskeleton stay within the integument and protect surface structures. Dermal armor of ostracoderms and bony scales of fishes are examples. Other bones have sunk inward, merging with deeper bones and cartilaginous elements of the endoskeleton to form composite structures. As a practical matter, this makes it difficult to examine the exoskeleton and the endoskeleton separately. Parts of one are often found in company with the other. Instead, we select composite structural units and follow their evolution. This way of dividing the skeleton for study gives us two

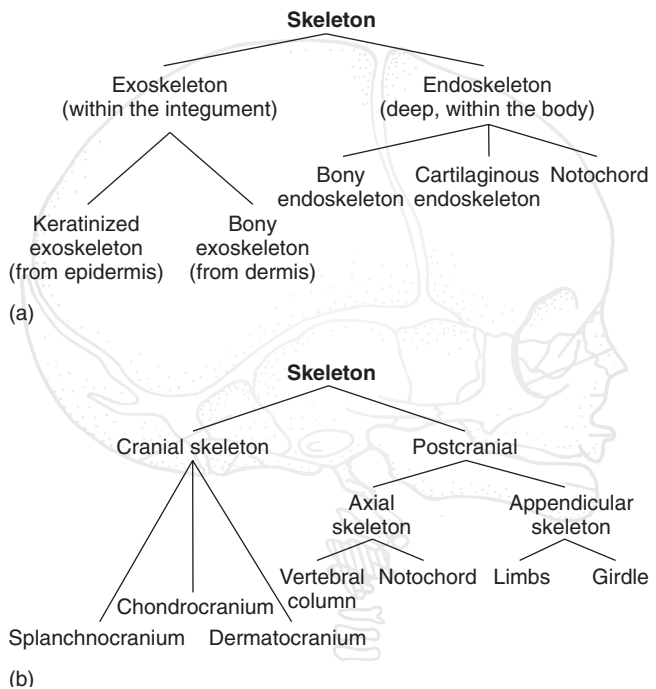


FIGURE 7.1 Organization of skeletal tissues in vertebrates. Components of the skeletal system function together as a unit but, as a convenience, they can be divided into manageable parts for closer analysis. (a) As a protective and supportive system, the skeleton can be divided into structures on the outside (exoskeleton) and inside (endoskeleton) of the body. (b) On the basis of position, the skeleton can be treated as two separate components, the cranial skeleton (skull) and the postcranial skeleton. The postcranial skeleton includes the axial and appendicular skeletons.

units: the skull, or **cranial skeleton**, and the **postcranial skeleton** (figure 7.1b). The postcranial skeleton includes the vertebral column, limbs, girdles, and associated structures, such as ribs and shells. In chapters 8 and 9, we examine the postcranial skeleton. Our discussion of the skeleton begins with the skull.

Introduction

Although merged into a harmonious unit, the vertebrate skull, or **cranium**, is actually a composite structure formed of three distinct parts. Each part of the skull arises from a separate phylogenetic source. The most ancient part is the **splanchnocranium (visceral cranium)**, which first arose to support pharyngeal slits in protochordates (figure 7.2a). The second part, the **chondrocranium**, underlies and supports the brain and is formed of endochondral bone or of cartilage, or both (figure 7.2b). The third part of the skull is the **dermatocranium**, a contribution that in later vertebrates forms most of the outer casing of the skull. As its name suggests, the dermatocranium is composed of dermal bones (figure 7.2c).

Endochondral and dermal bone (p. 179)

In addition to these formal components, two general terms apply to parts of the cranium. The **braincase** is a collective term that refers to the fused cranial components immediately surrounding and encasing the brain. Structures of the dermatocranium, the chondrocranium, and even the splanchnocranium can make up the braincase, depending on the species. The **neurocranium** is used as an equivalent term for the chondrocranium by some morphologists. Others expand the term to include the chondrocranium along with fused or attached sensory capsules—the supportive nasal, optic, and otic capsules. Still others consider the neurocranium to be only the ossified parts of the chondrocranium. Be prepared for slightly different meanings in the literature. Although we use the term *neurocranium* sparingly, neurocranium is understood to include the braincase (ossified or not) plus associated sensory capsules.

Chondrocranium

Elements of the chondrocranium appear to lie in series with the bases of the vertebrae. This arrangement inspired several morphologists of the nineteenth century to propose that the primitive vertebral column initially extended into the head to produce the skull. By selective enlargement and fusion, these intruding vertebral elements were seen as the evolutionary source of the chondrocranium. Consequently, the idea grew that the head was organized on a segmental plan like the vertebral column that produced it. Today this view is not held as confidently, although many allow that the occipital arch forming the back wall of the skull may represent several ancient vertebral segments that now contribute to the posterior wall of the chondrocranium (table 7.1).

In elasmobranchs, the expanded and enveloping chondrocranium supports and protects the brain within. However, in most vertebrates, the chondrocranium is primarily an embryonic structure serving as a scaffold for the developing brain and as a support for the sensory capsules.

Embryology

Although the embryonic formation of the chondrocranium is understood, details may differ considerably from one species to another. Generally, condensations of head mesenchyme form elongate cartilages next to the notochord. The anterior pair are the **trabeculae**, the posterior pair the **parachordals**, and in some vertebrates, a pair of **polar cartilages** lies between them (figure 7.3a). Behind the parachordals, several **occipital cartilages** usually appear as well. In addition to these cartilages, the sensory capsules associated with the nose, eyes, and ears develop supporting cartilages: **nasal**, **optic**, and **otic capsules**, respectively. Two types of embryonic cells differentiate to form the chondrocranium. Neural crest cells contribute to the nasal capsule, trabeculae (possibly only the anterior

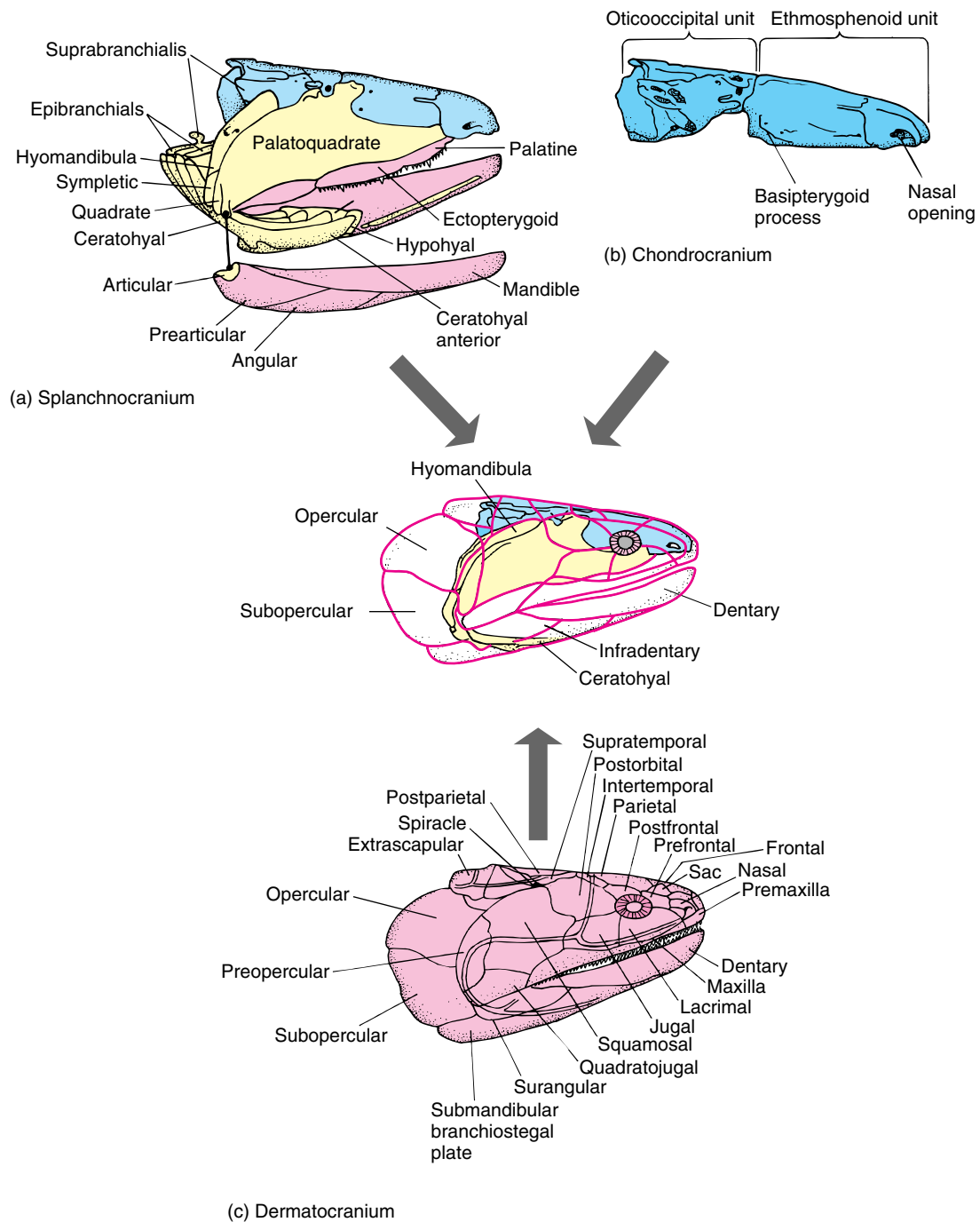


FIGURE 7.2 Composite skull. The skull is a mosaic composed of three primary contributing parts: the chondrocranium, the splanchnocranium, and the dermatocranium. Each has a separate evolutionary background. The skull of *Eusthenopteron*, a Devonian rhipidistian fish, illustrates how parts of all three phylogenetic sources contribute to the unit. (a) The splanchnocranium (yellow) arose first and is shown in association with the chondrocranium (blue) and parts of the dermatocranium (red). The right mandible is lowered from its point of articulation better to reveal deeper bones. (b) The chondrocranium in *Eusthenopteron* is formed by the union between the anterior ethmosphenoid and the posterior oticooccipital units. (c) The superficial wall of bones composes the dermatocranium. The central figure depicts the relative position of each contributing set of bones brought together in the composite skull. (Sac: nasal series)

TABLE 7.1 Endochondral Contributions to the Chondrocranium

Endochondral Structure	Fishes (Teleost)	Amphibians	Reptiles/Birds	Mammals
Occipital bones	Supraoccipital Exoccipital Basioccipital	Supraoccipital Exoccipital Basioccipital	Supraoccipital Exoccipital Basioccipital	Supraoccipital Exoccipital Basioccipital
Mesethmoid bone	Mesethmoid ^a (internasal)	Absent	Absent	Mesethmoid (absent in primitive mammals, ungulates)
Ethmoid region	Ossified	Unossified	Unossified	Turbinals (ethmo-, naso-, maxillo-)
Sphenoid bones Sphenethmoid Orbitosphenoid Basisphenoid Pleurosphenoid	Sphenethmoid Orbitosphenoid [Basisphenoid] ^b Pleurosphenoid	Sphenethmoid Orbitosphenoid Basisphenoid ?	Sphenethmoid Orbitosphenoid Basisphenoid Pleurosphenoid (crocodilians, amphisbaenians)	Presphenoid Orbitosphenoid Basisphenoid Absent
Laterosphenoid			Laterosphenoid (snakes)	Absent
Otic capsule Periotic	{ Prootic Epiotic Sphenotic	Prootic Opisthotic	{ Prootic Opisthotic Epiotic (absent in birds)	Petrosal with mastoid process

^aThis bone is of dermal origin, so it is not strictly homologous to tetrapod mesethmoid.

^bThis bone is usually absent or reduced in some fishes.

^cAlisphenoid from the splanchnocranium contributes.

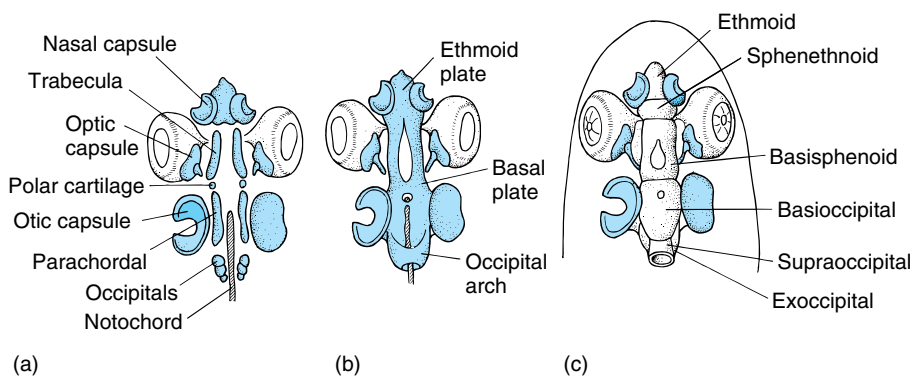


FIGURE 7.3 Embryonic development of the chondrocranium. Cartilage (blue) appears first but in most vertebrates is replaced by bone (white) later in development. The chondrocranium includes these cartilaginous elements that form the base and back of the skull together with the supportive capsules around sensory organs. Early condensation of mesenchymal cells differentiates into cartilage (a) that grows and fuses together to produce the basic ethmoid, basal, and occipital regions (b) that later ossify (c), forming basic bones and sensory capsules.

After deBeer.

part), and perhaps to part of the otic capsule (figure 7.4a). Mesenchyme of mesodermal origin contributes to the rest of the chondrocranium (figure 7.4b). As development proceeds, these cartilages fuse. The region between the nasal capsules formed by the fusion of the anterior tips of the trabeculae is the **ethmoid plate**. The parachordals grow together across the midline to form the **basal plate** between the otic capsules. The occipitals grow upward and around

the nerve cord to form the **occipital arch** (figure 7.3b). Collectively, all of these expanded and fused cartilages constitute the chondrocranium.

In elasmobranchs, the chondrocranium does not ossify. Instead the cartilage grows still farther upward and over the brain to complete the protective walls and roof of the braincase. In most other vertebrates, the chondrocranium becomes partly or entirely ossified (figure 7.3c).

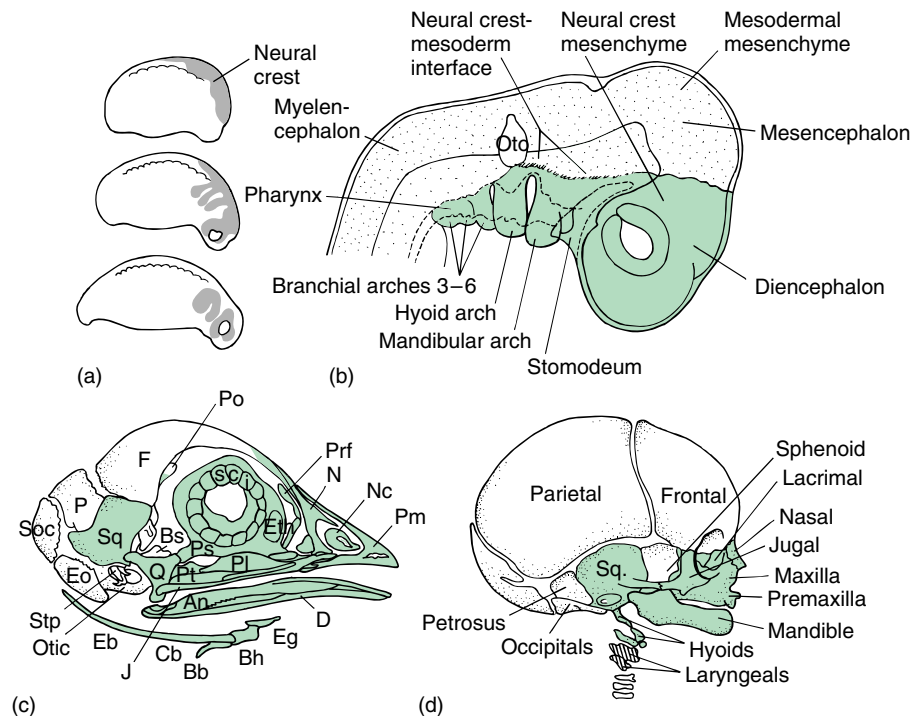


FIGURE 7.4 Neural crest contributions to the skull. (a) Salamander embryo illustrating the sequential spread of neural crest cells. During early embryonic development, neural crest cells contribute to the head mesenchyme, which is called the ectomesoderm because of its neural crest origin. (b) Also contributing to the head mesenchyme are cells of mesodermal origin, the mesodermal mesenchyme. The position of the mesodermal (stippled) and the neural crest (shaded) mesenchyme, and the approximate interface between them, are indicated in the chick embryo. Skull of a chick (c) and a human fetus (d) show bones or portions of bones derived from neural crest cells (shaded). Abbreviations: angular (An), basibranchial (Bb), basihyal (Bh), basisphenoid (Bs), ceratobranchial (Cb), dentary (D), epibranchial (Eb), entoglossum (Eg), exoccipital (Eo), ethmoid (Eth), frontal (F), jugal (J), nasal (N), cartilage nasal capsule (Nc), parietal (P), palatine (Pl), premaxilla (Pm), postorbital (Po), prefrontal (Prf), parasphenoid (Ps), pterygoid (Pt), quadrate (Q), scleral ossicle (Sci), supraoccipital (Soc), squamosal (Sq), stapes (Stp).

After Noden.

Splanchnocranium

The splanchnocranium is an ancient chordate structure. In amphioxus, the splanchnocranium, or at least its forerunner, is associated with the filter-feeding surfaces.

Among vertebrates, the splanchnocranium generally supports the gills and offers attachment for the respiratory muscles. Elements of the splanchnocranium contribute to the jaws and hyoid apparatus of gnathostomes.

Embryology

The mistaken view that the splanchnocranium developed from the same embryonic source as the walls of the digestive tract inspired the name “visceral” cranium, a name that unfortunately has stuck despite being a misnomer. Embryologically, the splanchnocranium arises from neural crest cells, *not* from lateral plate mesoderm like the smooth muscle in the walls of the digestive tract. In protochordates, neural crest cells are absent. Pharyngeal bars, composed of fibrous connective tissue, but never bone or cartilage, arise from mesoderm and form the unjointed branchial basket,

the phylogenetic predecessor of the vertebrate splanchnocranium. In vertebrates, cells of the neural crest depart from the sides of the neural tube and move into the walls of the pharynx between successive pharyngeal slits to differentiate into the respective pharyngeal arches. Pharyngeal arches of aquatic vertebrates usually are associated with their respiratory gill system. Because of this association, they are referred to as **branchial arches**, or **gill arches**.

Each arch can be composed of a series of up to five articulated elements per side, beginning with the **pharyngobranchial** element dorsally and then, in descending order, the **epibranchial**, **ceratobranchial**, **hypobranchial**, and **basibranchial** elements (figure 7.5). One or more of these anterior branchial arches may come to border the mouth, support soft tissue, and bear teeth. Branchial arches that support the mouth are called **jaws**, and each contributing arch is numbered sequentially or named. The first fully functional arch of the jaw is the **mandibular arch**, the largest and most anterior of the modified series of arches. The mandibular arch is composed of the **palatoquadrate** dorsally and **Meckel’s cartilage** (mandibular cartilage) ven-

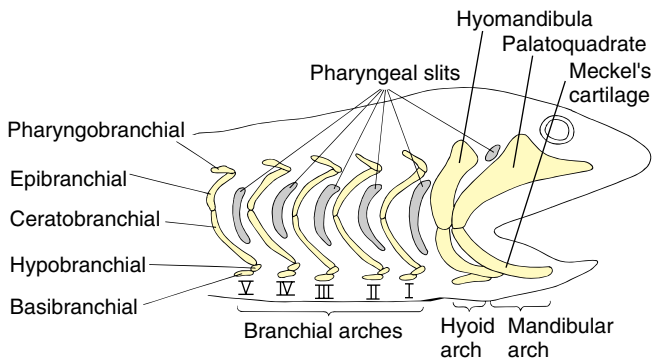


FIGURE 7.5 Primitive splanchnocranium. Seven arches are shown. Up to five elements compose an arch on each side, beginning with the pharyngobranchial dorsally and in sequence to the basibranchials most ventrally. The first two complete arches are named: mandibular arch for the first and hyoid arch for the second that supports it. The characteristic five-arch elements are reduced to just two in the mandibular arch: the palatoquadrate and Meckel's cartilage. The large hyomandibula, derived from an epibranchial element, is the most prominent component of the next arch, the hyoid arch. Behind the hyoid arch are variable numbers of branchial arches I, II, and so on. Labial cartilages are not included.

trally. The **hyoid arch**, whose most prominent element is the **hyomandibula**, follows the mandibular arch. A varying number of branchial arches, often designated with roman numerals, follow the hyoid arch (figure 7.5).

Origin of Jaws

In agnathans, the mouth is neither defined nor supported by jaws. Instead, the splanchnocranium supports the roof of the pharynx and lateral pharyngeal slits. Lacking jaws, ostracoderms would have been restricted to a diet of small, particulate food. The ciliary-mucous feeding surfaces of protochordates probably continued to play a large part in the food-gathering technique of ostracoderms. In some groups, small teethlike structures, derived from surface scales, surrounded the mouth. Perhaps ostracoderms used these rough “teeth” to scrape rock surfaces and dislodge encrusted algae or other organisms. As these food particles became suspended in water, ostracoderms drew them into their mouth with the incurrent flow of water. The mucus-lined walls of the pharynx collected these dislodged food particles from the passing stream.

Jaws appear first in acanthodian and placoderm fishes that used them as food traps to grab whole prey or take bites from large prey. Within some groups, jaws also served as crushing or chewing devices to process food in the mouth. With the advent of jaws, these fishes became more free-ranging predators of open waters.

Jaws arose from one of the anterior pair of gill arches. Evidence supporting this comes from several sources. First, the embryology of sharks suggests that jaws and branchial

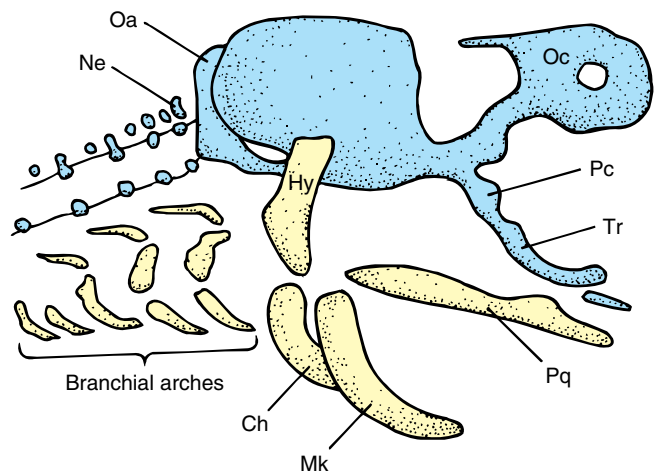


FIGURE 7.6 Shark embryo, the dogfish *Scyllium*. Jaws appear to be in series with the branchial arches. The mandibular arch is first, followed by the hyoid and then several branchial arches. Such a position of the jaws, in series with the arches, is taken as evidence that the jaws derive from the most anterior branchial arch. Abbreviations: ceratohyal (Ch), hyomandibula (Hy), Meckel's cartilage (Mk), neural arch (Ne), occipital arch (Oa), orbital cartilage (Oc), polar cartilage (Pc), palatoquadrate (Pq), trabecula (Tr). Labial cartilages are not included.

After deBeer.

arches develop similarly in series (figure 7.6) and both arise from neural crest. The spiracle appears to have once been a full-sized gill slit, but in modern sharks it is crowded and much reduced by the enlarged hyoid arch next in series. Furthermore, nerves and blood vessels are distributed in a pattern similar to branchial arches and jaws. Finally, the musculature of the jaws appears to be transformed and modified from branchial arch musculature.

So it seems reasonable to conclude that branchial arches phylogenetically gave rise to jaws. But the specifics remain controversial. For example, we are not sure whether jaws represent derivatives of the first, second, third, or even fourth branchial arches of primitive ancestors. Derivation of the mandibular arch also excites some controversy. The **serial theory** is the simplest view and holds that the first or perhaps second ancient branchial arch gave rise exclusively to the mandibular arch, the next branchial arch exclusively to the hyoid arch, and the rest of the arches to the branchial arches of gnathostomes (figure 7.7a).

Erik Jarvik, a Swedish paleontologist, proposed the **composite theory**, a more complex view based on his examination of fossil fish skulls and embryology of living forms (figure 7.7b). He hypothesized that ten branchial arches were present in primitive species, the first and following arches being named terminal, premandibular, mandibular, hyoid, and six branchial arches. Rather than the “one arch, one mandible” view, he envisioned a complex series of losses or fusions between selective parts of several arches that came together to produce the single composite mandible.

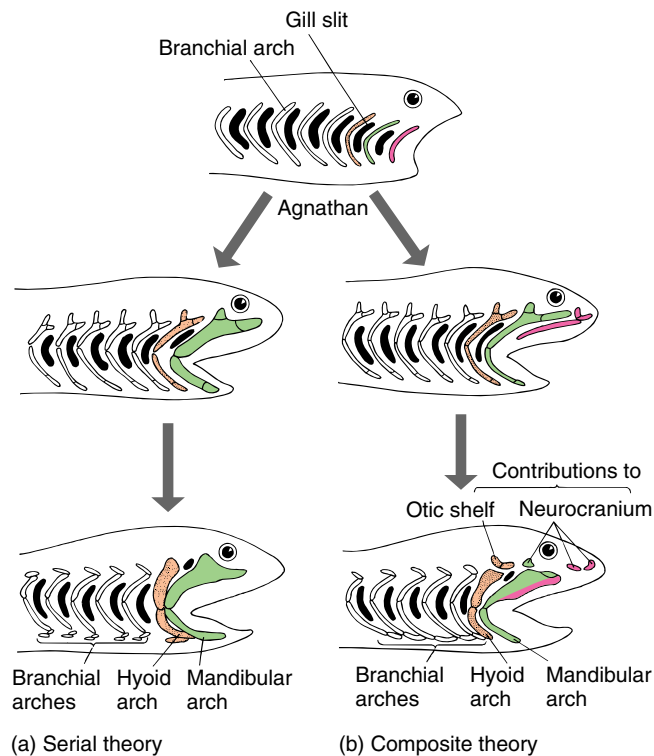


FIGURE 7.7 Serial and composite theories of jaw development. (a) The serial theory holds that jaws arise completely from one of the anterior branchial arches. Elements may be lost within it, but other elements from other arches do not contribute. (b) In the composite theory, the mandibular arch is formed from elements of several adjacent arches that also contribute to the neurocranium.

According to his theory, the mandibular arch of gnathostomes is formed by fusion of parts of the premandibular arch and parts of the mandibular arch of jawless ancestors. The palatoquadrate forms from the fusion of the epibranchial of the premandibular arch with the epibranchial and one pharyngobranchial of the mandibular arch. Meckel's cartilage arises from the expanded ceratobranchial element. Next, the hyoid arch arises phylogenetically from the epibranchial, ceratobranchial, and hypobranchial elements of the third primitive gill arch. The remaining branchial arches persist in serial order. The other elements of the primitive arches are lost or fused to the neurocranium.

Descriptive embryology provides much of the evidence put forth in these theories. However, descriptive embryology alone cannot trace arch components from embryo to adult structures with complete confidence. We can look forward to the use of more modern techniques to help settle this. For example, populations of cells can be marked with chemical or cellular markers early in embryonic development and followed to eventual sites of residence in the adult. These markers would permit us to detect the contributions of gill arches to jaws or chondrocranium.

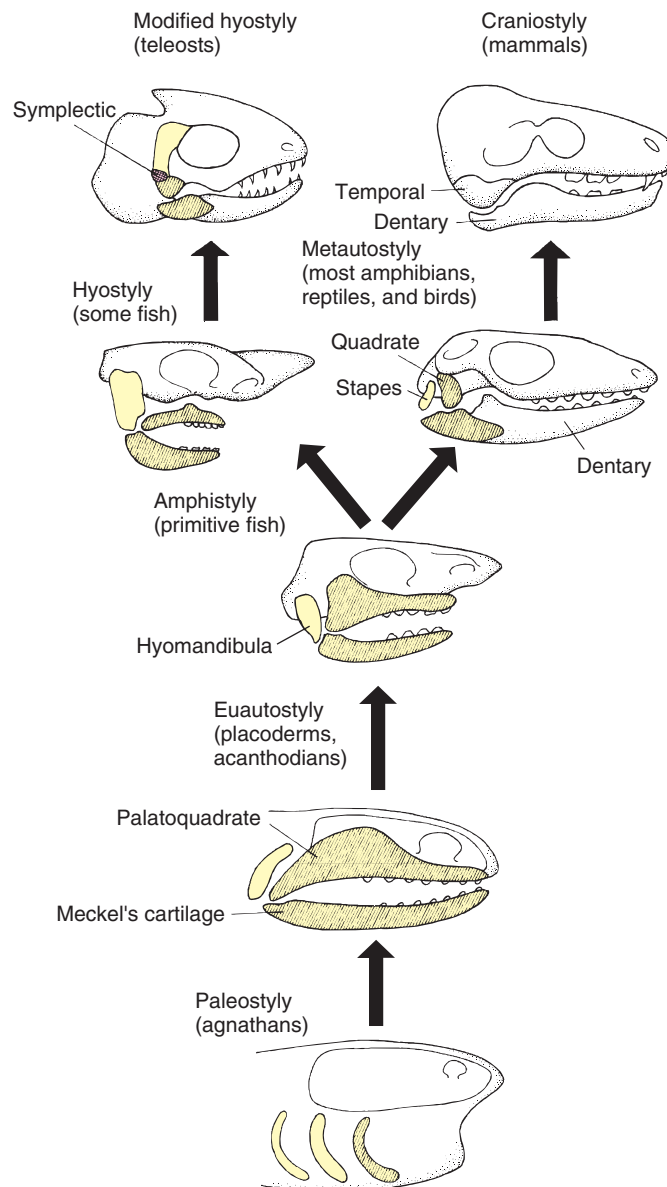


FIGURE 7.8 Jaw suspension. The points at which the jaws attach to the rest of the skull define the type of jaw suspension. Note the mandibular arches (yellow, crosshatched areas) and hyoid arches (yellow areas). The dermal bone (white areas) of the lower jaw is the dentary.

Nevertheless, even though some argue over details, we know in general that vertebrate jaws are derivatives of ancient gill arches (table 7.2).

Types of Jaw Attachments

Because of the mandible's prominence, evolution of the jaws is often traced through how the mandible is attached (i.e., its **suspensorium**) to the skull (figure 7.8). Agnathans represent the earliest **paleostylic** stage in which none of the arches attach themselves directly to the skull. The earliest jawed condition is **euaustostylic**, found in placoderms and

TABLE 7.2 Derivatives of Branchial Arches in Sharks, Teleosts, and Tetrapods

Arch	Sharks	Teleosts	Amphibians	Reptiles/Birds	Mammals
I	Meckel's cartilage	Articular ^a	Articular	Articular	Malleus ^b
	Palatoquadrate	Quadrate Epipterygoid	Quadrate Epipterygoid	Quadrate Epipterygoid	Incus ^b Alisphenoid
II	Hyomandibula	Hyomandibula Symplectic Interhyal	{ Stapes Extracolumella	Stapes Extracolumella	Stapes ^b
	Ceratohyal	Ceratohyal Hypohyal	Ceratohyal Hypohyal	Ceratohyal	Anterior horn hyoid
	Basihyal	Basihyal		Body of hyoid	Body of hyoid
III	Pharyngobranchial	Pharyngobranchial	Body of hyoid	Second horn of hyoid	Second horn of hyoid
	Epibranchial	Epibranchial			
	Ceratobranchial	Ceratobranchial			
	Hypobranchial	Hypobranchial			
IV	Branchial arch		Last horn and body of hyoid Laryngeal cartilages (?)	Last horn and body of hyoid Laryngeal cartilages (?)	Thyroid cartilages (?)
V	Branchial arch	Branchial arch	Laryngeal cartilages (?)	Laryngeal cartilages (?)	Laryngeal cartilages
VI	Branchial arch	Branchial arch	Not present	Not present	Not present
VII	Branchial arch	Branchial arch			

^aSometimes dermal bone contributes.^bSee figure 7.53 and related text for discussion of middle ear evolution.

acanthodians. The mandibular arch is suspended from the skull by itself (hence, “auto”), without help from the hyoid arch. In early sharks, some osteichthyans, and rhipistians, jaw suspension is **amphistylic**; that is, the jaws are attached to the braincase through two primary articulations, anteriorly by a ligament connecting the palatoquadrate to the skull and posteriorly by the hyomandibula. Many, perhaps most, modern sharks exhibit a variation of amphistylic jaw suspension. In most modern bony fishes, jaw suspension is **hyostylic** because the mandibular arch is attached to the braincase primarily through the hyomandibula. Often a new element, the **symplectic bone**, aids in jaw suspension. The visceral cranium remains cartilaginous in elasmobranchs, but within bony fishes and later tetrapods, ossification centers appear, forming distinctive bony contributions to the skull. In most amphibians, reptiles, and birds, jaw suspension is **metautostylic**. Jaws are attached to the braincase directly through the quadrate, a bone formed in the posterior part of the palatoquadrate (figure 7.8). The hyomandibula plays no part in supporting the jaws; instead, it gives rise to the slender **columella** or **stapes**, involved in hearing. Other elements of the second arch and parts of the third contribute to the **hyoid** or **hyoid apparatus** that supports the tongue and the floor of the mouth. In mammals, jaw suspension is **cranioistylic**. The entire upper jaw is incorporated into the braincase, but the lower jaw is suspended from the dermal **squamosal** bone of the braincase. The lower jaw of mammals consists entirely of the **dentary** bone, which is also of dermal origin. The palatoquadrate and Meckel's cartilages still develop, but they remain cartilaginous except at their posterior ends, which give rise to the **incus** and **malleus** of the

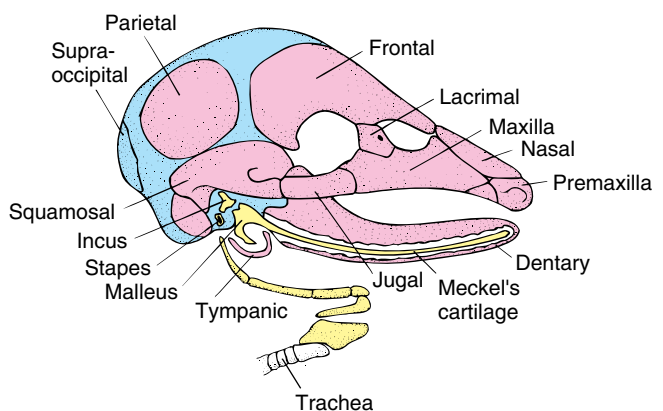


FIGURE 7.9 Skull of armadillo embryo. During embryonic formation of the three middle ear ossicles (incus, stapes, malleus), the incus and stapes arise from the mandibular arch, testifying to the phylogenetic derivation of these bones from this arch. The dermal dentary is cut away to reveal Meckel's cartilage, which ossifies at its posterior end to form the malleus. (Blue, chondrocranium contribution; yellow, splanchnocranium contribution; red, dermatocranium.)

After Goodrich.

middle ear, respectively (figure 7.9). Thus, in mammals, the splanchnocranium does not contribute to the adult jaws or to their suspension. Instead, the splanchnocranium forms the hyoid apparatus, styloid, and three middle ear bones: malleus, incus, and stapes. Through Meckel's cartilage, the splanchnocranium contributes the scaffolding around which the dentary bone forms.

Dermatocranium

Dermal bones that contribute to the skull belong to the dermatocranium. Phylogenetically, these bones arise from the bony armor of the integument of early fishes and sink inward to become applied to the chondrocranium and splanchnocranium. Bony elements of the armor also become associated with the endochondral elements of the pectoral girdle to give rise to the dermal components of this girdle.

Dermal girdle (p. 330)

Dermal bones first become associated with the skull in ostracoderms. In later groups, additional dermal bones of the overlying integument also contribute. The dermatocranium forms the sides and roof of the skull to complete the protective bony case around the brain; it forms most of the bony lining of the roof of the mouth, and encases much of the splanchnocranium. Teeth that arise within the mouth usually rest on dermal bones.

As the name suggests, bones of the dermatocranium arise directly from mesenchymal and ectomesenchymal tissues of the dermis. Through the process of intramembranous ossification, these tissues form dermatocranial bones.

Parts of the Dermatocranium

Dermal elements in modern fishes and living amphibians have tended to be lost or fused so that the number of bones present is reduced and the skull simplified. In amniotes, bones of the dermatocranium predominate, forming most of the braincase and lower jaw. The dermal skull may contain a considerable series of bones joined firmly at sutures in order to box in the brain and other skull elements. As a convenience, we can group these series and recognize the most common bones in each (figure 7.10; table 7.3).

Dermal Bone Series

Facial Series The facial series encircles the external naris and collectively forms the snout. The **maxilla** and **premaxilla** (incisive) define the margins of the snout and usually bear teeth. The **nasal** lies medial to the naris. The **septomaxilla** is a small dermal bone of the facial series that is often absent. When present, it is usually sunken below the surface bones and aids in forming the nasal cavity.

Orbital Series The dermal bones encircle the eye to define the orbit superficially. The **lacrimal** takes its name from the nasolacrimal (tear) duct of tetrapods that passes through or near this bone. The **prefrontal**, **postfrontal**, and **postorbital** continue the ring of bones above and behind the orbit. The **jugal** usually completes the lower rim of the orbit. Not to be confused with these dermal bones are the **scleral ossicles** of neural crest origin that, when present, reside within the orbit defined by the ring of dermal bones.

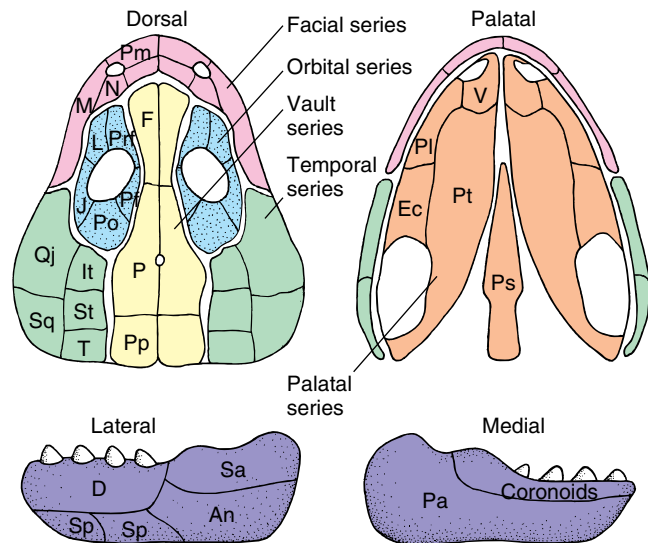


FIGURE 7.10 Major bones of the dermatocranium.

Sets of dermal bones form the facial series surrounding the nostril. The orbital series encircles the eye, and the temporal series composes the lateral wall behind the eye. The vault series, the roofing bones, run across the top of the skull above the brain. Covering the top of the mouth is the palatal series of bones. Meckel's cartilage (not shown) is encased in the mandibular series of the lower jaw. Abbreviations: angular (An), dentary (D), ectopterygoid (Ec), frontal (F), intertemporal (It), jugal (J), lacrimal (L), maxilla (M), nasal (N), parietal (P), prearticular (Pa), palatine (Pl), premaxilla (Pm), postorbital (Po), postparietal (Pp), prefrontal (Prf), parasphenoid (Ps), pterygoid (Pt), quadratojugal (Qj), surangular (Sa), splenial (Sp), squamosal (Sq), supratemporal (St), tabular (T), vomer (V).

Temporal Series The temporal series lies behind the orbit, completing the posterior wall of the braincase. In many primitive tetrapods, this series is indented posteriorly by a **temporal notch**. Once thought in life to suspend an eardrum, this notch was named accordingly an otic notch. This now seems unlikely, and instead the notch perhaps accommodated a spiracle, a respiratory tube. Openings called **fenestrae** (sing., *fenestra*) arise within this region of the outer braincase in many tetrapods in association with the jaw musculature. A row of bones, the **intertemporal**, **supratemporal**, and **tabular**, make up the medial part of the temporal series. This row is reduced in early tetrapods and usually lost in later species. Laterally, the **squamosal** and **quadratojugal** complete the temporal series and form the "cheek."

Vault Series The vault, or **roofing bones**, run across the top of the skull and cover the brain beneath. These include the **frontal** anteriorly and the **postparietal** (interparietal) posteriorly. Between them is the large **parietal**, occupying the center of the roof and defining the small **parietal foramen** if it is present. The parietal foramen is a tiny skylight in the skull roof that exposes the pineal gland, an endocrine gland, to direct sunlight.

TABLE 7.3 Major Dermal Bones of the Skull

B R A I N C A S E						M A N D I B L E
Facial Series	Orbital Series	Temporal Series	Vault Series	Palatal Series	Mandibular Series	
Premaxilla	Lacrima	Intertemporal	Frontal	Vomer	Lateral bones:	
Maxilla	Prefrontal	Supratemporal	Parietal	Palatine	Dentary (teeth)	
Nasals (septomaxilla)	Postfrontal Postorbital	Tabular	Postparietal	Ectopterygoid	Splenials (2)	
	Jugal	Squamosal Quadratojugal		Pterygoid Parasphenoid (unpaired)	Angular Surangular	
					Medial bones: Prearticular Coronoids	

Palatal Series The dermal bones of the **primary palate** cover much of the roof of the mouth. The largest and most medial is the **pterygoid**. Lateral to it are the **vomer**, **palatine**, and **ectopterygoid**. Teeth may be present on any or all four of these palatal bones. In fishes and lower tetrapods, there also is an unpaired medial dermal bone, the **parasphenoid**.

Mandibular Series Meckel's cartilage is usually encased in dermal bones of the mandibular series. Laterally, the wall of this series includes the tooth-bearing **dentary** and one or two **splenials**, the **angular** at the posterior corner of the mandible and the **surangular** above. Many of these bones wrap around the medial side of the mandible and meet the **prearticular** and one or several **coronoids** to complete the medial mandibular wall. Left and right mandibles usually meet anteriorly at the midline in a **mandibular symphysis**. If firm, the mandibular symphysis unites them into an arched unit. Most notably in snakes, the mandibular symphysis is composed of soft tissues, permitting independent movement of each mandible.

Overview of Skull Morphology

Braincase

In chondrichthyan fishes, the braincase is an elaborate cartilaginous case around the brain. The dermatocranium is absent, reflecting the elimination of almost all bone from the skeleton. However, in most bony fishes and tetrapods, the braincase is extensively ossified with contributions from several sources. For descriptive purposes, it is useful to think of the braincase as a box with a platform of endoskeletal elements supporting the brain, all encased in exoskeletal bones (figure 7.11). The endoskeletal platform is assembled from a series of **sphenoid** bones. The **occipital** bones, which apparently are derived from anterior vertebrae, form the end of this sphenoid platform. These occipital bones, up to four in number (**basioccipital**, **supraoccipital**, and paired **exoccipitals**), close the posterior wall of the braincase except for a large hole they define, the **foramen magnum**, through which the spinal cord runs. Articulation of the skull with

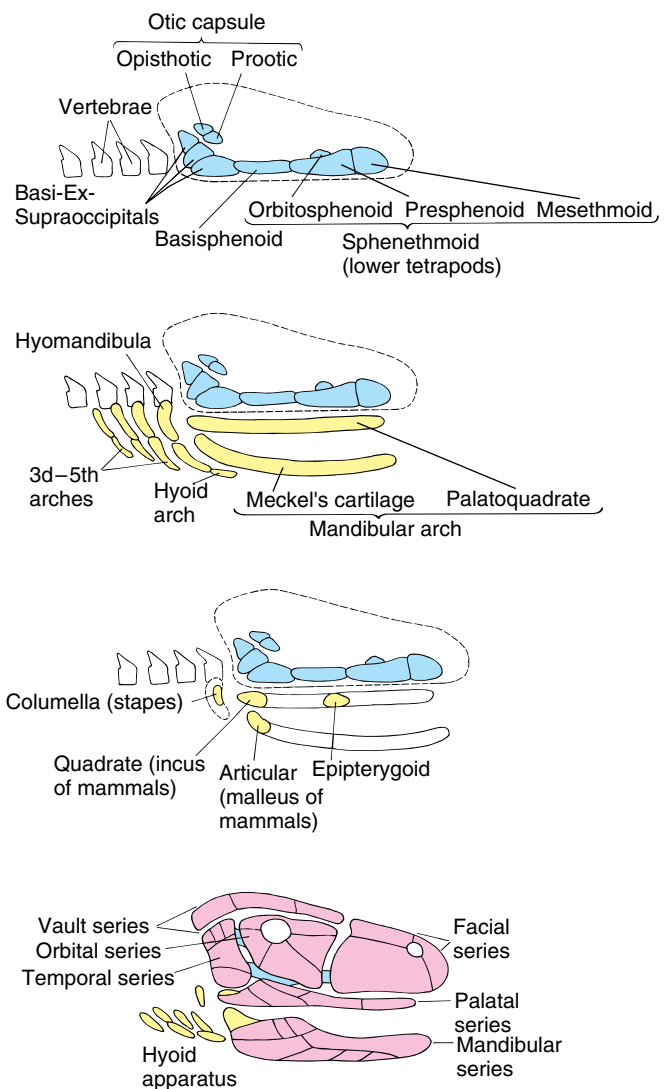


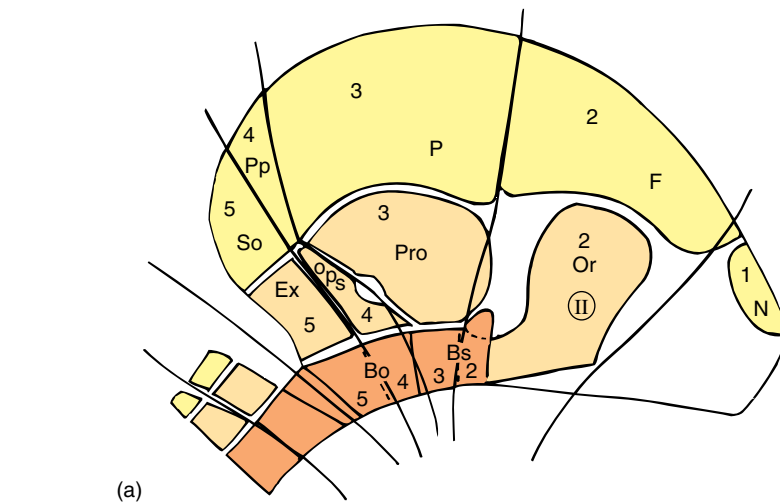
FIGURE 7.11 Contributions to the skull. The chondrocranium (blue) establishes a supportive platform that is joined by contributions from the splanchnocranium (yellow), in particular the epipterygoid. Other parts of the splanchnocranium give rise to the articular, quadrate, and hyomandibula, as well as to the hyoid apparatus. The dermatocranium (red) encases most of the chondrocranium together with contributions from the splanchnocranium.

BOX ESSAY 7.1

Getting a Head

The idea that the skull is derived from serial compacted vertebrae dates to the eighteenth century. The German naturalist and poet, W. Goethe (1749–1832), was apparently the first to think of but not the first to publish this idea. Goethe gave us the word *morphology*, which meant to him the search for underlying meaning in organic design or form. Among his discoveries was the observation that plant flowers are modified stem petals compacted together. His venture into vertebrates and vertebrate skulls in particular occurred in 1790 whilst he was strolling in an old cemetery in Venice. He spied a dried ram's skull disintegrated at its bony sutures but held in sequence by the soil. The separated bones of the ram's skull seemed to be the fore-shortened anterior vertebrae of the backbone, but Goethe did not publish this idea until about 1817. Public credit for this idea and for elaborating it goes to another German naturalist, L. Oken (1779–1851). In 1806, Oken was strolling in a forest and came upon a dried sheep skull. He was similarly struck by its serial homology with the vertebrae, and shortly thereafter published the idea (box figure 1a).

Next, the vertebral theory of skull origin fell into the hands of Richard Owen and became part of his much embellished theoretical view on animal archetypes (box figure 1b). Because of Owen's prominence in early nineteenth-century science, the idea of skull from vertebrae became a central issue within European scientific communities. One of the most persuasive dissenters from this view of a vertebral source for the skull was T. H. Huxley, who based his critique upon a detailed comparative study of vertebrate skulls and their development. This came to a head (no pun intended) in an invited lecture, the Croonian lecture of 1858, in which Huxley argued that the development of the skull showed that it was not composed of vertebrae. He suggested that the "skull was no more derived from vertebrae, than vertebrae are derived from

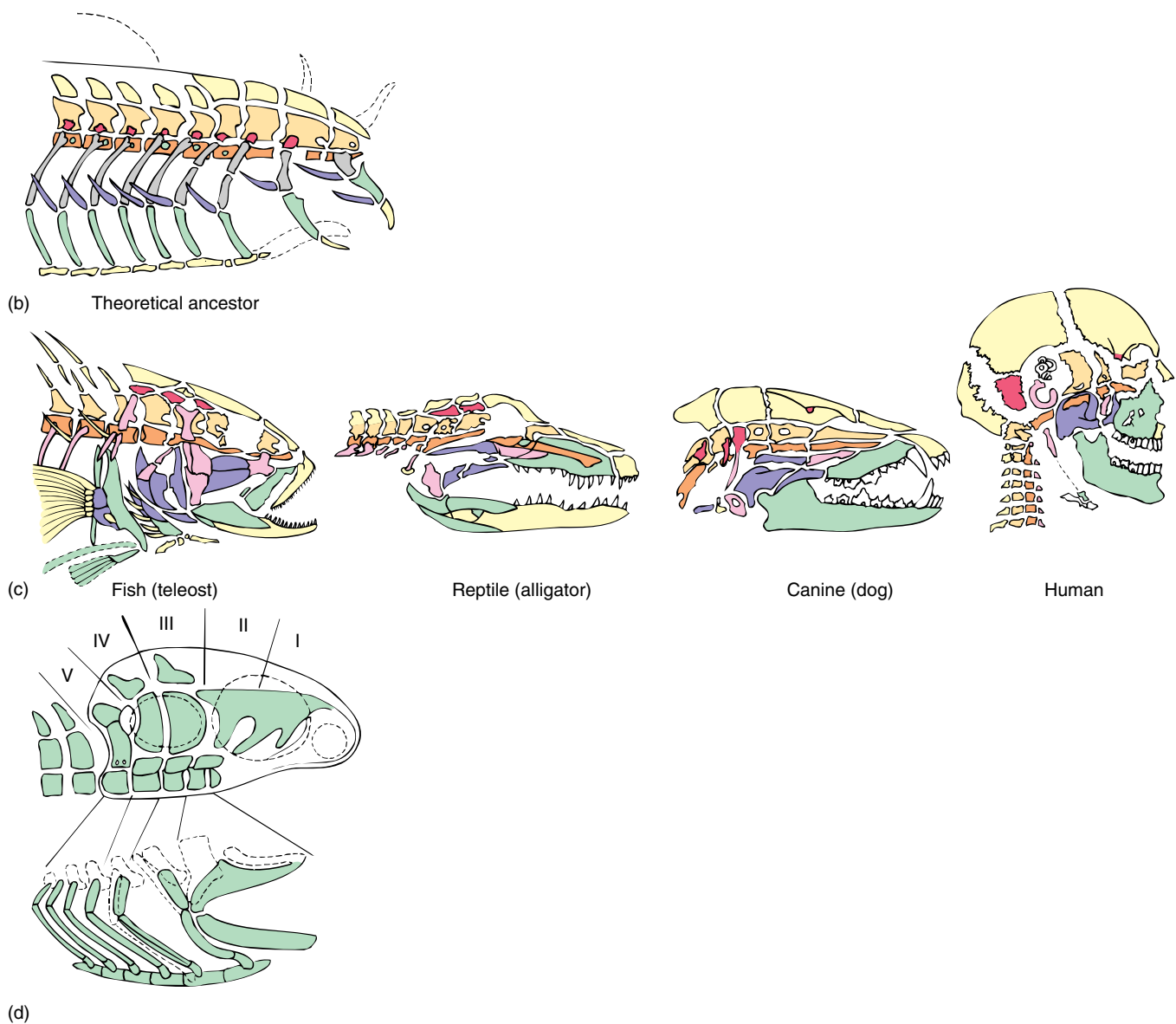


BOX FIGURE 1 Getting a head. Derivation of the head from anterior vertebrae was proposed separately by Goethe and Oken. Owen expanded on their ideas. (a) Ram's skull, showing how its presumed segmental pattern might be interpreted as being derived from parts of anterior vertebrae that expanded. (b) Richard Owen's elaborated view of head segmentation from vertebrae. Owen proposed that anterior vertebrae within the body moved forward to contribute to skeletal elements to the head. Therefore, Owen believed, the bony elements of the head could be homologized to the parts of a fundamental vertebral pattern. (c) Taking several vertebrates, he indicated how named parts of the skull might represent respective parts of this underlying vertebral pattern from which they derive. (d) T. H. Huxley proposed alternatively that, rather than being derived from vertebrae moved forward into the head, the components of the head were derived from a basic segmentation unrelated to the vertebral segmentation behind the skull. These basic segments (roman numerals) are laid out across a generalized vertebrate skull to show the respective contributions to specific parts. Abbreviations: basioccipital (Bo), basisphenoid (Bs), exoccipital (Ex), frontal (F), nasal (N), opisthotic (Ops), orbitosphenoid (Or), parietal (P), postparietal (Pp), prootic (Pro), supraoccipital (So).

(a) After Jollie.

the skull." The skull, Huxley argued, arose in much the same way in most vertebrates, by fusing into a unit, not as a jointed series. Skull ossification showed no similarity with ossification of the following vertebrae. Although Huxley was probably right about this for most of the skull, the occipital region does ossify in a manner similar to vertebrae.

While disposing of the vertebral theory, Huxley substituted a segmental theory, tracing the segmentation to somites, not to vertebrae (box figure 1c). He took the otic capsule housing the ear as a "fixed" landmark and envisioned four somites (preotic) in front and five somites (postotic) behind it as segmental sources for segmental adult derivatives of the head.



(b–c) After Reader; (d) after Jollie.

Today, some would argue that the head is a unique developmental system without any tie to the segmental somites (somitomeres). The neural crest cells that also contribute to parts of the skull show no

segmental pattern in the head. However, at least in fishes, the branchial arches are segmental, as is the head paraxial mesoderm (somitomeres), and segmentation apparently can be carried into the accompanying

neurocranium. Matched shading in vertebrate series (box figure 1c) shows derivatives from parts of theoretical ancestor (box figure 1b).

the vertebral column is established through the **occipital condyle**, a single or double surface produced primarily within the basioccipital but with contributions from the exoccipitals in some species.

The otic capsule rests on the posterior part of the endoskeletal platform and encloses the sensory organs of the ear. The splanchnocranium contributes the **epipterygoid** (**alisphenoid** of mammals) to the endoskeletal platform and gives rise to one (columella/stapes) or more (malleus and incus of mammals) of the middle ear bones housed in the otic capsule.

In most vertebrates, these endoskeletal elements, along with the brain and sensory organs they support, are enclosed by the exoskeletal elements, derivatives of the dermis, to complete the braincase.

Jaws

The **upper jaw** consists of the endoskeletal palatoquadrate in primitive vertebrates. The palatoquadrate is fully functional in the jaws of chondrichthyans and primitive fishes, but in bony fishes and tetrapods, the palatoquadrate usually makes limited contributions to the skull through its two derivatives: the epipterygoid, which fuses to the neurocranium, and the **quadrate**, which suspends the lower jaw except in mammals. The dermal maxilla and premaxilla replace the palatoquadrate as the upper jaw.

The **lower jaw**, or **mandible**, consists only of Meckel's cartilage in chondrichthyans. In most fishes and tetrapods, Meckel's cartilage persists but is enclosed in exoskeletal bone of the dermatocranium, which also supports teeth. Meckel's cartilage, encased in dermal bone, usually remains unossified, except in some tetrapods where its anterior end ossifies as the **mental** bone. In most fishes and tetrapods (except mammals), the posterior end of Meckel's cartilage can protrude from the exoskeletal case as an ossified **articular** bone.

In mammals, the lower jaw consists of a single bone, the dermal dentary. The anterior tooth-bearing part of the dentary is its **ramus**. Jaw-closing muscles are inserted on the **coronoid process**, an upward extension of the dentary. Posteriorly, the dentary forms the transversely expanded **mandibular condyle**, a rounded process that articulates with the **glenoid fossa**, a depression within the temporal bone of the braincase. Thus, in mammals, the mandibular condyle of the dentary replaces the articular bone as the surface of the lower jaw through which is established mandibular articulation with the braincase.

Hyoid Apparatus

The hyoid or hyoid apparatus is a ventral derivative of the splanchnocranium behind the jaws. In fishes, it supports the floor of the mouth. Elements of the hyoid apparatus are derived from the ventral parts of the hyoid arch and from parts of the first few branchial arches. In larval and paedomorphic amphibians, the branchial bars persist but form a

reduced hyoid apparatus that supports the floor of the mouth and functional gills. In adults, the gills and the associated part of the hyoid apparatus are lost, although elements persist within the floor of the mouth usually to support the tongue. Typically, the hyoid apparatus includes a main body, the **corpus**, and extensions, the **cornua** ("horns"). In many mammals, including humans, the distal end of the hyoid horn fuses with the otic region of the braincase to form the **styloid process**.

Cranial Kinesis

Kinesis means movement. Cranial kinesis refers literally then to movement within the skull. But if left this general, the definition becomes too broad to provide a useful context in which to discuss skull function. Some authors restrict the term to skulls with a transverse, hingelike joint across the skull roof and a transverse, sliding basal joint in the roof of the mouth. But this restricted definition precludes most teleost fishes, despite their highly mobile skull elements. Here, we use cranial kinesis to mean movement between the upper jaw and the braincase about joints between them (figure 7.12a). Such **kinetic skulls** characterize most vertebrates. They are found in ancient fishes (crossopterygians and probably palaeoniscoids), bony fishes (especially teleosts), very early amphibians, most reptiles (including most Mesozoic forms), birds, and early therapsid ancestors to mammals. Kinetic skulls are not present in modern amphibians, turtles, crocodiles, and mammals (with the possible exception of rabbits). The widespread presence of cranial kinesis among vertebrates, but its essential absence among mammals, seems to create a problem for humans. Because we, like most other mammals, have **akinetic skulls** with no such movement between upper jaw and braincase, we tend to underestimate its importance (figure 7.12b).

Kinesis and akinesis each have advantages. Cranial kinesis provides a way to change the size and configuration of the mouth rapidly. In fishes and other vertebrates that feed in water, rapid kinesis creates a sudden reduction of pressure in the buccal cavity so that the animal can suck in a surprised prey. This method of prey capture, which takes advantage of a sudden vacuum to gulp in water carrying the intended food, is known as **suction feeding**. Cranial kinesis also allows tooth-bearing bones to move quickly into strategic positions during rapid feeding. Some teleost fishes, for instance, swing their anterior tooth-bearing bones forward at the last moment to reach out quickly at the intended prey. In many venomous snakes, linked bones along the sides of the skull can rotate forward. The venomous viper erects the maxillary bone bearing the fang and swings it from a folded position along its upper lip to the front of the mouth, where it can more easily deliver venom into prey. In many fishes and reptiles with kinetic skulls, teeth on the upper jaw can be reoriented with respect to the prey in order to assume a more favorable position during prey capture or to align

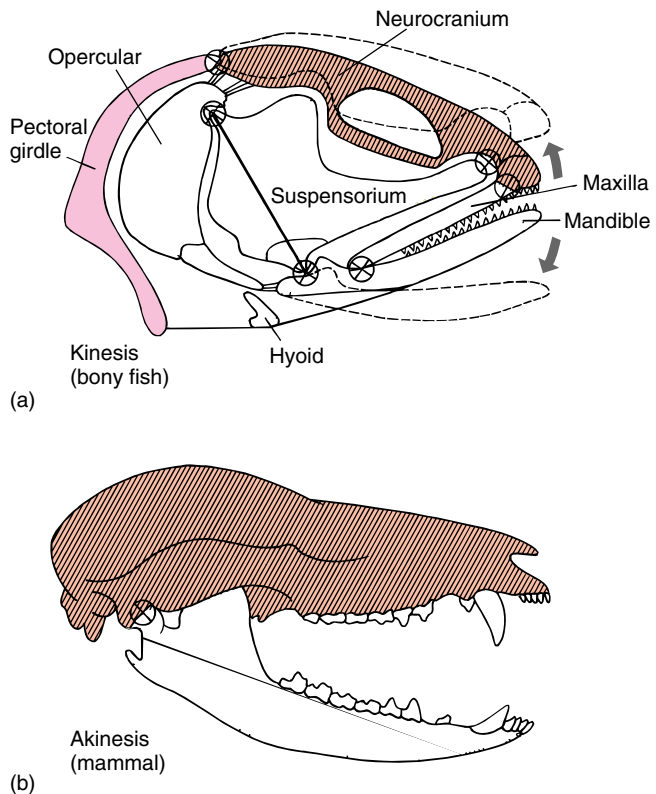


FIGURE 7.12 Mobility of skull bones. (a) The fish skull is kinetic. The upper jaw and other lateral skull bones rotate upon each other in a linked series, resulting in displacements of these bones (dashed outline) during feeding. Circles represent points of relative rotation between articulated elements. (b) The mammal skull is akinetic because no relative movement occurs between the upper jaw and the braincase. In fact, the upper jaw is incorporated into and fused with the braincase. There are no hinge joints through the braincase nor any movable linkages of lateral skull bones.

crushing surfaces better during swallowing. Here, cranial kinesis brings near simultaneous contact and closure of both upper and lower jaws on the prey. Without this, the first jaw to make contact singly would tend to knock prey away, foiling capture. On the other hand, loss of kinesis in mammals leaves them with an akinetic skull, which allows infants to suckle easily. Juvenile and adult mammals can chew firmly with sets of specialized teeth that work accurately from a secure, akinetic skull.

Tooth structure and occlusion (p. 500)

Phylogeny of the Skull

The skull is a composite structure derived from the splanchnocranium, dermatocranium, and chondrocranium. Each component of the skull comes from a separate phylogenetic source. The subsequent course of skull evolution is complex,

reflecting complex feeding styles. With a general view of skull structure now in mind, we can turn to a more specific look at the course of this evolution.

Agnathans

Ostracoderms

Osteostracans were one of the more common groups of ostracoderms. They possessed a head shield formed from a single piece of arched dermal bone, two close-set eyes dorsally placed with a single pineal opening between them, and a median nostril in front of the pineal opening. Along the sides of the head shield ran what are believed to be sensory fields, perhaps electrical field receptors or an early lateral line system sensitive to currents of water.

The broad, flattened head shield lowered the profile of ostracoderms, perhaps allowing them to hug the bottom surface, and their slight body suggests that they were benthic-dwelling fishes. The head shield formed the roof over the pharynx and held the sequential branchial arches that stretched like beams across the roof of the pharynx. Paired **gill lamellae** supported on **interbranchial septa** were stationed between these bars. Reconstructions of the head of *Hemicyclopsis*, a cephalaspidomorph, indicate that a plate, presumably of cartilage, stretched across the floor of the pharynx (figure 7.13a). Muscle action is thought to have raised and lowered this plate to draw a stream of water first into the mouth, and then over the gills, and finally out the branchial pores along the ventral side of the head. Suspended particles held in the stream of water could be captured within the pharynx before the water was expelled (figure 7.13b).

Anaspids were another group of early ostracoderms. Instead of a single bony shield, many small bony scales covered the head (figure 7.14a–c). The eyes were lateral, with a pineal opening between them and a single nostril in front. The body was streamlined, suggesting a slightly more active life than other ostracoderms enjoyed.

Heterostracans had flat to bullet-shaped heads composed of several fused bony plates (figure 7.15a). Their eyes were small and laterally placed, with a median pineal opening but no median nostril. Presumably, water flowed through the mouth, across the gill slits of the large pharynx, into a common tunnel, and out a single exit pore. The mouth of some heterostracans was rimmed with sharp, pointed oral scales that could have been used to dislodge food from rocks, allowing it to join the stream of water that entered the mouth (figure 7.15b).

Some scientists think that a few ostracoderms were predaceous, using the buccal cavity to gather up large prey, but because ostracoderms lacked strong jaws, feeding could not be based on powerful biting or crushing. The heavily plated heads and slight bodies of most ostracoderms argue for a relatively inactive lifestyle spent feeding on detritus and organic debris stirred up and drawn into the pharynx.

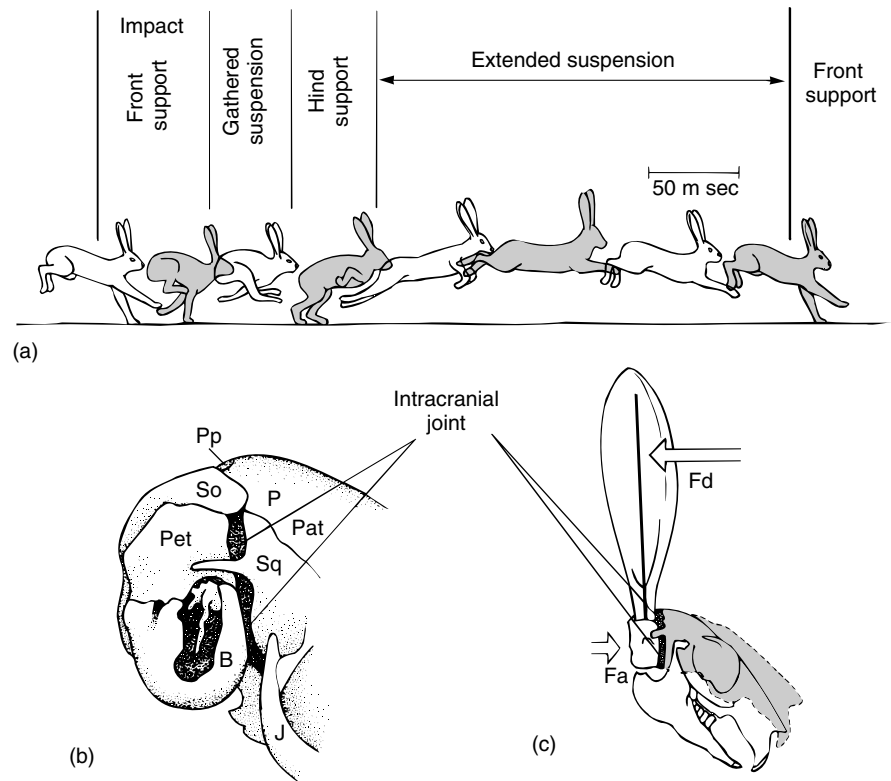
BOX ESSAY 7.2

Cranial Kinesis in Hares?

In hares or “jackrabbits” (but not in distantly related pikas or in their fossil ancestors), a suture between regions of the fetal braincase remains open in the adult, forming an intracranial joint (box figure 1). This intracranial joint runs along the sides and base of the adult braincase and hinges across the top via the postparietal. The joint permits relative motion between anterior and posterior parts of the braincase. It has been hypothesized that this joint helps absorb the impact forces sustained as the forelimbs strike the ground when a rabbit runs. Upon impact, mechanical deformation of the joint would absorb some kinetic energy as the hinge is strained. This deformation and absorption would reduce the shock sustained by the anterior part of the braincase. Additionally, the impact forces would tend to drive blood from intracranial sinuses into a complex association of venous channels and spaces within the skull. This would help dissipate these kinetic forces further as they acted against resistance offered by the walls of the blood vascular system.

The external ears (pinnae) of hares radiate heat generated during strenuous activity, but apparently only after locomotor exercise ceases. During locomotion, the ears are usually held erect by strong muscles at their bases. It has been hypothesized that these erect ears help reopen the intracranial joint as the hare pushes off on another leap to accelerate again, thus in a sense “resetting” this cranial mechanism and preparing it to act as a shock-absorbing device when the forelimbs again strike the ground (box figure 1c).

The functional significance of the intracranial joint is still debated. However, if such hypotheses are confirmed, this specialized joint in hares, together with their projecting ears, might also serve to reduce



BOX FIGURE 1 Possible cranial kinesis in hares. (a) Phases during a running stride are illustrated. Note that the forelimbs receive the initial impact upon landing. (b) Posterior regions of the skull of the jackrabbit *Lepus*. The intracranial joint extends along the sides of the skull between squamosal (Sq) and otic regions and then along the base of the skull. The interparietal bone forms the hinge across the top of the skull. (c) External ears held erect and attached to the posterior part of the skull may help to reposition the posterior part of the skull relative to the anterior part during the extended suspension phase of running. The presumed motion (slightly exaggerated) of the anterior braincase relative to the posterior braincase is indicated. Fa is the force vector due to acceleration resulting from thrust, and Fd is the force vector due to drag of the ears in the oncoming wind. Abbreviations: bulla (B), postparietal (Pp), jugal (J), parietal (P), petrosal (Pet), supraoccipital (So), squamosal (Sq).

jarring of the eyes carried in the anterior braincase. Among mammals, rabbit kinesis represents an independent and apparently unique condition that did not evolve from

therapsid kinesis. Further, it evolved not for its advantages during feeding but rather for its advantages during rapid locomotion. (Based on the research of D. Bramble.)

Cyclostomes

Lampreys and hagfishes are the only surviving agnathans and heirs of the ostracoderms. However, subsequent specializations have left cyclostomes with anatomies quite unlike those of the early ostracoderms. Cyclostomes lack bone entirely and are specialized for parasitic or scavenging lives

that depend on a rasping tongue to scrape up tissue for a meal. Lampreys have a single medial nostril and a pineal opening. Branchial pouches are present. The braincase is cartilaginous. Branchial arches, although present, form an unjointed branchial basket. Hagfishes have a median nostril but no external pineal opening.

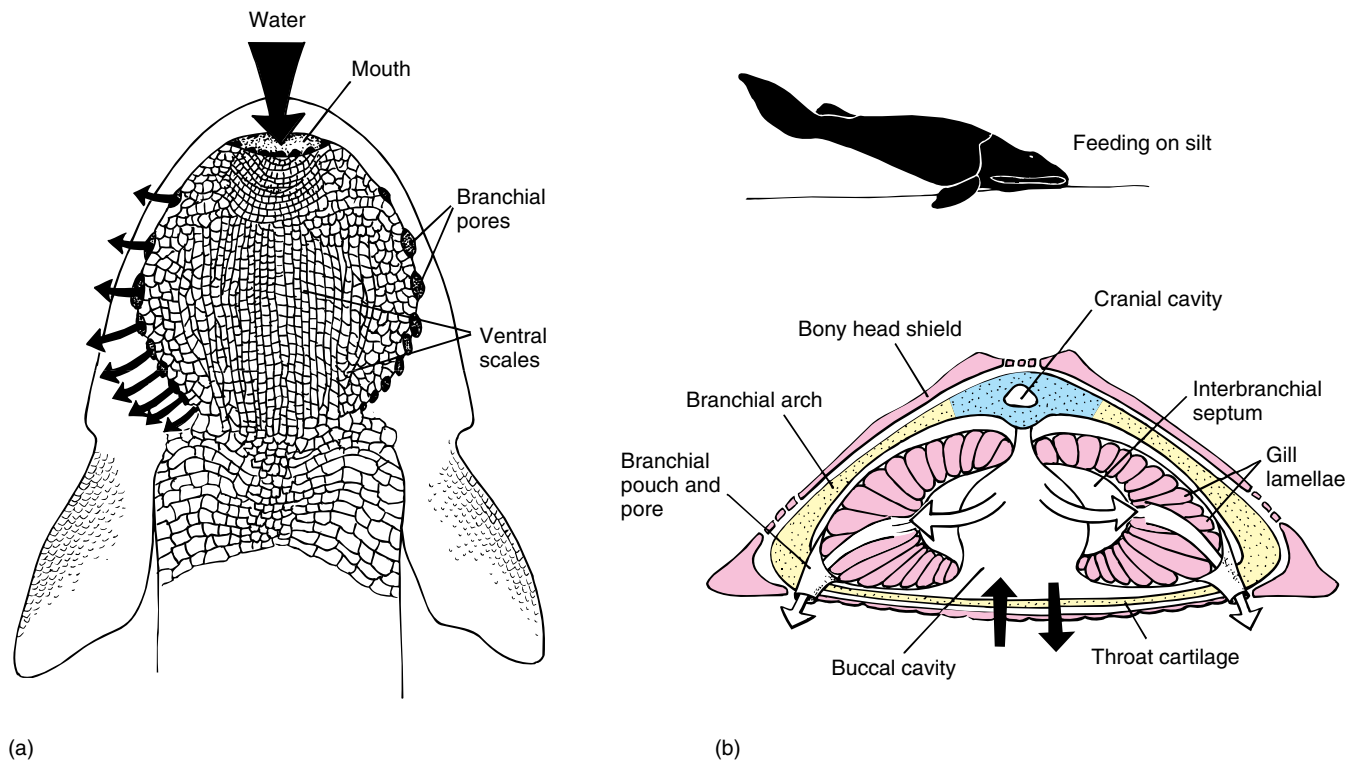


FIGURE 7.13 Ostracoderm *Hemicyclaspis*, a cephalaspidomorph. (a) Ventral view showing branchial pores, the presumed sites of exit for water moving through the pharynx. (b) Cross section through the pharynx illustrating respiratory gill lamellae and supporting branchial arch. Presumably, the floor of the pharynx could be raised and lowered to actively draw water into the mouth and drive it out through the several branchial pores. The current crossed the respiratory gills before exiting. Suspended food may have been collected in the pharynx and then passed to the esophagus.

After Jarvik.

Gnathostomes

All vertebrates, except agnathans, have jaws and form the embracing group gnathostomes (“jaw mouth”). Some biologists mark the advent of vertebrate jaws as one of the most important transitions in their evolution. Powerful closing muscles, derivatives of the branchial arch musculature, make the jaws strong biting or grasping devices. It is not surprising, then, that with the advent of jaws, gnathostomes experience a dietary shift away from suspension feeding of the ostracoderms to larger food items. With a change in diet also comes a more active lifestyle.

Fishes

Placoderms As much as a third to a half of the anterior placoderm body was composed of heavy plates of dermal bone that also enclosed the pharynx and braincase. The rest of the body was covered with small bony scales. The dermal plates of the head were thick and tightly joined into a unit termed the **cranial shield** (figure 7.16a,b). Although the pattern of these dermal plates has been compared to scales of bony fishes, their arrangement was sufficiently different that it seems best to follow the convention of using different names until some agreement is reached on their homologies.

The braincase was heavily ossified, and the upper jaws attached to it. In most, a well-defined joint existed between the braincase and the first vertebra. A spiracle was apparently absent. Water departing from the mouth exited posteriorly at the open junction between cranial and trunk shields. Most placoderms were 1 m in length, although one species possessing strong jaws reached nearly 6 m overall.

Acanthodians The gnathostomes with the earliest surviving fossil record are the acanthodians. Most were small, several centimeters in length, with streamlined bodies, suggesting an active swimming lifestyle. Their bodies were covered with nonoverlapping, diamond-shaped, dermal bony scales. The bony scales of the head region were enlarged into small plates. The pattern of cranial dermal scales resembled bony fishes, but as with placoderms, these are usually given their own names. Some species had an **operculum**, a bony flap that covered the exit gill slits. Eyes were large, suggesting that visual information was especially important to these fishes. *Acanthodes* (early Permian) possessed a **lateral cranial fissure**, a gap that partially divided the posterior braincase. This fissure is an important fixture in actinopterygian fishes, where it allows exit of the tenth cranial nerve. The mandibular arch that formed the jaws was

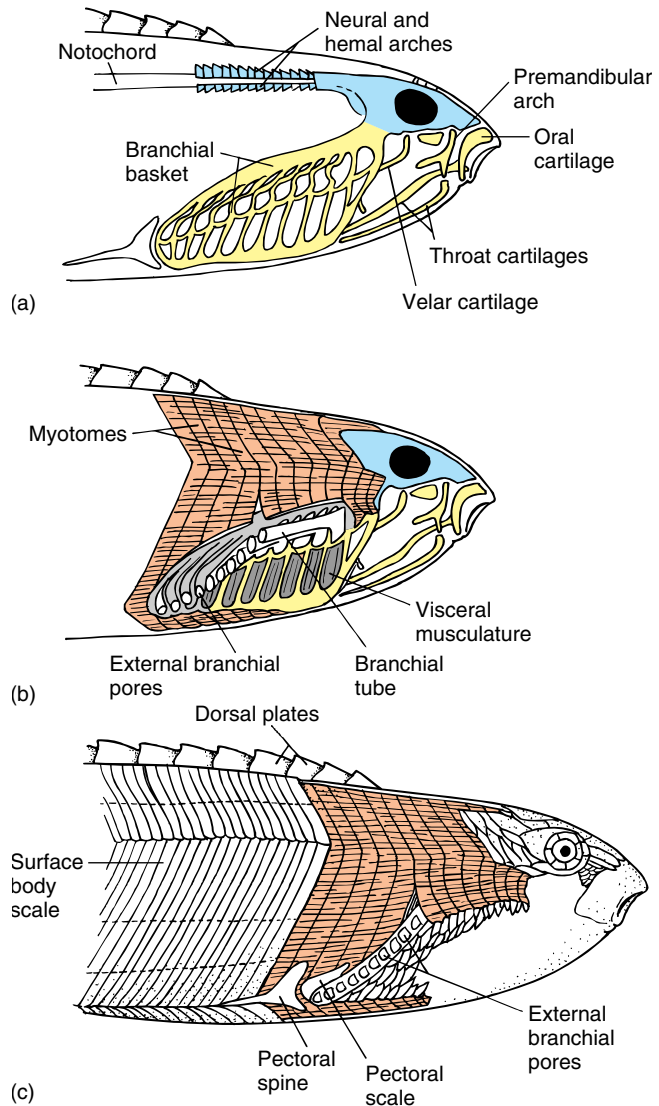


FIGURE 7.14 Ostracoderm *Pterolepis*, an anaspid.

(a) Exposed skull. The splanchnocranium included a few elements around the mouth, and the chondrocranium held the eye. A notochord was present and vertebral elements rested on it. (b,c) Restoration of muscles and some of the surface scales. The throat cartilages supported the floor of the buccal cavity, which might have been part of a pump to draw water into the mouth and then force it across the gills and out through the external branchial pores.

After Stensiö.

much like that of sharks and bony fishes. Three centers of ossification appear within the palatoquadrate: The metapterygoid and **autopalatine** both articulated with parts of the braincase, and the posterior quadrate articulated with the ossified Meckel's cartilage (figure 7.17a). A dermal bone, the **mandibular**, reinforced the ventral edge of the lower jaw. A hyoid arch and five successive branchial arches were present in *Acanthodes* (figure 7.17b).

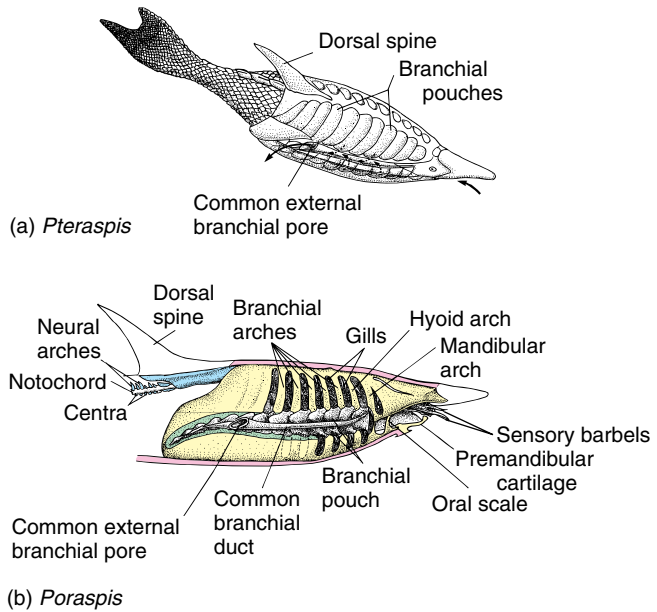


FIGURE 7.15 Ostracoderm feeding. (a) Lateral view of *Pteraspis*, a heterostracan. Water flowed through the mouth, over the gills, suspended in branchial pouches, and into a common chamber before finally exiting via the branchial pore. Large, fused bony plates formed the head shield. Throughout the tail, the bony scales were small to accommodate the lateral bending of the tail. (b) Schematic reconstruction of the head of a heterostracan. Pointed, rough oral scales rimmed the mouth and might have been used to scrape or dislodge food from rock surfaces. This reconstruction of a heterostracan is based primarily on *Poraspis*.

After Stensiö.

Chondrichthyans Cartilaginous fishes possess almost no bone. Denticles are present, vestiges of scales made up of the minerals enamel and dentin. A dermatocranium is absent. Instead, the chondrocranium has been expanded upward and over the top of the head to form the braincase. As a consequence, the chondrocranium is a much more prominent component of the skull than it is in most other vertebrates. The **ethmoid** and **orbital** anterior regions and posterior **oticooccipital** region are merged into an undivided braincase. The splanchnocranium is present. In primitive chondrichthyans, six gill arches trailed the mandibles (figure 7.18a,b). The upper jaw (palatoquadrate) of primitive sharks was supported by the braincase and probably by the hyomandibula.

Modern sharks usually lack a strong, direct attachment between hyomandibula and palatoquadrate. Instead, the jaws are suspended at two other sites, by the ceratohyal and Meckel's cartilage and by a strong, ligamentous connection running from the base of the nasal capsule to the orbital process of the palatoquadrate. As the ceratohyal, and to some extent the hyomandibula, have moved in to aid in supporting the jaws, the gill slit in front has become crowded, leaving only a small opening, the **spiracle**. In some sharks (great whites, makos, hammerheads) and in most bony

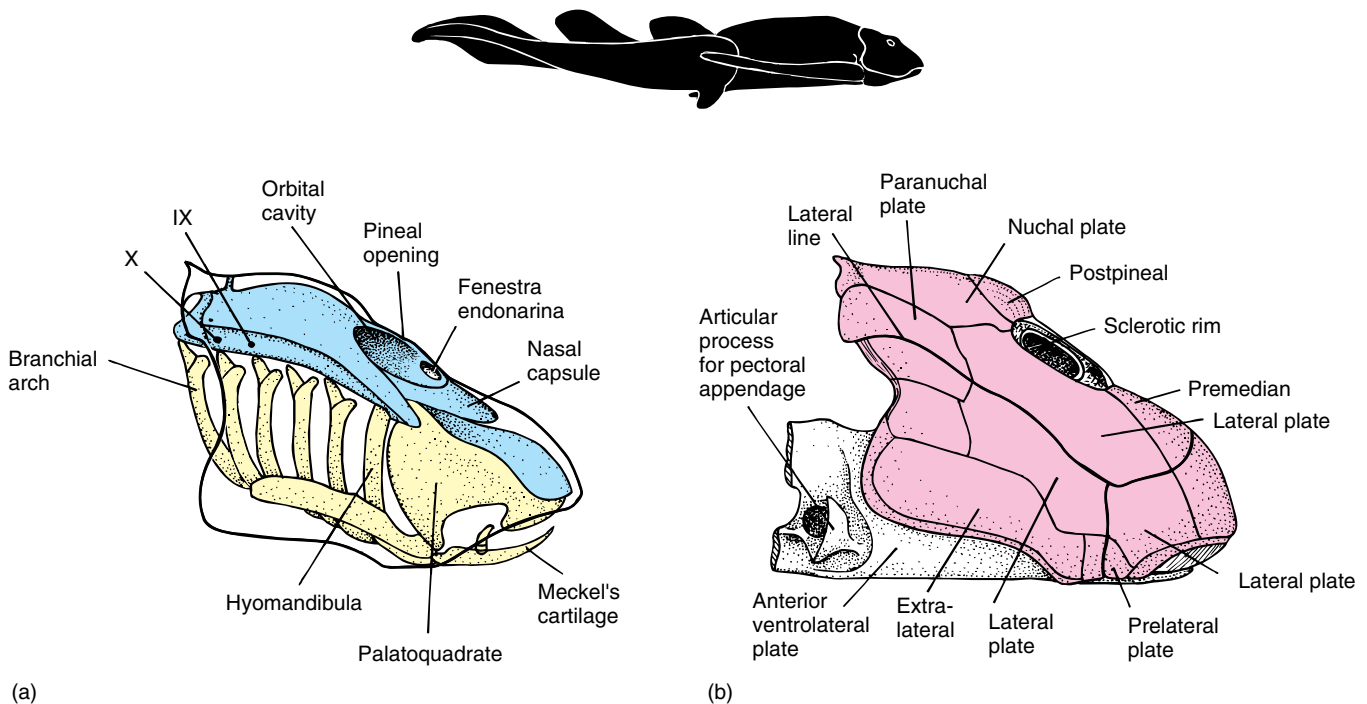


FIGURE 7.16 Placoderm skull. *Bothriolepis* was about 15 cm long and lived in the middle Devonian. (a) Lateral view of splanchnocranium and chondrocranium. (b) Skull with overlying dermatocranium in place. Note the dermal plates.

After Stensiö, 1969.

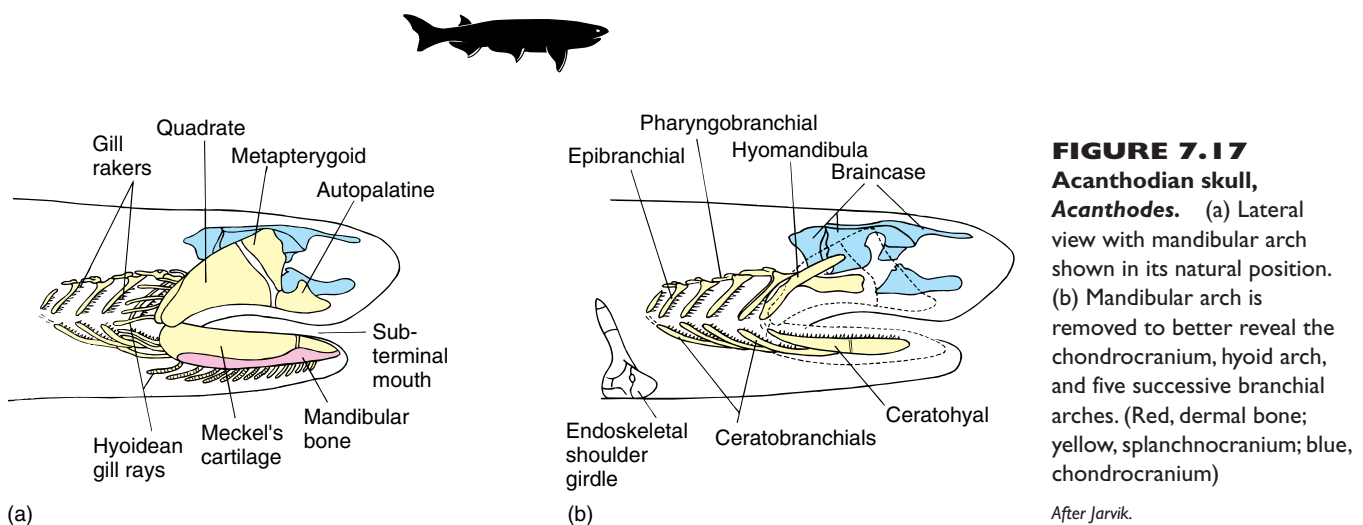


FIGURE 7.17 Acanthodian skull, *Acanthodes*. (a) Lateral view with mandibular arch shown in its natural position. (b) Mandibular arch is removed to better reveal the chondrocranium, hyoid arch, and five successive branchial arches. (Red, dermal bone; yellow, splanchnocranium; blue, chondrocranium)

After Jarvik.

fishes, the spiracle has vanished altogether. In chondrichthyans, such as holocephalans, the jaws mechanically crush hard shells of prey, but in active chondrichthyans, such as predaceous sharks, the jaws capture prey.

Sharks may use suction to draw small prey toward or into the mouth, but more commonly, they attack prey directly, approaching it head-on. As sharks raise their head, the lower jaw descends (figure 7.19a). Upper and lower jaws articulate with each other, and both in turn are suspended like a pendulum from the hyoid arch. The hyoid arch swings about its attachment to the braincase, which permits the

jaws to descend and shift downward and forward over the prey (figure 7.19b). Teeth along the upper (palatoquadrate) and lower (Meckel's cartilage) jaws are often oriented with their points in an erect position to engage the surface of the prey. Occasionally a nictitating membrane, a movable flap of opaque skin, is drawn protectively across each eye.

Jaw protrusion may also assist the synchronized meeting of upper and lower jaws on the prey. If the lower jaw alone was responsible for closing the mouth, it might prematurely strike the prey before the upper jaw was suitably positioned to assist. Protracting the mandibles away from

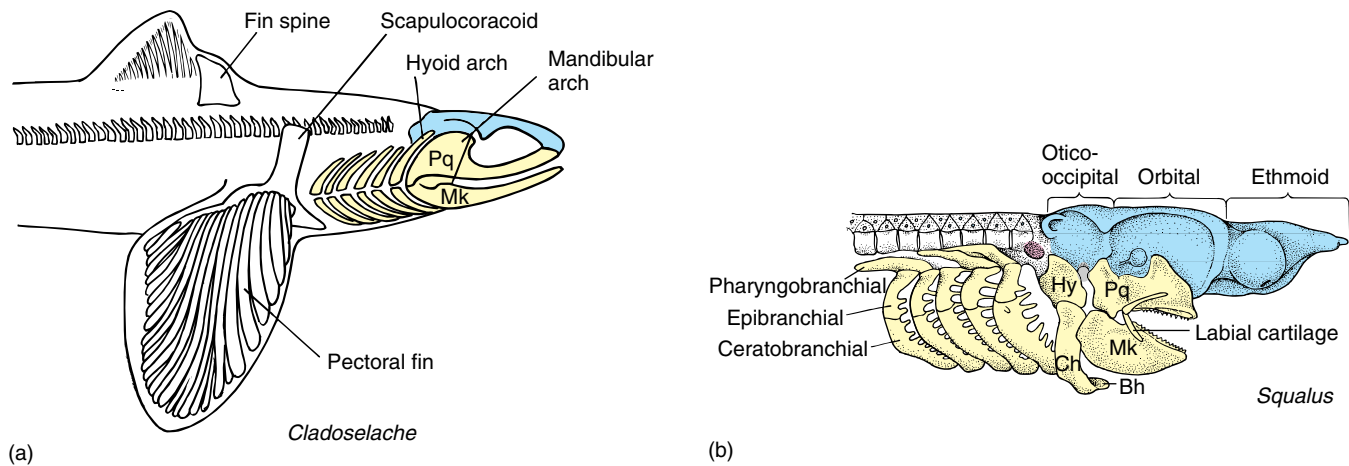


FIGURE 7.18 Shark skull. (a) Primitive shark *Cladoselache*, a late Devonian shark that reached perhaps 55 cm in length. Mandibles were followed by a complete hyoid arch and five branchial arches. Full gill slits were present between each arch. (b) Modern shark *Squalus*, the dogfish shark. The hyoid arch, second in series, is modified to support the back of the mandibular arch. As the hyoid moves forward to help suspend the jaw, the gill slit in front is crowded and reduced to the small spiracle. Although fused into one unit, the three basic regions of the chondrocranium are ethmoid, orbital, and otico-occipital. Abbreviations: basihyal (Bh), ceratohyal (Ch), hyomandibula (Hy), Meckel's cartilage (Mk), palatoquadrate (Pq).

(a) After Zangerl.

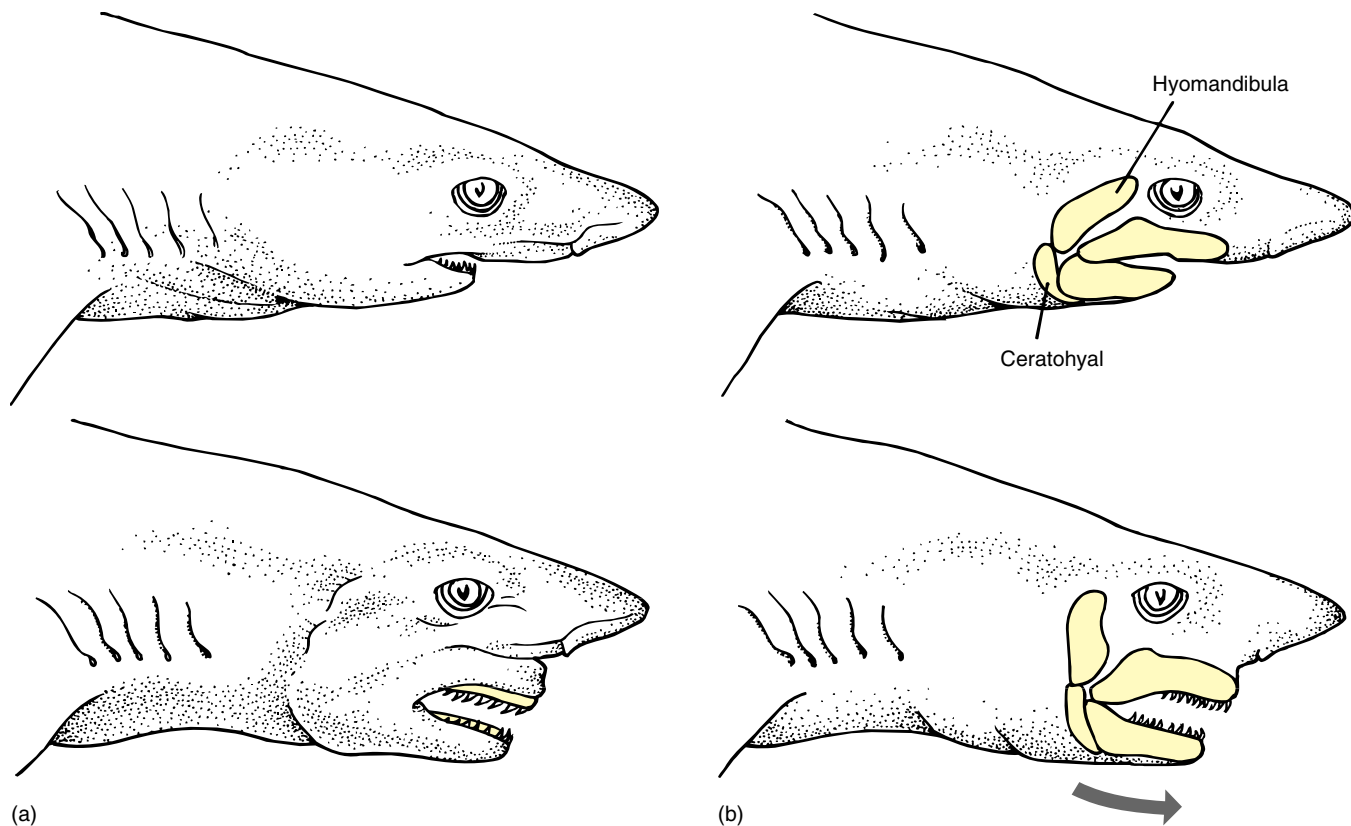


FIGURE 7.19 Feeding in sharks. (a) Sketches of shark with jaws retracted (top) and manually protracted (bottom). (b) Interpreted positional changes in the mandibular arch as it rides forward on its suspension from the ceratohyal. Position depicted is near the completion of jaw closure on the prey. Arrow indicates ventral and forward shift of the jaws.

Based on, and simplified from, the research of T. H. Frazzetta.

the head allows the jaws to assume a more favorable geometric configuration so that they meet the prey simultaneously and avoid deflecting it when they close. As the jaws clamp on the prey, the mandibular arch often is protracted near the end of closure. If the prey is large, the shark may violently shake its head to cut free a section of the prey and swallow it.

When protracted, the jaws disrupt the streamlined body silhouette characteristic of an active, open-water fish. Retraction of the jaws following feeding restores the hydrodynamic, streamlined shape of the fish and tucks the jaws back up against the chondrocranium.

Actinopterygians Early actinopterygians had relatively large eyes and small nasal capsules. The jaws were long, extending to the front of the head. The jaws carried numerous teeth, and an operculum covered the gill arches. The hyoid arch increased its support of the mandibles. Homologies of dermal bones in some groups have been difficult to assign, partly because of the proliferation of extra bones, especially facial bones. Around the external naris, there may be many tiny bones variously ascribed by position to nasals, rostral, antorbitals, and others. One common scheme is shown in figure 7.20a,b, but several varieties occur as well. Notice in particular the set of **opercular bones** covering the gills and the set of **extrascapulars** at the dorsal, posterior rim of the skull. These are major dermal bones in actinopterygians that are lost in tetrapods (figure 7.21a,b).

Within actinopterygians, an extraordinary radiation occurred that continues to the present. It is difficult to generalize about trends within the skull because so many varied specializations of modern bony fishes are part of this radiation. If a common trend exists, it is for increased liberation of bony elements to serve diversified functions in food procurement.

Most actinopterygians employ rapid suction feeding, with prey capture completed within 1/40 of a second. The almost explosive expansion of the buccal cavity creates a vacuum to accomplish swift capture. Negative pressure, relative to ambient pressure, sucks a pulse of water carrying the prey into the mouth. Once captured, teeth hold the prey. Compression of the buccal cavity expels excess water posteriorly out the gill slits. Fishes that feed by suction take in larger chunks of food than suspension feeders. Larger food particles have more inertia and require a stronger feeding device. Suction feeders consequently possess a well-muscularized buccal cavity and powerful, kinetic jaws.

In primitive actinopterygians, such as the fossil *Cheirolepis* and living *Amia* (figures 7.21a,b and 7.22a,b), the feeding apparatus includes several units. One is the neurocranium, to which the premaxilla and maxilla are usually fused. The posterior part of the neurocranium articulates with and is free to rotate on the anterior vertebra. The opercular bones form a unit along the side of the head. The **suspensorium** is formed from the fusion of various bones in different species but usually includes the hyomandibula, var-

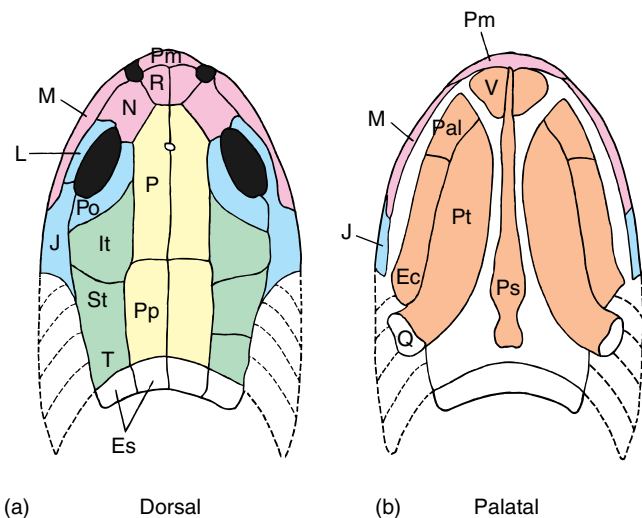


FIGURE 7.20 Major skull bones of an actinopterygian fish. (a) Dorsal view. (b) Palatal (ventral) views. Opercular bones are represented by dashed lines. Abbreviations: ectopterygoid (Ec), extrascapulars (Es), intertemporal (It), jugal (J), lacrimal (L), maxilla (M), nasal (N), parietal (P), palatine (Pal), premaxilla (Pm), postorbital (Po), postparietal (Pp), parasphenoid (Ps), pterygoid (Pt), quadrate (Q), rostral (R), supratemporal (St), tabular (T), vomer (V).

ious pterygoids, and quadrate. The suspensorium is shaped like an inverted triangle, its two upper corners articulating with the snout and braincase, its third lower corner articulating with the mandible. During jaw opening, epaxial muscles of the trunk raise the neurocranium and the attached upper jaw. Sternohyoideus muscles in the throat move the hyoid apparatus to lower the mandible (figure 7.23a,b). Strong adductor muscles of the jaws run from the suspensorium directly to the mandible to close the lower jaw.

In advanced actinopterygians, the teleosts, there is usually even greater freedom of skull bone movement (figure 7.24a–e). The premaxilla and maxilla are now usually freely articulated with each other and with the neurocranium (figure 7.25). During jaw opening, the neurocranium is raised, and the mandible is lowered. In addition, the geometric arrangement of the jaws allows it to move forward. The hyoid apparatus forms struts within the floor of the buccal cavity. When pulled backward by the throat musculature, these hyoid struts help push the lateral walls of the buccal cavity apart and so contribute to its sudden enlargement and creation of suction within.

Sarcopterygians In early lungfishes, the upper jaw (palatoquadrate) was fused to the ossified braincase, which was a single unit with teeth flattened into plates. This suggests that the earliest lungfishes fed on hard foods, like their living counterparts that have similar tooth plates and jaws for feeding on shellfishes, snails, and crustaceans. The other group of sarcopterygians, the rhipidistians, had strong jaws with small, pointed teeth. However, in contrast to the teeth

FIGURE 7.21 Skull of the primitive palaeoniscoid fish *Cheirolepis*, from the late Devonian.

Overall length of the fish was about 24 cm. (a,b) Dorsal and lateral views of the skull, respectively. Bones of the pectoral girdle (red) are tightly connected to the posterior wall of the skull. Abbreviations: angular (Ang), branchiostegals (Br), clavicle (Cl), cleithrum (Ct), dentary (D), dermohyal (Dhy), external naris (En), lateral extrascapular (Esl), intertemporal (It), jugal (J), lacrimal (L), maxilla (M), nasal (N), opercular (O), accessory opercular (Opa), parietal (P), premaxilla (Pm), postorbital (Po), preopercular (Pop), posttemporal (Pot), postparietal (Pp), preorbital (Pro), quadratojugal (Qj), rostral (R), sclerotic ring (Sc), supracleithrum (Sct), subopercular (Sop), supraorbital (Spo), supratemporal (St).

After Carroll.

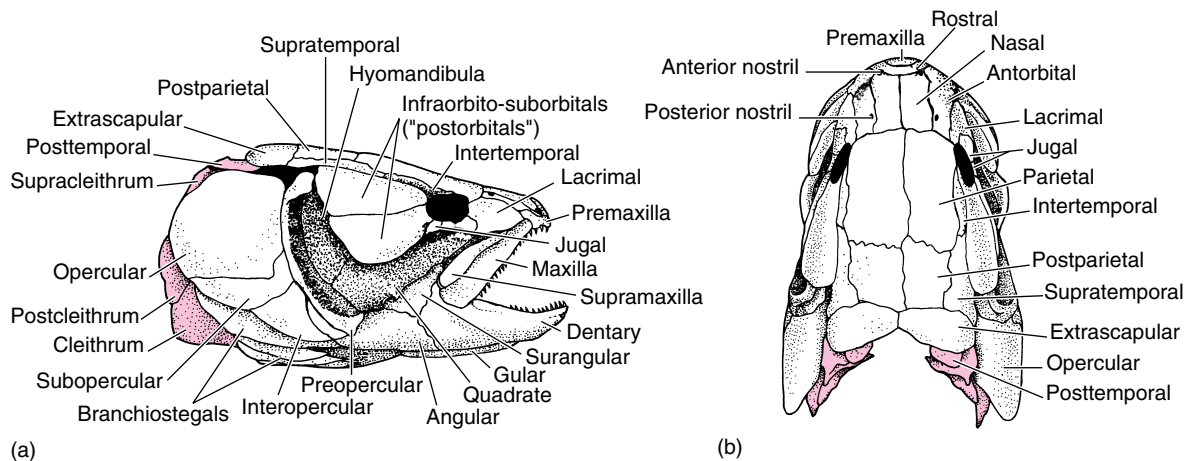
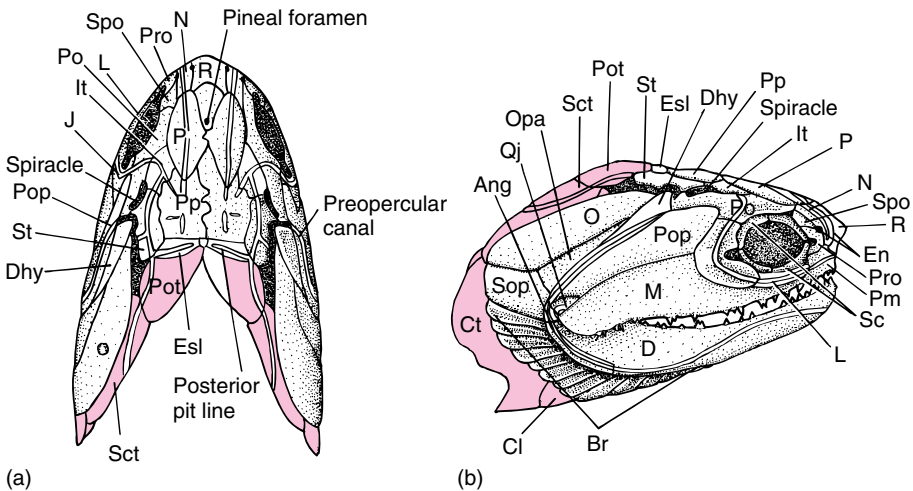


FIGURE 7.22 Skull of the bowfin, *Amia*, a chondrosteian. Lateral (a) and dorsal (b) views.

of other fishes, the walls of rhipidistian teeth were extensively infolded, producing distinct **labyrinthodont teeth**. Large teeth were carried on the dentary of the lower jaw and along the lateral bones of the palate—vomer, palatine, ectopterygoid. Bones of the dermatocranium resembled those of actinopterygians, and like actinopterygians, the palatoquadrate articulated anteriorly with the nasal capsule and laterally with the maxilla. Unlike actinopterygians and extant lungfishes, the braincase of rhipidistians typically ossified into two articulated units: an anterior **ethmoid unit** (ethmosphenoid unit) and a posterior oticooccipital unit, with a flexible joint between them. In the dermal roofing bones above this joint, a hinge formed between the parietal

and postparietal. Consequently, the snout could rotate upward about the rest of the skull, a displacement thought to be important during feeding (figure 7.26). The functional notochord also extended well forward into the head, passing through a tunnel in the oticooccipital segment, eventually abutting the back of the ethmoid unit and perhaps bringing added support into this region of the skull.

Labyrinthodont teeth (p. 505)

Nasal Capsules From fishes to tetrapods, the nasal capsules have had a complex history. The nasal capsules hold the olfactory epithelium in the form of a paired **nasal sac**

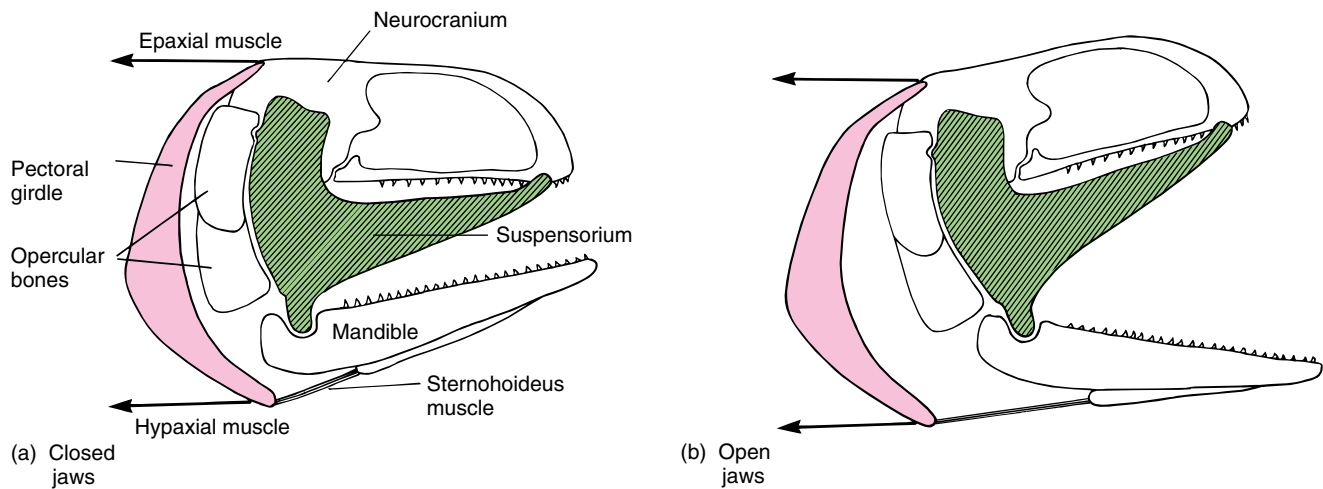


FIGURE 7.23 Jaw opening in a primitive actinopterygian fish. (a) Jaws are closed. (b) Jaws are open. The mandible rotates on its articulation with the suspensorium, which in turn is articulated with the opercular bones. The pectoral girdle remains relatively fixed in position, but the neurocranium rotates on it to lift the head. Lines of action of major muscles are shown by arrows.

After Lauder.

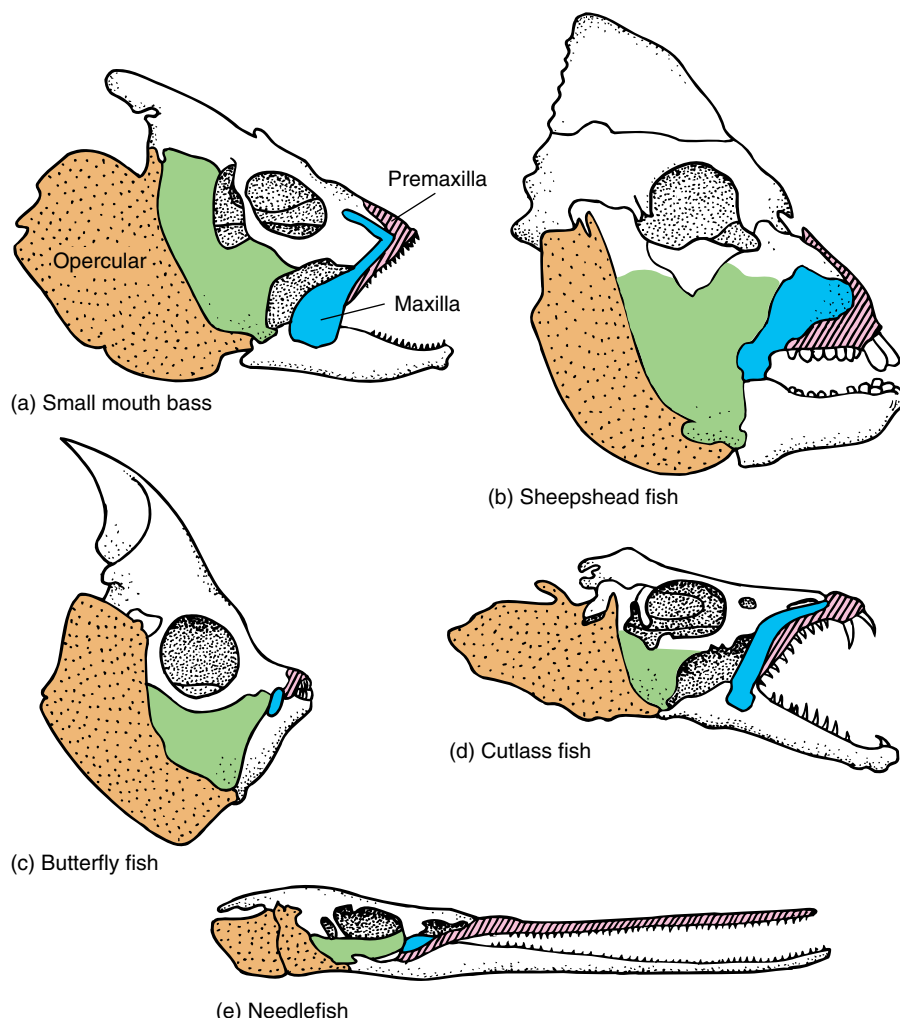


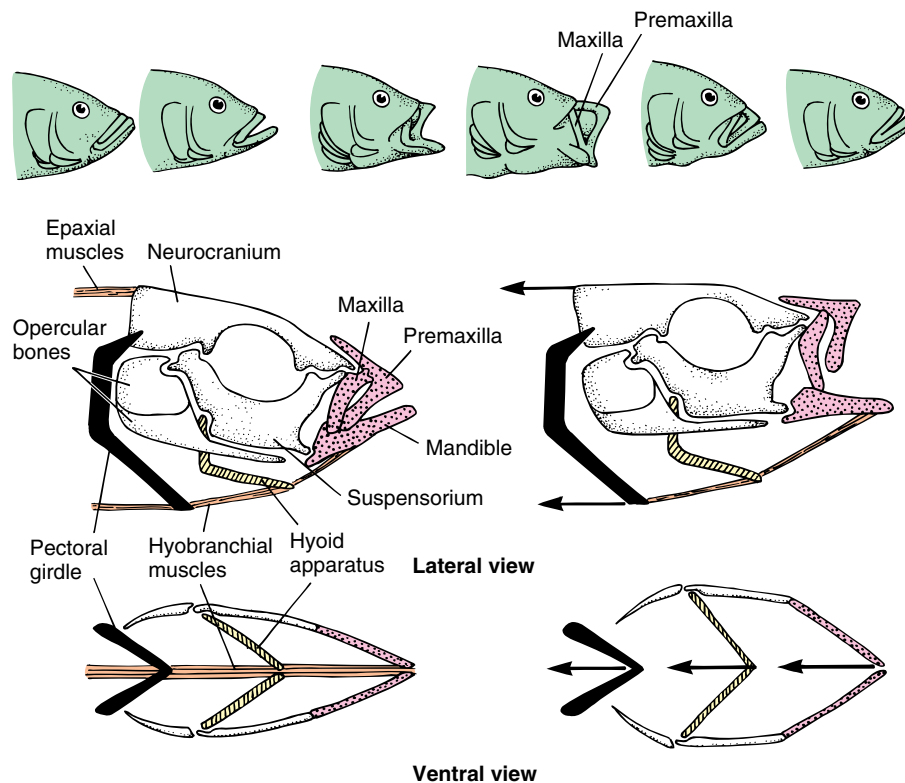
FIGURE 7.24 Teleost skulls.

Despite the great diversification of teleosts in many habits, the basic pattern of skull bones is preserved. (a) Small mouth bass (*Micropterus dolomieu*). (b) Sheepshead fish (*Archosargus probatocephalus*). (c) Butterfly fish (*Chaetodon ocellatus*). (d) Cutlass fish (*Trichiurus lepturus*). (e) Needlefish (*Tylosurus marinus*).

After Radinsky.

FIGURE 7.25 Suction feeding of a teleost fish. Top series are traces from a high-speed film of jaw opening (food not shown). Note changes in position of the jaws. Lateral and ventral views, respectively, of the major kinetic bones of the skull are shown when jaws are closed (left) and when they are open (right). Note the forward movement of the jaws (stippled areas) and outward expansion of the buccal cavity. Lines of muscle action are shown by arrows.

After Liem.



(figure 7.27a). In actinopterygians, the nasal sac typically does not open directly into the mouth. Instead, its anterior (incurrent) and posterior (excurrent) narial openings establish a route for one-way water flow across the olfactory epithelium, delivering to it fresh chemical odors. By contrast, each nasal sac of tetrapods opens directly into the mouth via an internal naris, or **choana** (figure 7.27b). Each nasal sac also opens to the exterior by way of an **external naris** (nostril), thus establishing a respiratory route for airflow in and out of the lungs. In addition to internal and external nares, a third opening within the nasal sac begins as a tube, the **nasolacrimal duct**, that runs toward the orbit in order to drain away excess secretions of the adjoining lacrimal gland after helping to moisten the surface of the eye.

Olfactory organs (p. 666)

Among sarcopterygians, the nasal capsules of rhipidistians are similar to those of tetrapods. In rhipidistians, the nasolacrimal duct is an adaptation that benefits surface fishes that poke their eyes and nostrils out of the water. The lacrimal gland moistens exposed sensory organs that are subjected to drying. The nasolacrimal duct is probably homologous to the posterior (excurrent) naris of actinopterygian fishes. Rhipidistians (but not coelacanth) also possess internal nares, apparently representing a new derivative of the nasal sac connecting it with the mouth. However, lungfishes probably lack internal nares, although this is still debated. In lungfishes, the posterior (excurrent) naris opens near the

margin of the mouth but does not pierce the palatal series of dermal bones as does the true internal naris of rhipidistians and tetrapods.

Early Tetrapods

The earliest tetrapods arose from rhipidistian ancestors and retained many of their skull features, including most of the bones of the dermatocranium. Numerous bones in the snout were reduced, leaving a distinct nasal bone occupying a position medial to the external naris (figure 7.28a,b). Beginning in tetrapods, the hyomandibula ceases to be involved in jaw suspension and instead becomes dedicated to hearing as the stapes (or columella) within the middle ear. The opercular series of bones covering the gills are typically lost. Extrascapulars across the back of the fish skull also disappear in primitive tetrapods. Along with this, the pectoral girdle loses its attachment to the back of the skull. Roofing bones and chondrocranium become more tightly associated, reducing the neurocranial mobility of the snout in comparison with rhipidistians.

The lateral line system, an aquatic sensory system, is evident in skulls of the earliest tetrapods, at least among the juveniles that were presumably aquatic stages (figure 7.29a,c). The skull is flattened, and in some a temporal notch at the back of the skull is present. The stapes conveys sound vibrations to the inner ear. But the stapes in early tetrapods is still a robust bone that also seems to be a buttress between the braincase and the palatoquadrate. Teeth were conical in labyrinthodonts, with the

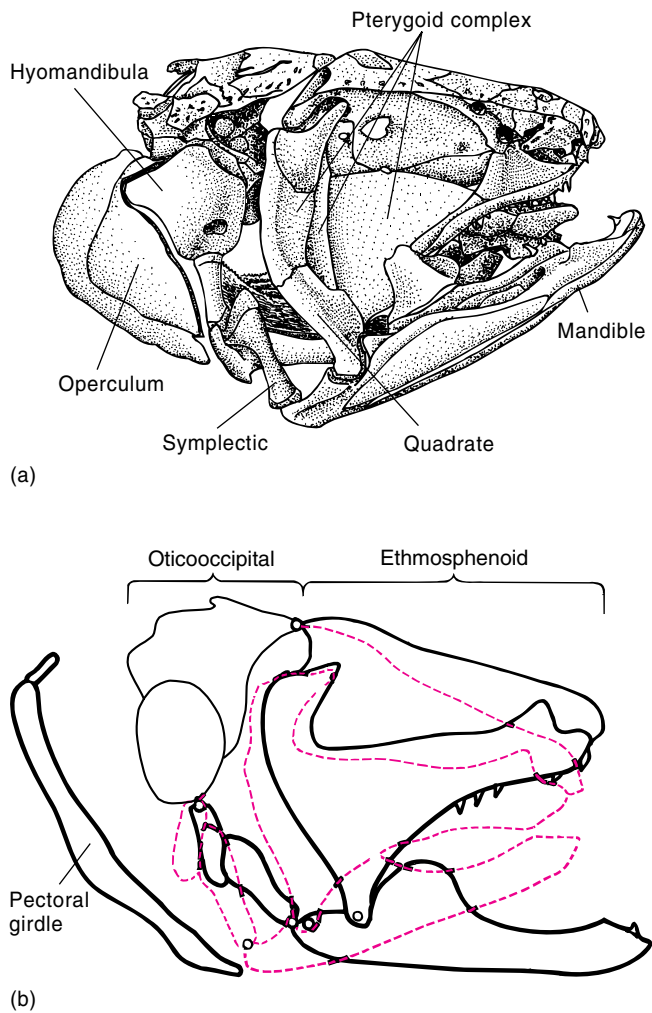


FIGURE 7.26 Cranial kinesis of a coelacanth, *Latimeria*. (a) Lateral view of the skull. (b) Biomechanical model of major functional elements showing displacement pattern during jaw opening (solid lines) compared with closed position (dashed lines). Pterygoid complex includes entopterygoid, ectopterygoid, and epipterygoid.

(a) After Millot, Anthony, and Robineau; (b) based on Lauder.

enamel folded into complex patterns. Teeth of lepospondyls lacked the highly folded enamel, and the otic notch was absent.

The skulls of modern amphibians are greatly simplified compared with those of their fossil ancestors, with many of the dermal bones being lost or fused into composite bones. Caecilian skulls are compact and firmly ossified, although the pattern of dermal bones can be quite varied. In salamanders, the chondrocranium consists primarily of **orbitosphenoid** and **prootic** bones, with exoccipitals closing the posterior wall of the braincase (figure 7.30). Nasal bones are usually present. Up to four pairs of roofing bones contribute to the skull: Frontals and parietals are present in all, but prefrontals and lacrimals vary among groups. In anurans (figure 7.31), ossification of the chondrocranium is highly

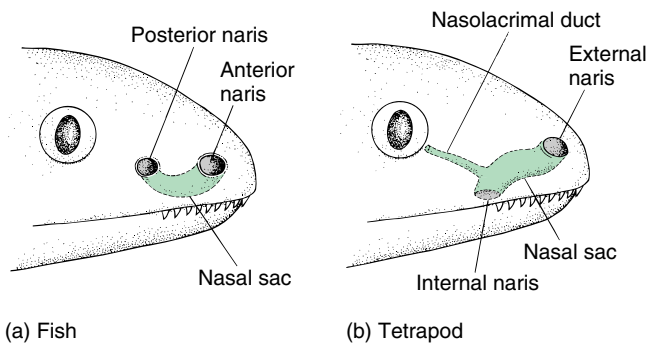


FIGURE 7.27 Openings of the nasal sac. (a) In an actinopterygian fish, the nasal sac typically has an anterior naris through which water enters and a posterior naris through which water exits, but the nasal sac does not open into the mouth. (b) In a tetrapod, the nasal sac has an external naris (homologous with the anterior naris of the fish) and a nasolacrimal duct to the orbit (presumed homologue of the posterior naris of the fish). In addition to these, a third extension of the nasal sac, the internal naris, opens into the buccal cavity through the roof of the mouth.

variable, usually with just five bones present, a single sphenethmoid and paired prootics and exoccipitals. A nasal bone is present, but only a paired, composite **frontoparietal** remains of the roofing bones. In both frogs and salamanders, the single parasphenoid has expanded to form a large plate that has crowded other palatal bones.

The splanchnocranium, a major component of the fish skull, is reduced in amphibians. In modern amphibians, the hyomandibula plays no role in jaw suspension. This task is taken over exclusively by the articular and quadrate bones through which the mandible articulates with the skull. The branchial arches composing the hyobranchial apparatus support external respiratory gills in the larvae, but when the larvae metamorphose into the adult, these arches are reduced to the hyoid apparatus that supports the action of the tongue.

Salamanders commonly use suction feeding in water. The floor of the throat is rapidly expanded and the jaws parted enough so that the pulse of water carrying the intended prey enters (figure 7.32). Excess water gulped in with the prey exits at the back of the mouth through the gill slits. In salamanders, as in fishes, there is a **unidirectional** flow of food and water into the mouth and out the gill slits. In metamorphosed salamanders and in adult frogs, gill slits are absent, so excess water entering the mouth during feeding must reverse its flow to exit via the mouth. Such flow is said to be **bidirectional**. On land, amphibians commonly use a sticky, projectile tongue. At close range, muscles catapult the tongue over the parted mandibles and into contact with the prey. At longer range, muscle action works in cooperation with fluid-filled spaces within the tongue to accelerate it along the hyoid apparatus. Retraction of the tongue returns the attached food to the mouth, and teeth close on it to control the struggling prey.

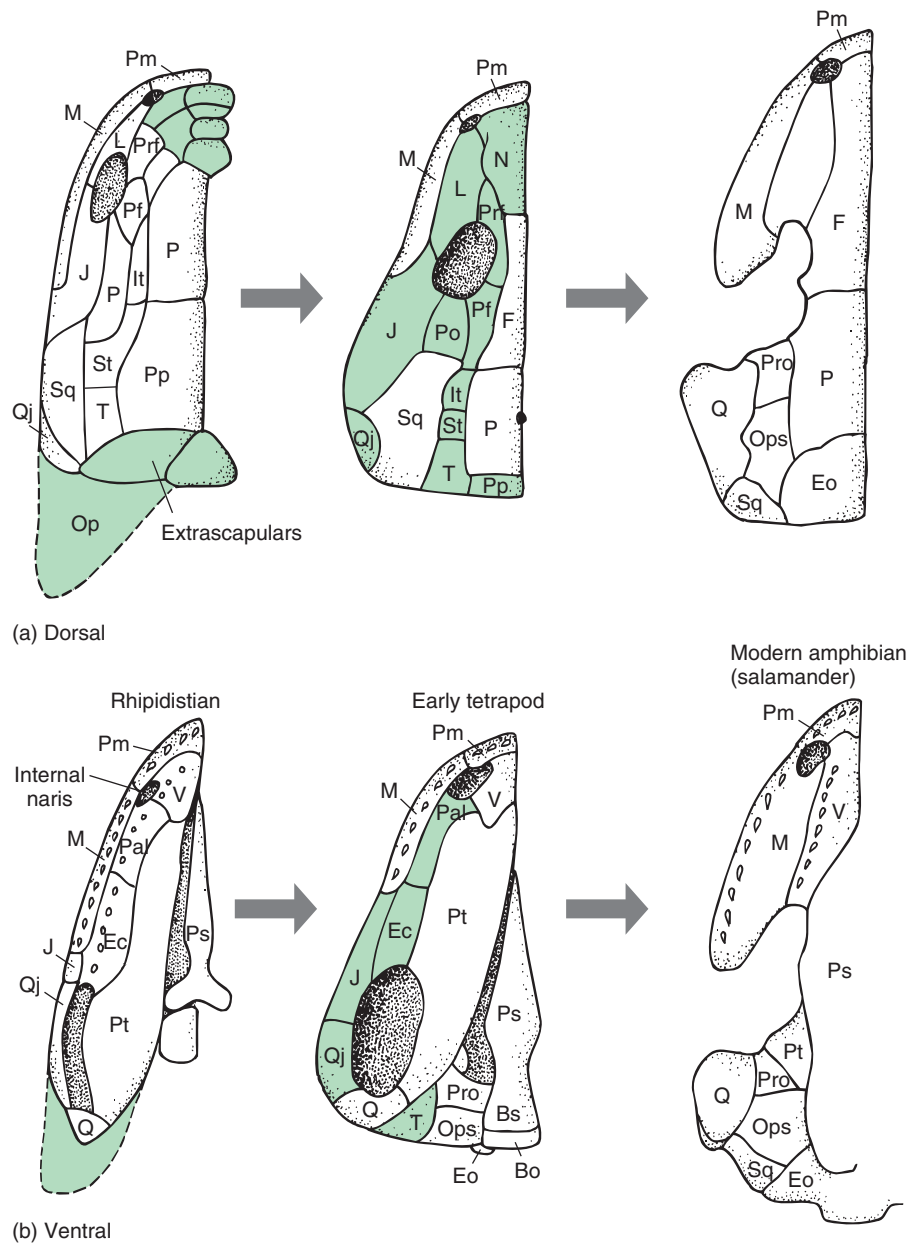


FIGURE 7.28 Diagrammatic views of skull modifications from rhipidistian to early tetrapod to modern amphibian (salamander).

(a) Dorsal views. (b) Ventral (palatal) views. Skull bones lost in the derived group are shaded in the skull of the preceding group. Abbreviations: basioccipital (Bo), basisphenoid (Bs), ectopterygoid (Ec), exoccipital (Eo), frontal (F), intertemporal (It), jugal (J), lacrimal (L), maxilla (M), nasal (N), opercular (Op), opisthotic (Ops), parietal (P), palatine (Pal), postfrontal (Pf), premaxilla (Pm), postorbital (Po), prefrontal (Prf), prootic (Pro), postparietal (Pp), parasphenoid (Ps), pterygoid (Pt), quadrate (Q), quadratojugal (Qj), supratemporal (St), squamosal (Sq), tabular (T), vomer (V).

Primitive Amniotes

The first amniotes were small and would probably remind us of lizards in general appearance. The skull roof, like that of early amphibians, was formed from the dermatocranium, with openings for eyes, pineal organ, and nostrils (figure 7.33a–d). Robust attachment flanges and processes are evidence of strong jaw-closing muscles. The palatoquadrate of the mandibular arch was reduced to the small epipterygoid and separate quadrate. The hyoid arch produced a stapes, a stout bone that braced the back of the dermatocranium against the chondrocranium. These early tetrapods lacked a temporal notch. Sound transmission to the inner ear may have occurred along bones of the lower jaw.

Skull Fenestrae As mentioned earlier, the temporal region of the dermatocranium contains features particularly revealing of amniote lineages (figure 7.34). Fenestrae are openings in the outer dermatocranium. The anapsid skull lacks temporal fenestrae. In recent turtles, **emarginations** often encroach upon the posterior margin of the skull roof. These emarginations are large notches that function like fenestrae, but they are independent phylogenetic derivatives. The diapsid skull includes two temporal fenestrae, a condition carried forward in *Sphenodon* and in crocodiles and their allies. However, the lower and upper temporal bars are often lost in other modern forms. This gives us several contemporary varieties of a modified diapsid skull in which the diapsid condition is substantially altered, such as birds, lizards, and especially snakes.

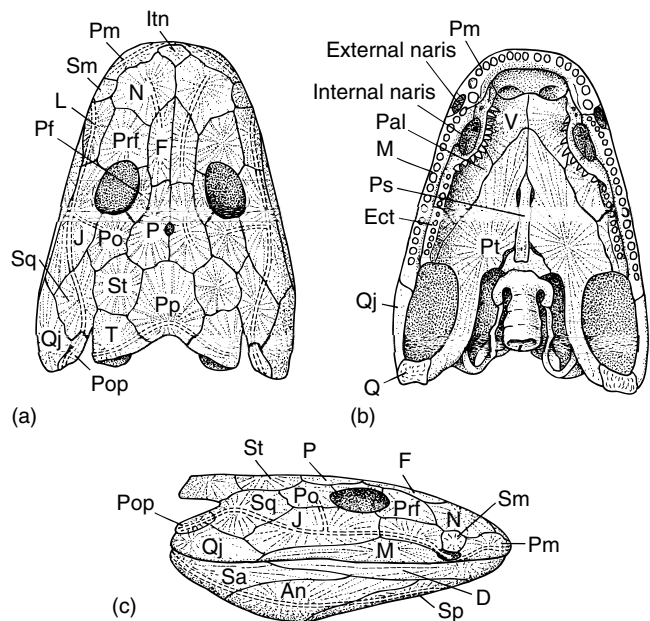


FIGURE 7.29 Skull of *Ichthyostega*, a primitive tetrapod of the late Devonian. Dorsal (a), ventral (b), and lateral (c) views. Parallel tracks of dashed lines indicate course of the aquatic lateral line system on the skull bones. Abbreviations: angular (An), dentary (D), ectopterygoid (Ect), frontal (F), internasal (ltn), jugal (J), lacrimal (L), maxilla (M), nasal (N), parietal (P), palatine (Pal), postfrontal (Pf), premaxilla (Pm), postorbital (Po), preopercular (Pop), postparietal (Pp), prefrontal (Prf), parasphenoid (Ps), pterygoid (Pt), quadrate (Q), quadratojugal (Qj), surangular (Sa), septomaxilla (Sm), splenial (Sp), supratemporal (St), squamosal (Sq), tabular (T), vomer (V).

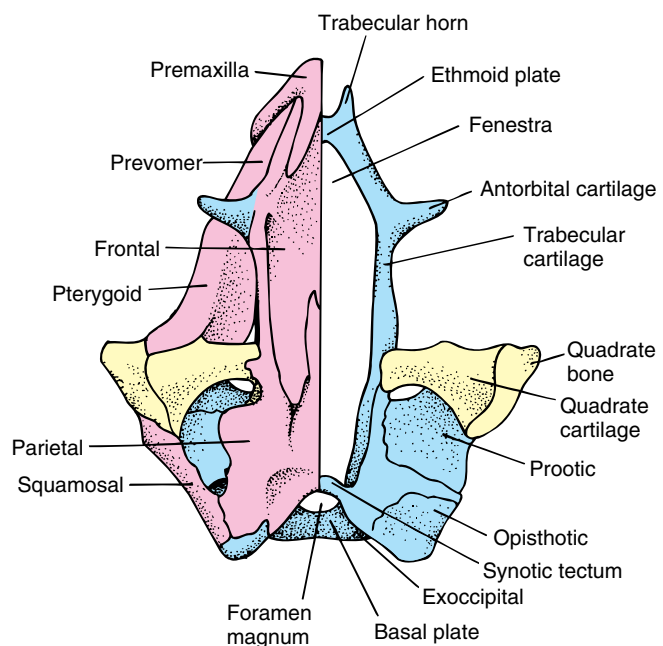


FIGURE 7.30 Skull of *Necturus*, a modern amphibian. Superficial skull bones are indicated on the left. These bones have been removed to reveal the chondrocranium and derivatives of the splanchnocranium on the right.

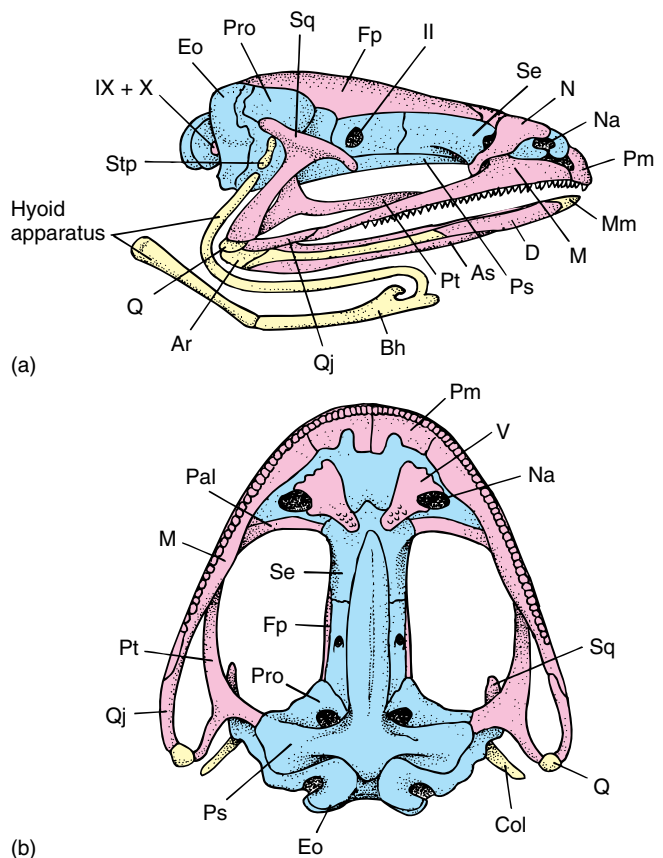


FIGURE 7.31 Frog skull. Lateral (a) and ventral (b) views. Abbreviations: articular (Ar), angulosphenoid (As), basihyal (Bh), dentary (D), exoccipital (Eo), frontoparietal (Fp), maxilla (M), mento-Meckelian (Mm), nasal (N), naris (Na), palatine (Pal), premaxilla (Pm), prootic (Pro), parasphenoid (Ps), pterygoid (Pt), quadrate (Q), quadratojugal (Qj), sphenethmoid (Se), squamosal (Sq), stapes (Stp), vomer (V). Roman numerals indicate foramina serving specific cranial nerves.

After Marshall.

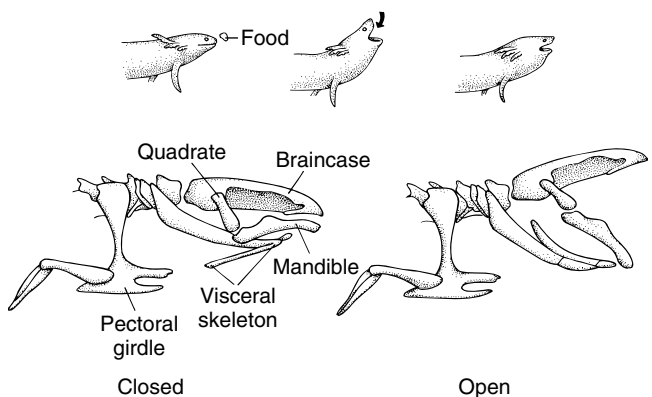


FIGURE 7.32 Suction feeding by an aquatic salamander. Before, during, and after suction feeding traced from a high-speed film feeding sequence (top series). Note the interpreted positions of the skull elements when the jaws are closed (bottom left) and open (bottom right).

After Lauder.

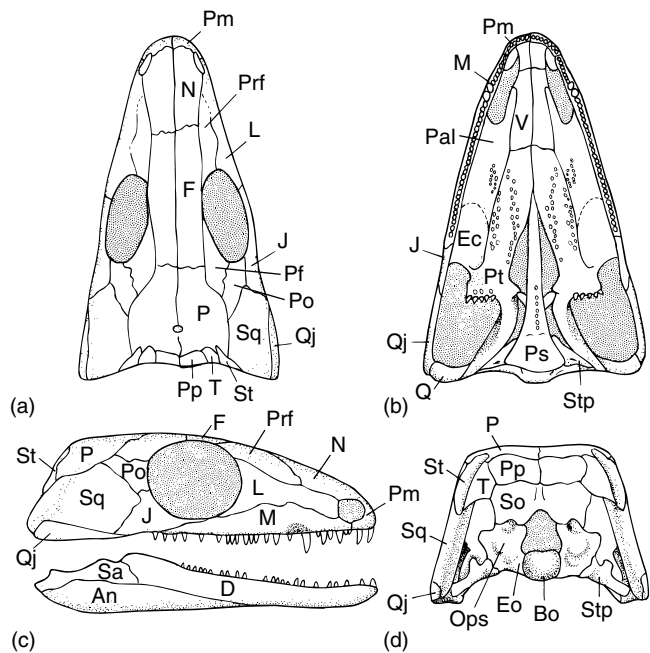


FIGURE 7.33 Skull of *Paleothyris*, an early amniote from the Carboniferous. Dorsal (a), ventral (b), lateral (c), and posterior (d) views. Abbreviations: angular (An), basioccipital (Bo), dentary (D), ectopterygoid (Ec), exoccipital (Eo), frontal (F), jugal (J), lacrimal (L), maxilla (M), nasal (N), opisthotic (Ops), parietal (P), palatine (Pal), postfrontal (Pf), premaxilla (Pm), postorbital (Po), postparietal (Pp), prefrontal (Prf), parasphenoid (Ps), pterygoid (Pt), quadrate (Q), quadratejugal (Qj), surangular (Sa), supraoccipital (So), supratemporal (St), squamosal (Sq), stapes (Stp), tabular (T), vomer (V).

After Carroll.

The synapsid skull of pelycosaurs, therapsids, and modern mammals contains a single temporal opening. Loss of the postorbital bone in modern mammals allows merging of the temporal fenestra with the orbit.

Taxonomic implications of temporal fenestrae (p. 107)

Although used by taxonomists to delineate phylogenetic lineages within tetrapods, the functional significance of fenestrae is not clear. With few exceptions, most notably lepospondyls, fenestrae are absent in early tetrapods and primitive reptiles. Because fenestrae are associated with strong jaw adductor muscles, it has been suggested that they open space in the skull for these muscles to bulge during contraction (figure 7.35a–c). But it is difficult to see how such a function could have afforded some initial advantage favoring their evolution. Initially fenestrae would have been too small to provide space for bulging muscles that presumably favored their appearance. Alternatively, some have suggested that unstressed bone of the dermatocranium might have little selective value if it did not contribute to muscle attachment. Its loss would have been expected, leading to

the initial appearance of fenestrae in these areas. More positively, it has been proposed that the rims of open fenestrae offer a more secure attachment site for muscles than does a flat surface. Muscle tendons merge with the periosteum, spread the tensile forces around the rim, and distribute them across the extended surface of the bone. This might render the attachment site less susceptible to being torn loose from the bone.

Whatever the function of fenestrae, their presence would be possible only if holes would not unduly weaken the ability of the skull to withstand stresses. Their absence in labyrinthodonts and primitive amniotes, their presence in later amniotes, and the appearance of emarginations by a different route in turtles imply a complex and not fully understood interaction between function and design in early tetrapods.

Cranial Kinesis in Reptiles Skull elements of reptiles exhibit varying degrees of mobility. The most extensive motions are found in the skulls of lizards and especially snakes. In these two groups, a transverse hinge extends across the skull roof, a **transcranial joint**. Depending on the position of this hinge, three names apply. Where a hinge passes across the back of the skull, permitting rotation between the neurocranium and outer dermatocranium, the skull is said to exhibit **metakinesis** (figure 7.36a). If a joint passes through the dermatocranium behind the eye, the skull exhibits **mesokinesis**. If a joint in the dermatocranium passes in front of the orbits, the skull exhibits **prokinesis**. Depending on the number of hinges, the skull may be **monokinetic**, having one joint, or **dikinetic** (amphikinetic), having two joints. Although rare, mesokinesis is possibly present in amphisbaenians and some burrowing lizards. Prokinesis is typical in snakes and birds. Most modern lizards are dikinetic, with both meta- and mesokinetic joints across their skull roofs.

The term **streptostyly** applies not to the skull roof but to the quadrate and describes the condition in which the quadrate is free to undergo some degree of independent rotation about its dorsal connection with the braincase (figure 7.36b). Most lizards, snakes, and birds are streptostylic.

Modern Reptiles

Modern turtles have anapsid skulls, but emarginations that develop from the posterior region forward often result in the opening of large regions within outer bones of the dermatocranium (figure 7.37a–e). Large jaw-closing muscles occupy this space. Although turtles lack teeth, the opposing surfaces of upper and lower jaws are usually covered with keratinized “tooth” plates that deliver powerful biting forces to food.

Several modern reptiles are surviving members of the diapsid radiation. In *Sphenodon*, complete upper and lower temporal bars firmly join the front and the back of the lateral skull wall (figure 7.38a–d). A mobile transcranial joint

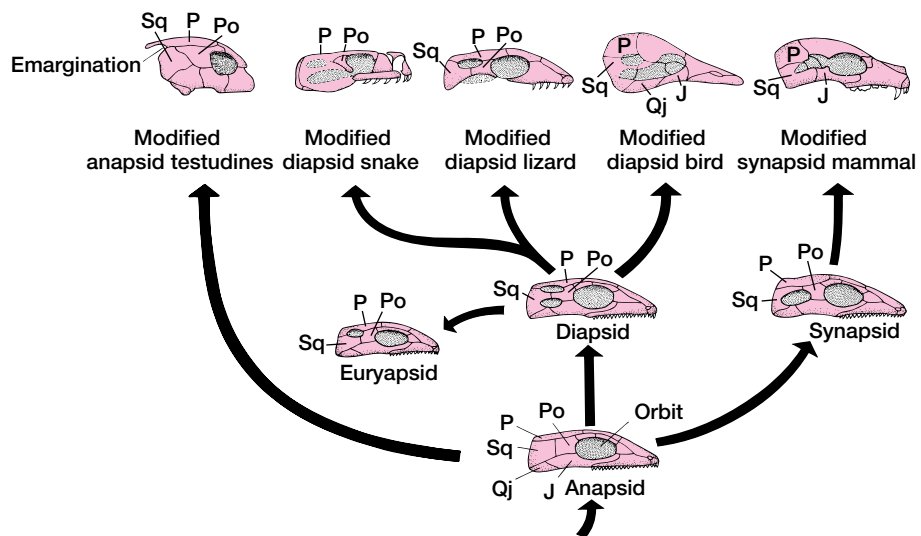


FIGURE 7.34 Major lineages of dermatocranium evolution within amniotes. The anapsid skull occurs in cotylosaurs and their modern descendants, turtles and tortoises. Two major groups, the diapsids and synapsids, independently evolved from the anapsids. *Sphenodon* and crocodilians retain the primitive diapsid skull, but it has been modified in diapsid derivatives such as snakes, lizards, and birds. Shading indicates positions of temporal fenestrae and orbit. Abbreviations: jugal (J), parietal (P), postorbital (Po), quadratojugal (Qj), squamosal (Sq).

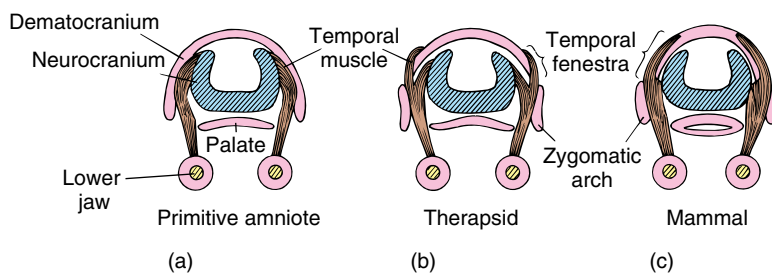


FIGURE 7.35 Temporal fenestrae. The shift in jaw muscle attachment to the skull is shown. (a) Anapsid skull. In early amniotes, temporal muscles run from the neurocranium to the lower jaw. Such a skull is retained in modern turtles. (b) Perforation in the dermatocranium opens fenestrae, and attachment of jaw muscles expands to the edges of these openings. (c) Extensive attachment of jaw muscles to the surface of the dermatocranium. Such development of fenestrae characterizes the diapsid and synapsid radiations.

After Smith.

and movable palate are absent. Consequently, no significant mobility is permitted within the dermatocranium. However, the mandible slides back and forth on the fixed quadrate from which it is suspended. The single row of teeth of the mandible moves between a double row of teeth on the upper jaw, an action that seems to be important in slicing through some types of prey.

Loss of the lower temporal bar produces the modified diapsid skull of lizards (figure 7.39). Loss of this lower bony strut laterally liberates the posterior part of the skull from the snout, thereby permitting streptostyly, and hence promoting the mesokinetic part of lizard dikinesis. Lizard ancestors, the younginiformes, apparently possessed a single metakinetic joint across the back of the skull. A second kinetic joint, the mesokinetic joint, has been added to this in most modern lizards, making the skulls of most lizards diakinetic. Although skulls of some specialized lizards, such as burrowers, anteaters, and some herbivores, seem monokinetic, this is likely a secondary condition. This kinetic machinery of lizard jaws has been modeled as a four-bar linkage system (figure 7.40a,b). One unit is the triangular-shaped snout. Its posterior wall forms one of the four

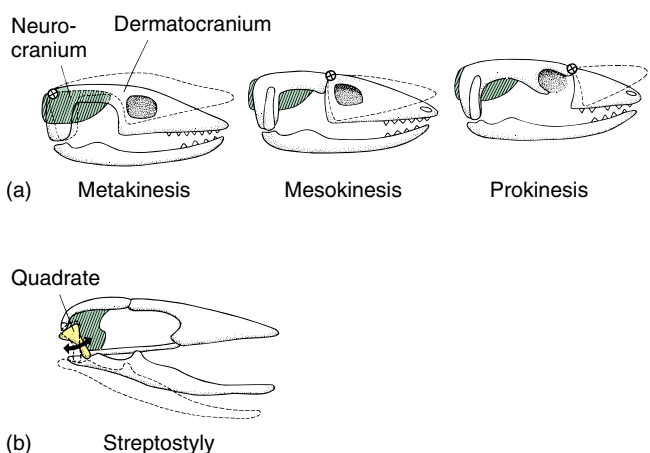


FIGURE 7.36 Cranial kinesis in squamates. (a) There are three types of cranial kinesis based largely on the position at which the hinge (X) lies across the top of the skull. The hinge may run across the back of the skull roof (metakinesis), behind the orbit (mesokinesis), or in front of the orbit where the snout articulates (prokinesis). (b) The ability of the quadrate to rotate about its dorsal end is called streptostyly.

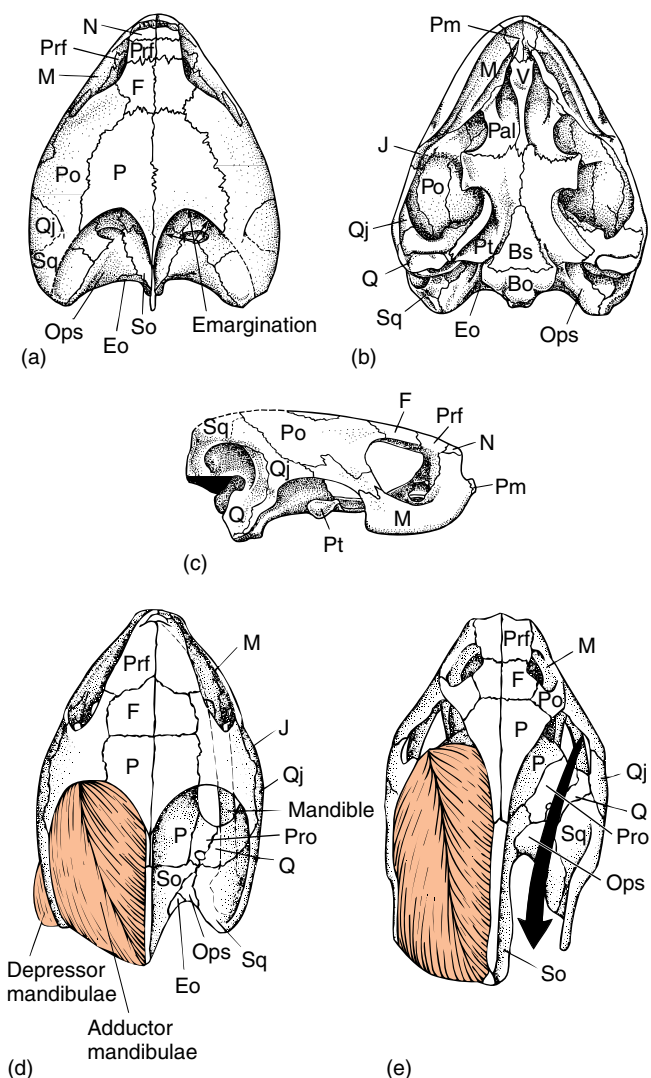


FIGURE 7.37 Turtle skulls. (a–c) Skull of *Pleisocheilus*, from the late Jurassic. *Pleisocheilus* is the earliest known member of the cryptodires. Note the absence of any temporal fenestrae but the presence of emarginations etched in the dorsal, posterior rim of the skull. Dorsal (a), ventral (b), and lateral (c) views. (d) European pond turtle *Emys*, showing site of residence of jaw opening (depressor mandibulae) and closing (adductor mandibulae) muscles in relation to emargination. (e) Modern softshell turtle *Trionyx*, showing line of action of adductor mandibulae, solid arrow, from lower jaw to skull within enlarged emargination. Abbreviations: basioccipital (Bo), basisphenoid (Bs), exoccipital (Eo), frontal (F), jugal (J), maxilla (M), nasal (N), opisthotic (Ops), parietal (P), palatine (Pal), prefrontal (Prf), premaxilla (Pm), prootic (Pro), postorbital (Po), pterygoid (Pt), quadrate (Q), quadratojugal (Qj), supraoccipital (So), squamosal (Sq), vomer (V).

(a–d) After Carroll; (e) after Romer.

linkages. The dorsal corner of the snout participates in the mesokinetic joint and forms a second mechanical link with the dorsal end of the quadrate through the top of the skull. The quadrate represents the third link. The fourth mechanical link connects the quadrate's lower end (where it meets the pterygoid) forward to the posterior lower corner of the snout to complete and close the four-bar kinematic chain.

Biomechanical mechanisms (p. 144)

Without such a kinematic series of linkages, jaw closure would be scissorslike, and jaw-closing forces on the prey would have a forward component that might deflect or squirt the prey out of the mouth, increasing the chance of prey loss (figure 7.40c). However, in the skull of many lizards, rotation of the four linkages permits changes in geometric configuration. As a consequence, these lizards can alter the angle of the tooth row borne by the snout as it closes on the prey. Upper and lower jaws close and meet the prey nearly simultaneously, delivering forces directed at the prey; thus the lizard is less likely to experience prey loss.

The metakinetic joint is not directly part of this linkage train of bones, although its transverse axis is coincident with the quadrate-parietal joint of the four-bar linkage mechanism. The metakinetic joint permits the dermatocranium, to which the linkage chain is joined, to move relative to the deeper neurocranium. The axis of the metakinetic joint is almost coincident with the superficial joint between the dorsal end of the quadrate and the braincase, but it is not part of this outer set of linkages. Thus, rotation about this metakinetic joint lifts the whole dermatocranium along with the entire set of linkages relative to the neurocranium.

Some lizards, like many terrestrial salamanders, project their tongues during feeding. When the tongue is prominently deployed, a lizard engages in **lingual feeding** (figure 7.41a). The jaws part, and the sticky tongue is projected at the prey. In chameleons, a circular **accelerator muscle** wraps around the **lingual process** of the hyoid apparatus (figure 7.41b,c). Upon contraction, the accelerator muscle squeezes the lingual process, picks up speed as it slides down the tapered process, perhaps like squeezing a slippery bar of soap, and carries along the glandular tip of the tongue (figure 7.41d). The gathered momentum of the tip of the tongue launches it out of the mouth toward the prey. Upon impact, the fleshy glandular tip of the tongue flattens against the target, establishing firm adhesion. Retraction of the tongue back into the mouth retrieves the prey. The jaws then close to hold the captured prey.

In snakes, the frontal and parietal roofing bones have grown down around the sides of the skull to form most of the walls of the braincase as well (figure 7.42). Their enlargement results in crowding or loss of many of the other dermal bones. Snake skulls are prokinetic. A joint across the skull forms in front of the orbit between frontal and nasal regions. However, most of the extensive mobility of the snake jaw results from changes in skull design in the lateral bones. Both upper and lower temporal bars are lost, thus removing

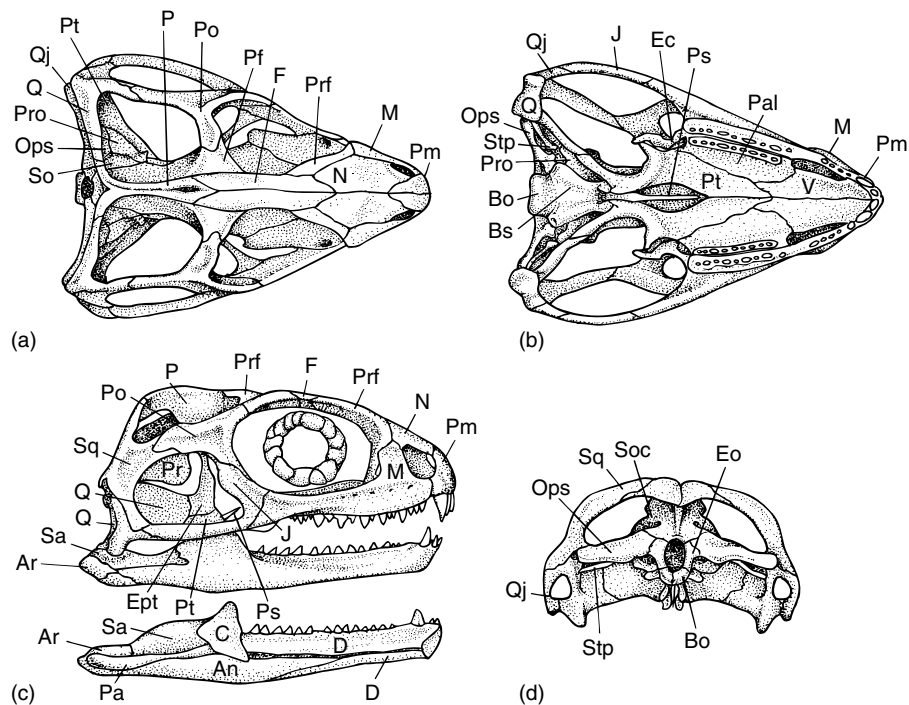


FIGURE 7.38 Living rhynchocephalian. The two temporal fenestrae are still bounded by bone in *Sphenodon*, a living diapsid. Dorsal (a), ventral (b), lateral (c), and posterior (d) views. Abbreviations: angular (An), articular (Ar), basioccipital (Bo), basisphenoid (Bs), coronoid (C), dentary (D), ectopterygoid (Ec), exoccipital (Eo), epipterygoid (Ept), frontal (F), jugal (J), maxilla (M), nasal (N), opisthotic (Ops), parietal (P), prearticular (Pa), palatine (Pal), postfrontal (Pf), premaxilla (Pm), postorbital (Po), prefrontal (Prf), prootic (Pro), parasphenoid (Ps), pterygoid (Pt), quadrate (Q), quadratojugal (Qj), surangular (Sa), supraoccipital (Soc), squamosal (Sq), stapes (Stp), vomer (V).

After Carroll.

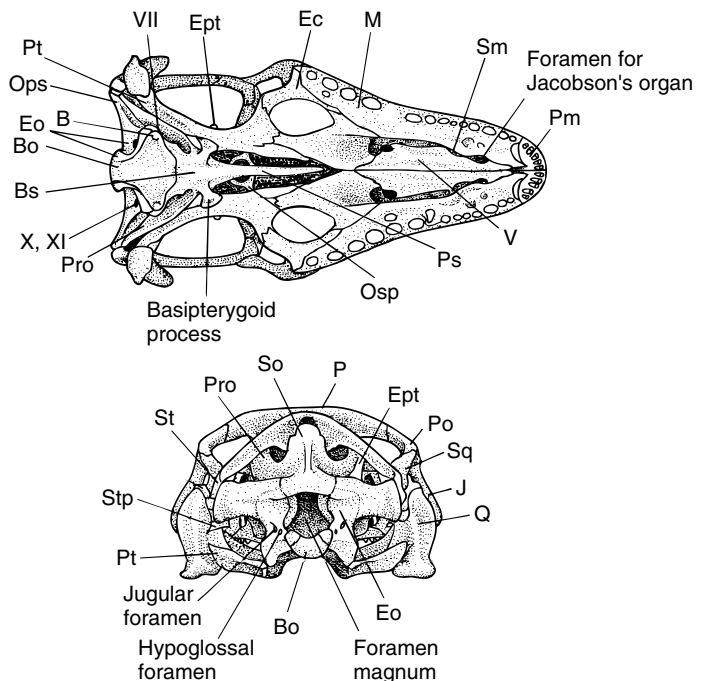
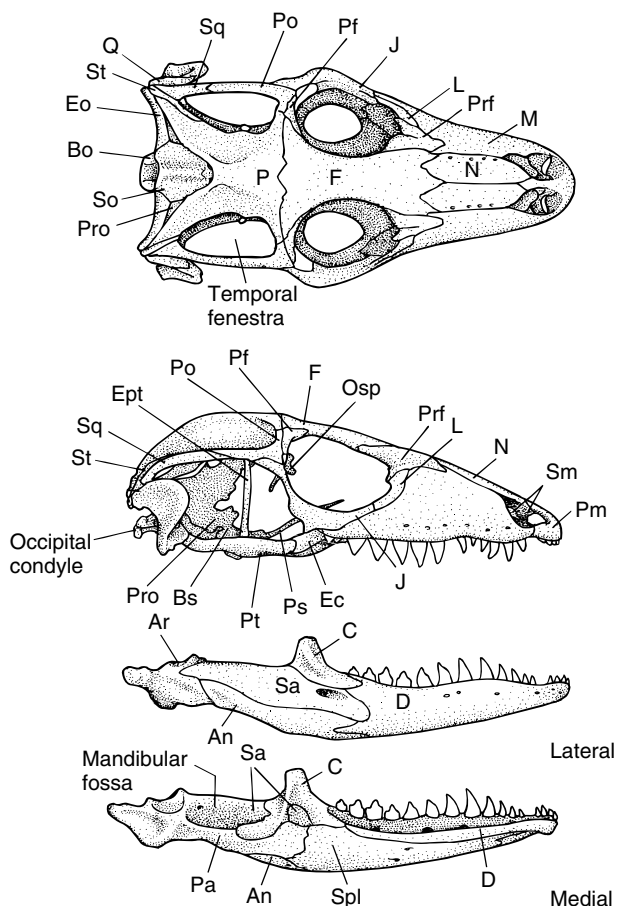


FIGURE 7.39 Lizard skull. Lizards are modified diapsids. Two fenestrae are present, but the ventral bony border of the lower fenestra is absent, a result of changes serving increased cranial kinesis. Abbreviations: angular (An), articular (Ar), basioccipital (Bo), basisphenoid (Bs), coronoid (C), dentary (D), ectopterygoid (Ec), exoccipital (Eo), epipterygoid (Ept), frontal (F), jugal (J), lacrimal (L), maxilla (M), nasal (N), opisthotic (Ops), orbitosphenoid (Osp), parietal (P), prearticular (Pa), postfrontal (Pf), premaxilla (Pm), postorbital (Po), prefrontal (Prf), parasphenoid (Ps), prootic (Pro), pterygoid (Pt), quadrate (Q), surangular (Sa), septomaxilla (Sm), splenial (Sp), supraoccipital (So), squamosal (Sq), supratemporal (St), stapes (Stp), vomer (V).

After Jollie.

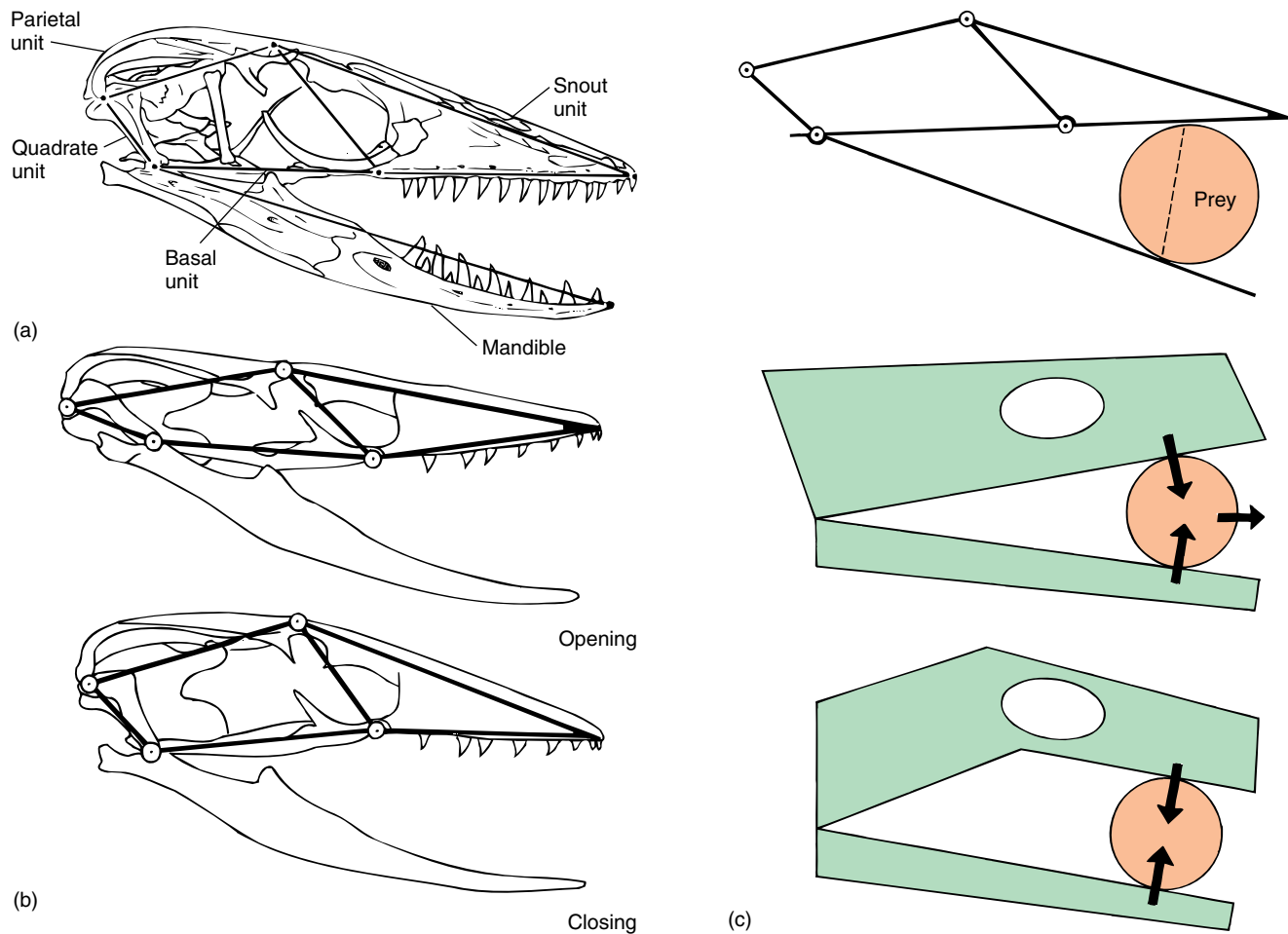


FIGURE 7.40 Kinesis of a lizard skull. (a) Joints within the skull allow the snout to lift upward or bend downward about its mesokinetic articulation with the rest of the braincase. This results in a change in the angle of closure of the teeth when the animal grabs its prey. (b) These movable units of the lizard skull can be represented as a kinematic mechanism by linkages (heavy lines) and points of rotation (circles). Compared with the rest position of these linkages (a), geometric changes are shown during opening (middle) and closing (bottom) on the prey. (c) The functional significance of cranial kinesis in lizards is related to the resulting change in angle of tooth rows. Kinesis bends the snout so that both rows close directly on the prey (bottom). Were this not the case (middle and top), jaw closure would be more of a scissors action, tending to squirt the prey back out of the mouth.

Based on the research of T. H. Frazzetta.

struts that in other diapsid skulls form restrictive braces across the temporal region. The kinematic machinery of the snake skull includes more elements than the linkage system of lizards (figure 7.43a–c). The quadrate, as in lizards, is streptostylic but more loosely articulated with the pterygoid. Muscle forces imparted directly to the pterygoid are transmitted to the tooth-bearing maxilla via the linking ectopterygoid. The maxilla rotates upon the prefrontal, from which it is suspended from the braincase. In many snakes, especially in advanced venomous snakes such as vipers, the prefrontal and supratemporal also enjoy some degree of rotation upon the braincase. Thus, the kinetic system can be modeled on a linkage chain with up to six links (supratemporal, quadrate, pterygoid, ectopterygoid, maxilla, prefrontal) suspended at either end from a seventh link, the braincase (figure 7.43d).

The mandible of snakes, suspended from the quadrate, includes a tooth-bearing dentary that articulates with a posterior **compound bone** derived from the fused surangular and angular. A tiny splenial is usually present on the medial side. Both halves of the lower jaw are joined at the mandibular symphysis, not by bony fusion but by flexible soft tissues that unite the tips of the mandible. Mandibular tips thus enjoy independent movement. Because there are no bony cross connections between chains of movable bones on left and right sides, each kinematic set of linkages can spread and move independently of the other on the opposite side. This is particularly important during swallowing when alternating left and right sets of bones are walked over the prey (see figure 7.63). It is a mistaken view that snakes “unhinge” their jaws when they swallow. Instead, the

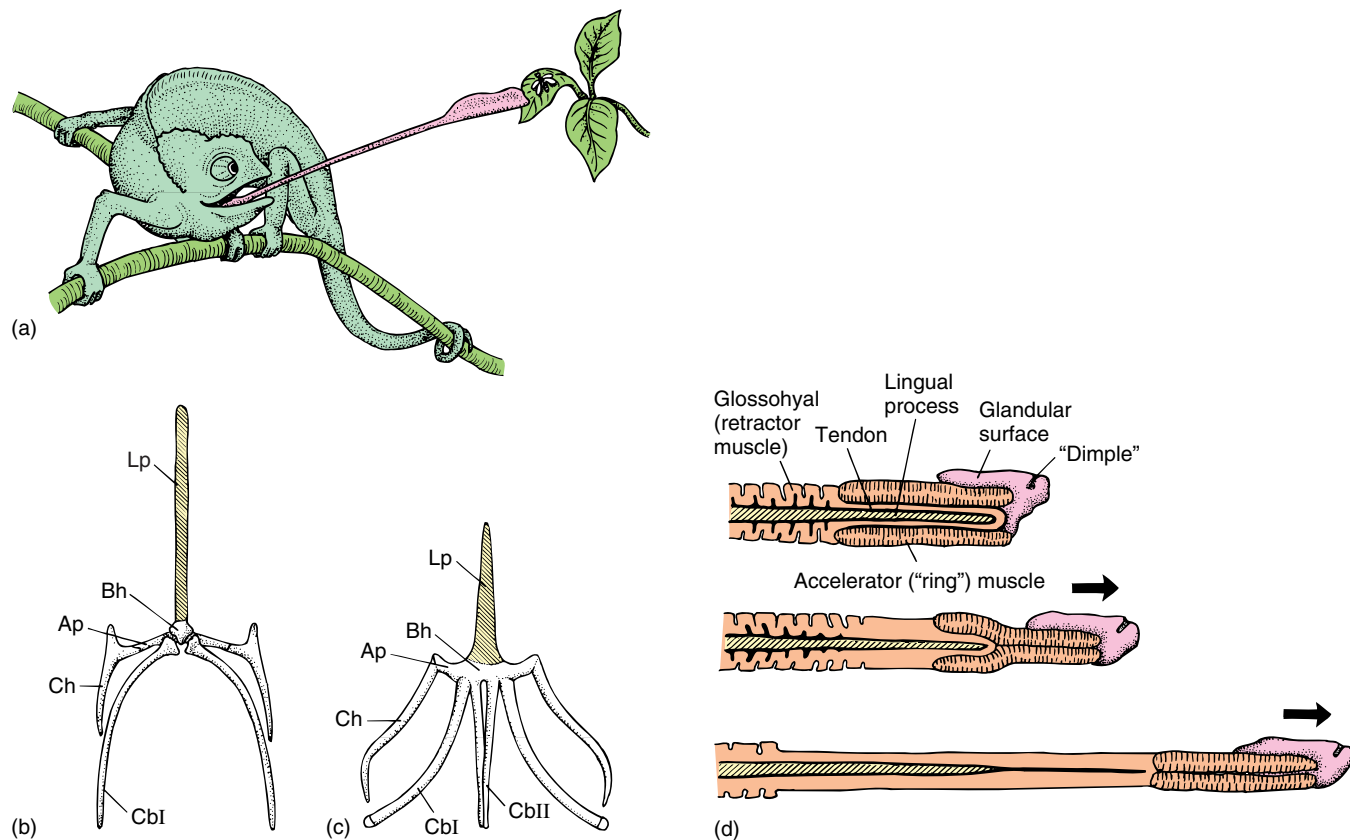


FIGURE 7.41 Lingual feeding in lizards. (a) Jackson's chameleon uses its projectile tongue to "shoot" long distances at prey. (b) Hyoid apparatus of the chameleon includes an elongated lingual process (Lp) along which the tongue slides during launch. (c) Hyoid apparatus of a lizard without a projectile tongue. (d) Mechanical basis of tongue projection. The accelerator muscle, a circular band around the lingual process, contracts to squeeze the lingual process. The squeeze of accelerator muscles causes the muscle to slide rapidly toward the tip of the lingual process, carrying with it the glandular surface of the tongue. With gathered momentum, the tongue is launched from the lingual process toward the prey. The folded glossohyal muscle attached to the tongue's tip is carried out as well and eventually is responsible for retrieving the tongue and the adhering prey. Abbreviations: anterior process (Ap), basihyal (Bh), ceratobranchials I and II (CbI and CbII), ceratohyal (Ch), lingual process (Lp).

(b,c) After Bramble and Wake.

great freedom of rotation between elements of the kinematic chains, the independent movement of each, and the ability of flaring the flexible jaws outward to accommodate bulky prey all account for the suppleness of snake jaws. These processes, not disarticulation, permit snakes to swallow (although slowly) relatively large, whole prey.

Crocodylians, together with *Sphenodon* and squamates, represent the surviving reptiles with a diapsid skull. The crocodilian skull is a composite of chondro-, dermato-, and splanchnocranial elements, although the dermatocranium tends to predominate (figure 7.44). Both temporal bars are present, and the skull is firm, without any evidence of cranial kinesis. However, crocodile ancestors possessed kinetic skulls, suggesting that modern forms have lost this feature. Further, crocodiles possess a secondary palate, a further departure from diapsid ancestors. Within the roof of the mouth, marginal bones (premaxilla, maxilla, palatine) grow inward to meet at the midline beneath the sphenoid region.

Together with the pterygoid, these marginal bones produce the bony secondary palate that separates the nasal passage-way from the mouth.

Birds

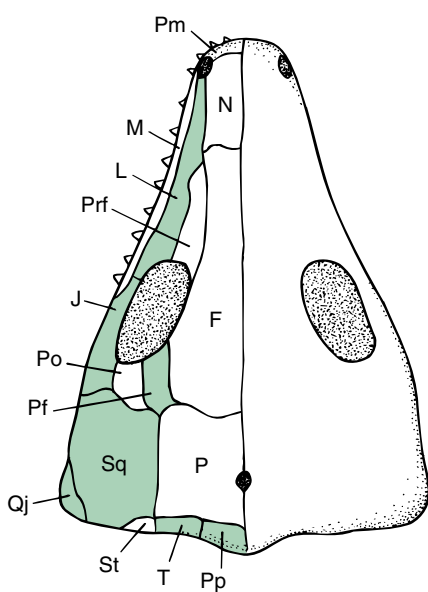
Birds also arise from a diapsid ancestry, but like squamates, they show considerable modification of this skull pattern (figure 7.45). The braincase is much inflated and ossified in birds, accommodating a relatively expanded brain within. Sutures between bones are usually overgrown in the adult so that boundaries are not easily delineated. The palatal bones are quite varied, but generally all show some degree of reduction and lightening. Vomers and ectopterygoids are small, pterygoids are short struts articulating with the quadrate, and epipterygoids are usually lost (figure 7.46a–d).

Like turtles and some dinosaurs, birds are toothless, and their jaws are covered by keratinized sheaths. Birds that feed on slippery prey, such as fish-eating shorebirds, have

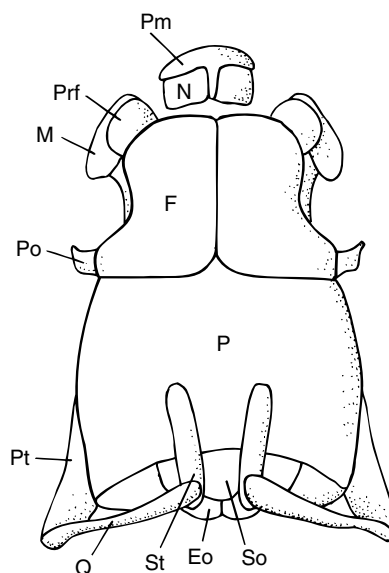
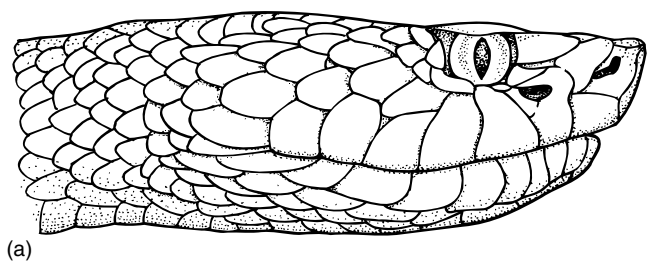
FIGURE 7.42

Diagrammatic comparison of a derived modern snake skull with an amniote skull. Bones lost in the modern snake are indicated by shading in the primitive captorhinomorph.

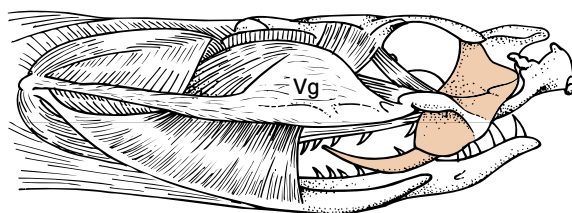
Abbreviations: exoccipital (Eo), frontal (F), jugal (J), lacrimal (L), maxilla (M), nasal (N), parietal (P), postfrontal (Pf), premaxilla (Pm), postorbital (Po), postparietal (Pp), prefrontal (Prf), pterygoid (Pt), quadrate (Q), quadratojugal (Qj), supraoccipital (So), squamosal (Sq), supratemporal (St), tabular (T).



Primitive amniote

Derived reptile
(viperid snake)

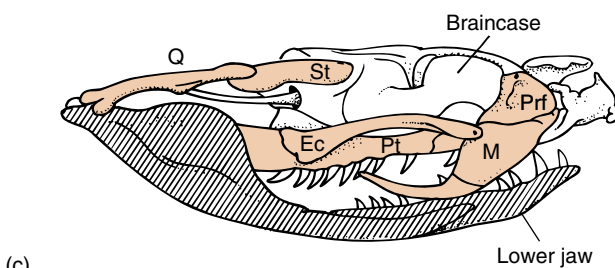
(a)



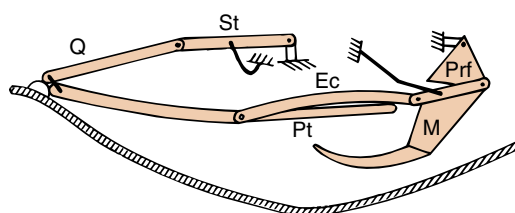
(b)

FIGURE 7.43 Kinematic model of movable skull bones in a venomous snake, the water moccasin. Whole head (a) with successive removal of skin and muscles (b) reveals bones of the skull (c). Linkage bones movable relative to the braincase are in color; lower jaw is crosshatched. (d) Biomechanical model of movable bones rotatable about pin connections. Movable bones include the ectopterygoid (Ec), maxilla (M), pterygoid (Pt), prefrontal (Prf), quadrate (Q), supratemporal (St). Location of the main venom gland (Vg) is shown as well.

After Kardong.



(c)



(d)

BOX ESSAY 7.3

Striking Features of Snakes

The jaws of snakes are highly kinetic, with great freedom of motion. Skull bones that in other reptiles are fixed to the braincase or have restricted movement are joined in snakes into linked chains with extensive motion relative to the braincase. Further, the series of linked bones on left and right sides are not joined directly; so they experience independent displacement, a feature allowing alternating left and right reciprocating motion of jaw bones over the prey

being swallowed. This independent motion and outward spreading of the jaws (not “unhinging” of the jaws) allows most snakes to swallow large prey. Little by little, the distended jaws are walked in alternating steps over the prey until it is completely engulfed.

During the rattlesnake strike, the forward swing of these linked bones erects the maxilla and the fang it carries into position to inject venom into the prey. Snake

fangs are modified teeth with hollow cores so that venom flows from their base into the prey. The fangs of most venomous snakes are longer than other teeth in the mouth, and the fangs of vipers and pit vipers are especially long. Extensive rotation of the fangbearing maxilla in such snakes allows this long fang to be folded up and out of the way along the upper lip when it is not in use.

beaks whose keratinized margins are serrated to improve friction grip. The jaws are drawn out into a **beak**. The upper temporal bar is absent, and the lower temporal bar is a slender rod called the jugal bar (quadratojugal-jugal bar), which extends from the beak posteriorly to the side of the movable (streptostylic) quadrate. The skull is prokinetic. A strong **postorbital ligament** extends from behind the eye to the lower jaw. In neognathous birds, the palate is functionally divided at the pterygo-palatine joint (figure 7.47a,b). The converging paired pterygoids meet or nearly meet at the midline to couple there with the palatines (figure 7.47b). At this coupling, these bones form a joint that slides along the ventral edge of the orbital septum. The nasofrontal and palato-maxilla joints are thin, flexible, bony joints, not synovial, but they can be represented as hinges about which rotation occurs. The mechanically important bones are modeled as a linkage system on each side (figure 7.47c). When inserting muscles pull the quadrate and palate forward, the divided palate slides along the septum pushing the palatines forward, which in turn push against the base of the beak, rotating it about the nasofrontal joint, and raising the beak. The coupled pair of gliding linkages is a **slider-crank mechanism**. (Muscles acting directly on the lower jaw activate its opening.) Jaw-closing muscles act in the opposite fashion to move the beak downward to grasp food, and return the kinetic machinery to the rest position. The thin jugal bar usually bows outward during jaw opening, but does not contribute significantly to the mechanism producing upper jaw elevation.

Many birds use their beak like a probe to reach buried grubs or insects embedded in tree bark or soft soil. Such birds often use a form of rhynchokinesis, the lifting of the beak tips about points of rotation within the jaws (figure 7.47e). The jaws need not be parted far to seize the food. Other birds have beaks that open tough seeds and short, stout jaws that concentrate closing forces at the base of their beaks.

In paleognathous birds, the pterygoids do not meet at the midline, but slide on projecting struts, the basipterygoid processes (figure 7.47d). So structurally distinct is the palate,

that it has been used to argue that all paleognaths (ratites and tinamous) represent a primitive condition and a monophyletic group.

Synapsids

Primitive Synapsids *Dimetrodon* represents a primitive synapsid. Therapsids continue the synapsid line and exhibit considerable diversity (figure 7.48). For a time in the Permian and early Triassic, they were fairly abundant. Some were herbivores; most were carnivores. Most skull bones of early amniotes persist, but characteristic of synapsids, the temporal region develops a single opening bound horizontally along its lower border by a bony connection between jugal and squamosal bones. In advanced therapsids and primitive mammals, the vertical bar dividing the orbit from the single temporal fenestra is lost, leaving the narrow bony connection between jugal and squamosal bowing outward in the cheek region. This bony squamosal-jugal bar is now commonly called the **zygomatic arch**. Within therapsids, there is a tendency for the temporal opening to move dorsally and for the zygomatic arch to become delineated.

Mammals The skull of mammals represents a highly modified synapsid pattern. Various dermal elements are lost in therian mammals, including the prefrontal, postorbital, postfrontal, quadratojugal, and supratemporal (figure 7.49). The postparietals, typically paired in reptiles, fuse into a single, medial **interparietal** in therapsids, which in mammals may incorporate the tabular and fuse with the occipital bones. Monotremes retain several early synapsid skull features, including prefrontal, postfrontal, and pleurospenoid bones together with unfused occipitals. Monotremes are somewhat specialized as well. The lacrimal of therians is absent in them, and the jugal bones are small (figure 7.50a–d). A tympanic ring encircles the middle ear bones of monotremes, but in most therians, this ring has expanded into a large swollen capsule, the **auditory bulla**, that houses the middle ear ossicle (figure 7.51a–c).

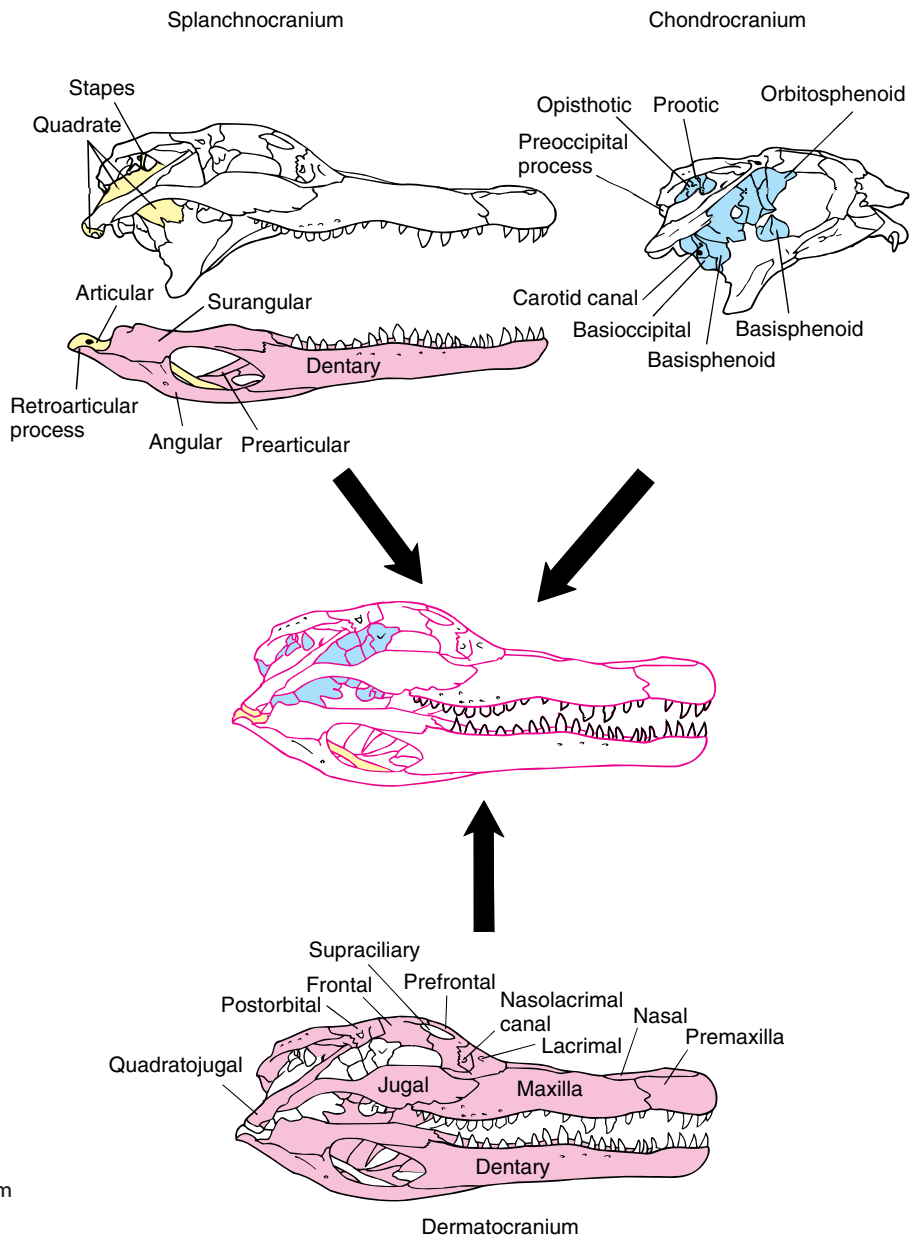


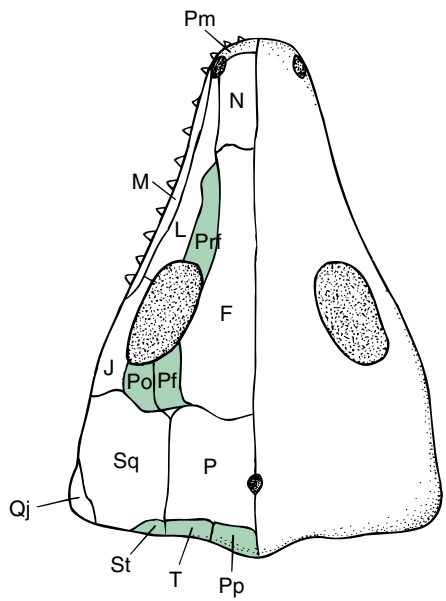
FIGURE 7.44 Alligator skull. A composite skull design characteristic of vertebrates. The skull is a combination of elements receiving contributions from the chondrocranium (blue), the splanchnocranium (yellow), and the dermatocranium (red).

Placental Mammals Fusions between separate centers of ossification produce composite bones in the skull of placental mammals. The single occipital bone represents the fusion of basioccipital, paired exoccipitals, supraoccipital, and interparietal (and perhaps tabular) (figure 7.52a). The occipital bone defines the foramen magnum and closes the posterior wall of the braincase. As in monotremes and marsupials, there is a ventrally located, bilobed occipital condyle that articulates with the **atlas**, the first vertebra of the cervical region. Dorsally, a raised **nuchal crest** may form across the back of the occipital region, offering a secure attachment site for neck muscles and ligaments that support the head.

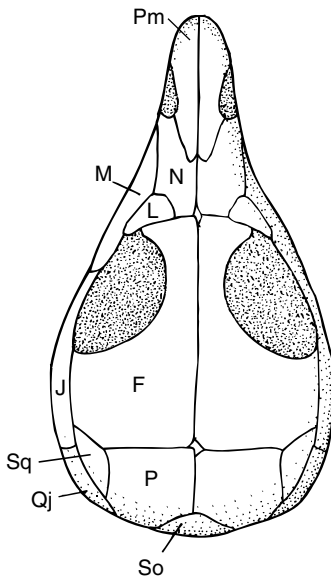
Several embryonic centers contribute to the sphenoid bone, representing the orbitosphenoid, presphenoid, basisphenoid, and a large alisphenoid (the epipterygoid of lower vertebrates) (figure 7.52b).

On the side of the braincase behind the orbit, a large **temporal** bone is formed by the fusion of contributions from all three parts of the skull (figures 7.52c and 7.53). The dermatocranium contributes the squamosal and the **tympanic bulla** (a derivative of the angular) in many mammals. The chondrocranium contributes the **petrosal**, itself a derivative of prootic and opisthotic bones (figure 7.52c). The petrosal often bears a ventrally directed projection, the **mastoid process**. The splanchnocranium contributes three tiny middle ear bones (malleus, incus, stapes) and the styloid (figure 7.54).

In most tetrapods, the nasal capsule remains unossified. However, in mammals, the ethmoid portion ossifies to form scroll-like **turbinates** (turbinals, conchae). There are usually three sets of turbinates attached to respective neighboring bones: the **nasoturbinate**, **maxilloturbinate**, and

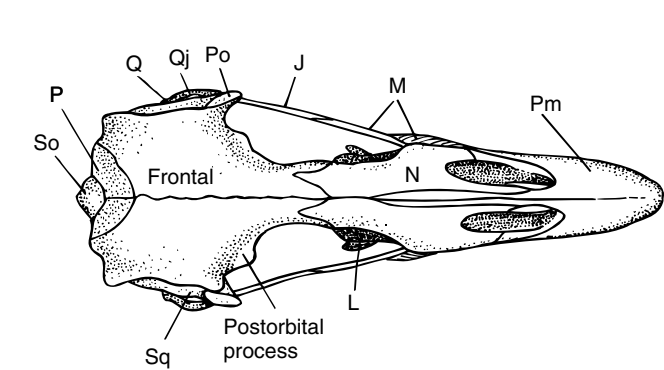


Primitive amniote

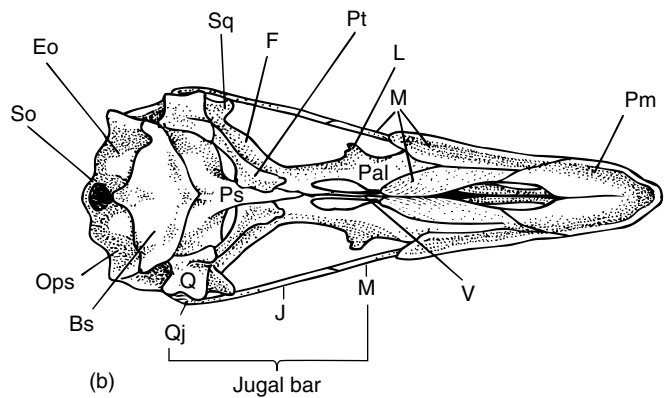


Bird

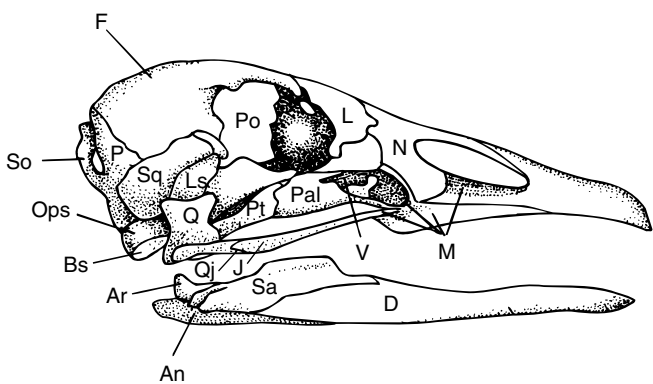
FIGURE 7.45 Diagrammatic comparison of a derived bird skull with a primitive amniote. Bones lost in birds are shaded in the primitive reptile. Abbreviations: frontal (F), jugal (J), lacrimal (L), maxilla (M), nasal (N), parietal (P), postfrontal (Pf), premaxilla (Pm), postorbital (Po), postparietal (Pp), prefrontal (Prf), quadratojugal (Qj), supraoccipital (So), squamosal (Sq), supratemporal (St), tabular (T).



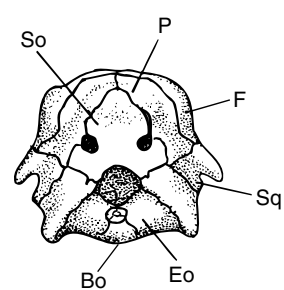
(a)



(b)



(c)



(d)

FIGURE 7.46 Bird skull. In the adult bird, sutures between skull bones fuse to obliterate identifiable borders. Dorsal (a), ventral (b), lateral (c), and posterior (d) views of the skull of a young gosling (*Anser*) before bones fuse. Abbreviations: angular (An), articular (Ar), basioccipital (Bo), basisphenoid (Bs), dentary (D), exoccipital (Eo), frontal (F), jugal (J), lacrimal (L), laterosphenoid (Ls), maxilla (M), nasal (N), opisthotic (Ops), parietal (P), palatine (Pal), premaxilla (Pm), postorbital (Po), parasphenoid (Ps), pterygoid (Pt), quadrate (Q), quadratojugal (Qj), surangular (Sa), supraoccipital (So), squamosal (Sq), vomer (V).

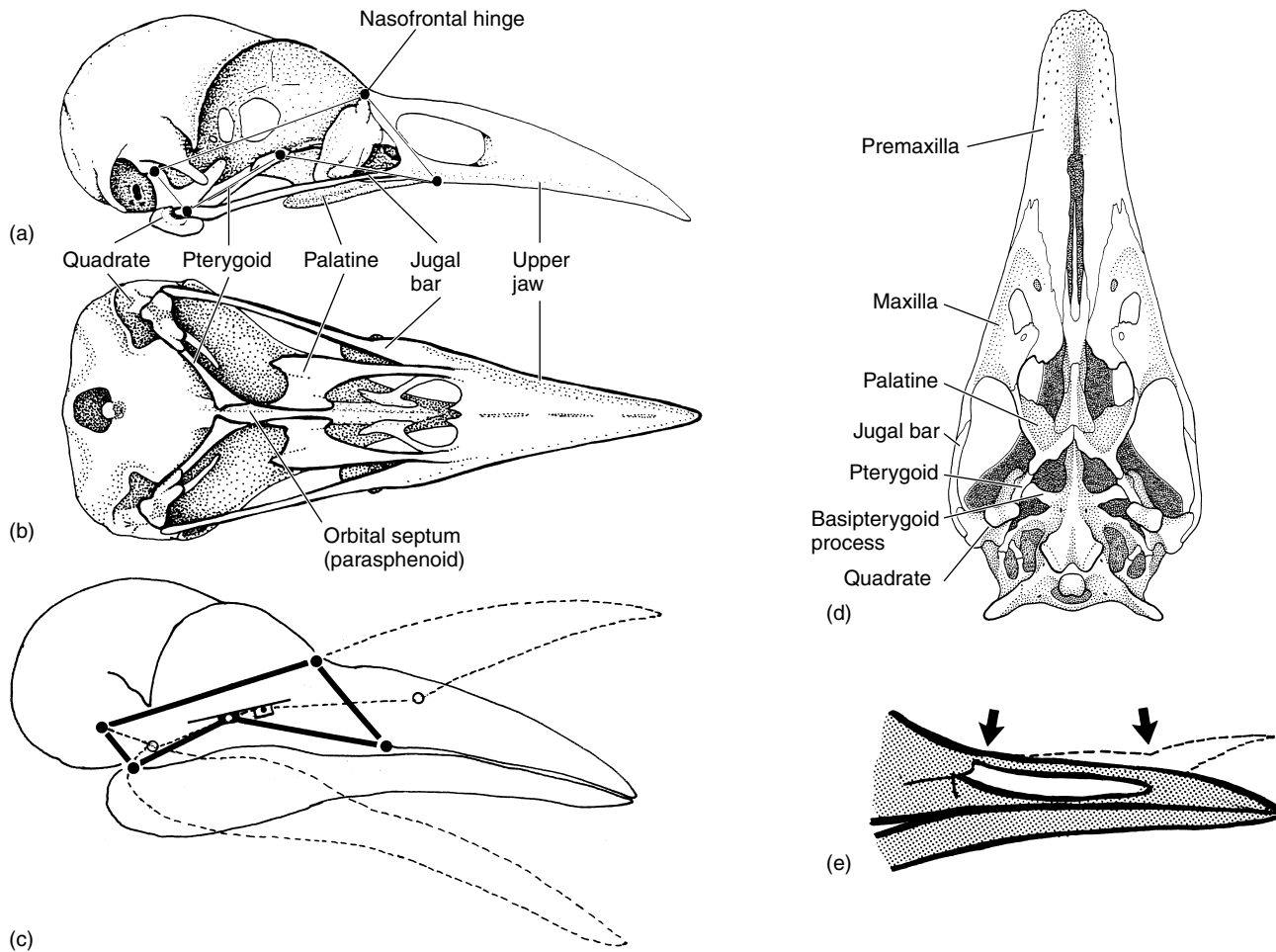


FIGURE 7.47 Cranial kinesis in the crow skull (*Corvus*). (a) Lateral view. (b) Ventral view. (c) Linkage model of cranial kinesis, slider-crank mechanism. From the rest position (solid lines), the point of coupling between pterygoids and palatines slides forward along the orbital septum to a new position (dashed lines), which lifts the upper jaw about the prokinetic joint (nasofrontal hinge). (d) Paleognath. Ostrich palate. (e) Rhynchokinesis. Flexions within the beak permit the tips of the upper and lower jaws to part without opening of the entire mouth.

ethmoturbinate. The coiled walls of the turbinates support the mucous membrane within the nasal passage. Air entering these passages is warmed and moistened before reaching the lungs, functions that are especially important in endotherms. Absent in ungulates but present in most other orders, such as rodents, carnivores, and primates, is another region of the nasal capsule, the mammal **mesethmoid**. This element forms the septum between the nasal capsules and usually remains cartilaginous. Between the nasal area and cranial cavity stands the transverse and finely perforated **cribriform plate** (figure 7.54). Olfactory nerves originating in the olfactory epithelium of the nasal capsule pass through this plate to reach the olfactory bulb of the brain.

Middle Ear Bones Two profound changes in the lower jaw mark the transition from therapsid to mammal (figure 7.55). Both changes go hand in glove. They result in such an alteration in skull design that some anatomists doubted them until the surprisingly good fossil record made the evolution-

ary transition undeniable. One of these changes is the loss of the postdentary bones of the lower jaw. The other is the presence of three middle ear bones. In vertebrates, the inner ear is embedded deep within the otic capsule and holds the sensory apparatus responsive to sounds. The hyomandibula or its derivatives deliver sound vibrations to the sensitive inner ear. In all tetrapods, the hyomandibula tends to become reduced to a slender, light bone called the stapes (= columella). Sometimes there is a second hyomandibula-derived bone, the **extracolumella**. The stapes is usually suspended in the middle ear cavity where damping by restrictive attachments is minimized. As sounds set the tympanum into motion, these vibrations are imparted to the small, responsive stapes. Its opposite end often expands to reach the sensitive inner ear apparatus that responds to the vibrations the stapes delivers.

In mammals, two tiny, additional bones join the stapes in the middle ear. Together these bones transmit sound to the inner ear. Specifically, these three middle ear bones are

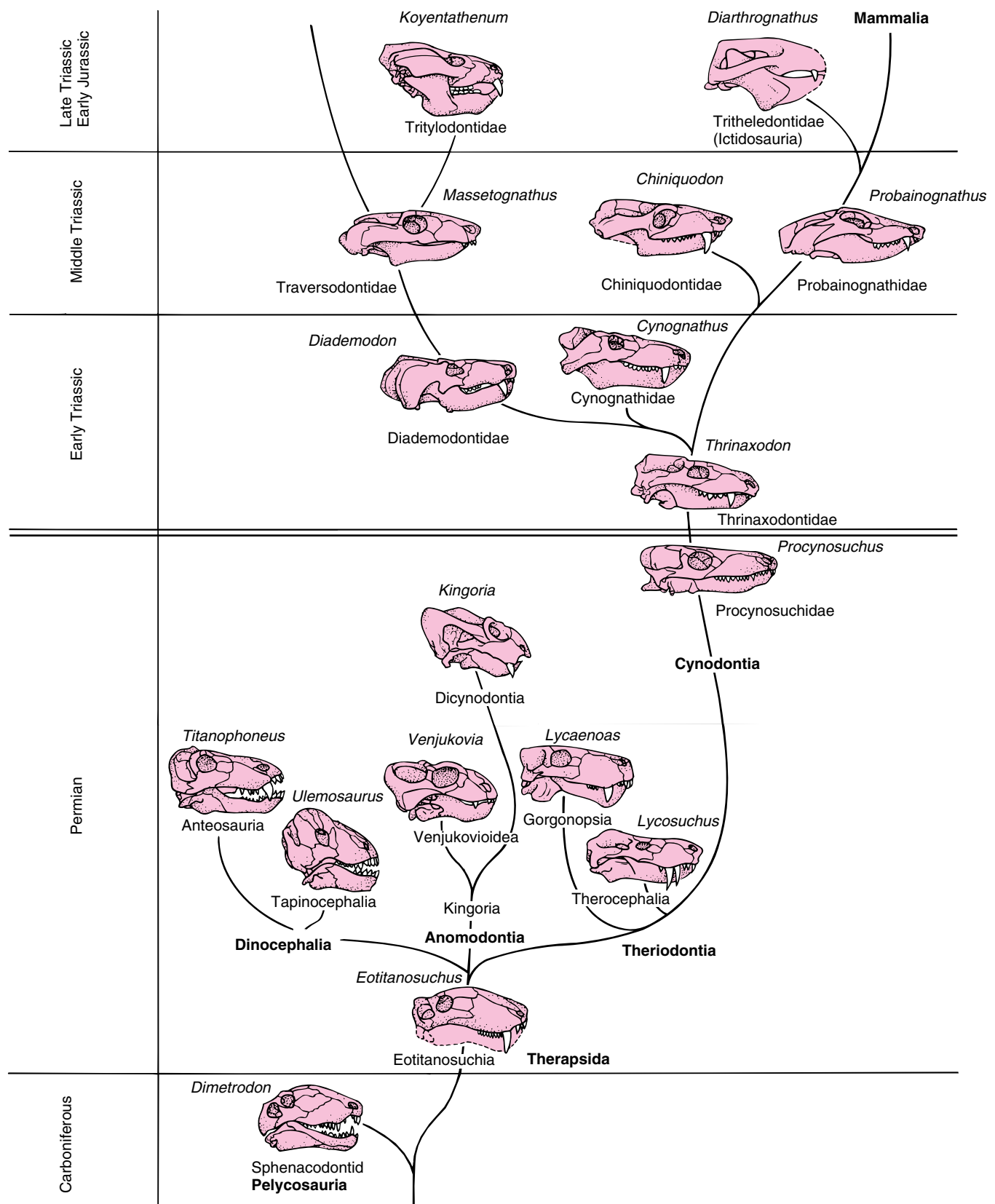


FIGURE 7.48 Radiation of therapsids. Therapsids continue the synapsid line and exhibit considerable diversity. For a time in the Permian and early Triassic, they were fairly abundant. Some were herbivorous; most were carnivorous.

Based on the research of James A. Hopson.

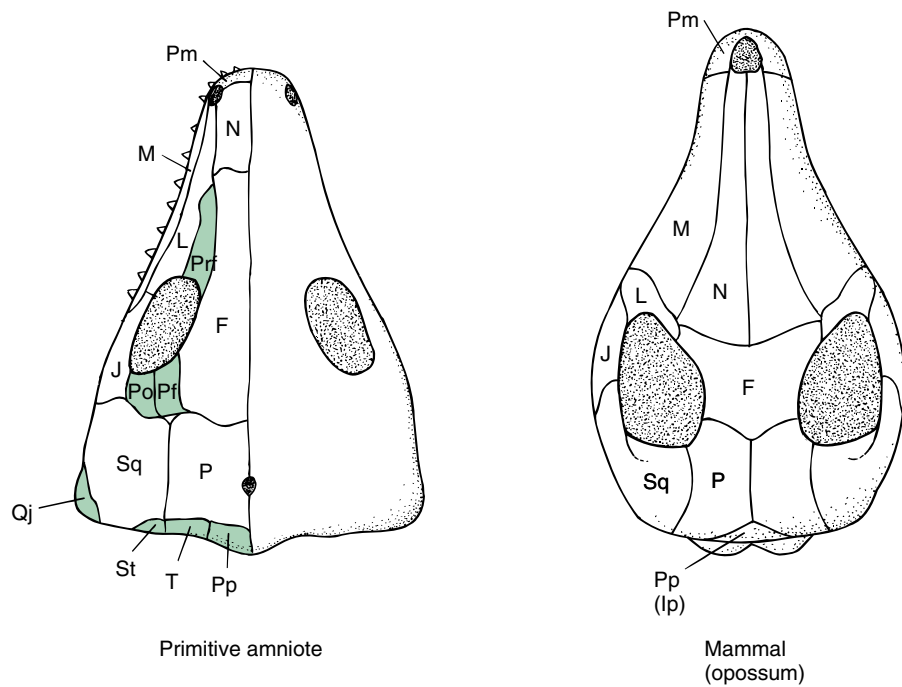


FIGURE 7.49 Diagrammatic comparison of a derived mammal skull with a primitive amniote skull.

Bones lost in the derived mammal are shaded in the primitive amniote. In mammals, orbital and temporal openings merge. Abbreviations: frontal (F), jugal (J), interparietal (Ip), lacrimal (L), maxilla (M), nasal (N), parietal (P), postfrontal (Pf), premaxilla (Pm), postorbital (Po), postparietal (Pp), prefrontal (Prf), quadratojugal (Qj), squamosal (Sq), supratemporal (St), tabular (T).

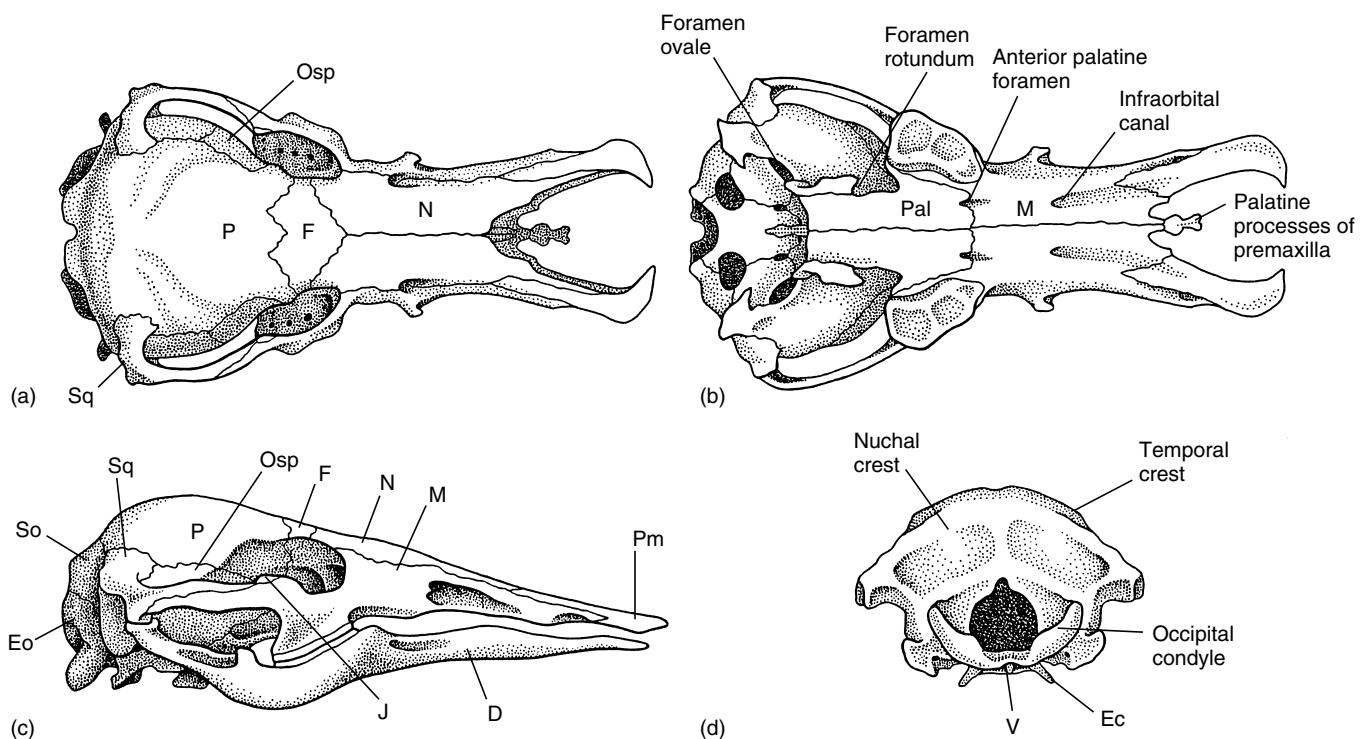


FIGURE 7.50 Monotreme, skull of the duckbill platypus *Ornithorhynchus*. Dorsal (a), ventral (b), lateral (c), and posterior (d) views. Abbreviations: dentary (D), ectopterygoid (Ec), exoccipital (Eo), frontal (F), jugal (J), maxilla (M), nasal (N), orbitosphenoid (Osp), parietal (P), palatine (Pal), premaxilla (Pm), supraoccipital (So), squamosal (Sq), vomer (V).

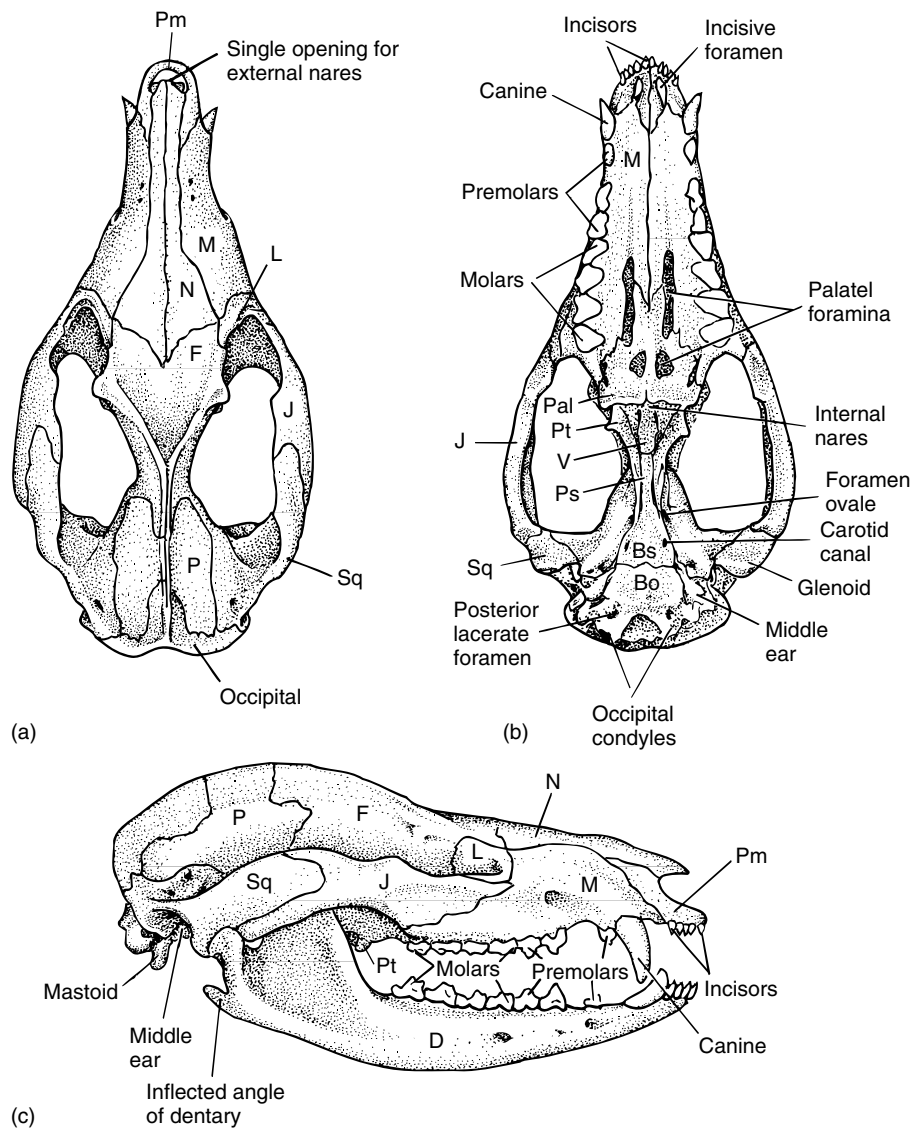


FIGURE 7.51 Marsupial, skull of the opossum *Didelphis*. Dorsal (a), palatal (b), and lateral (c) views. Abbreviations: basioccipital (Bo), basisphenoid (Bs), dentary (D), frontal (F), jugal (J), lacrimal (L), maxilla (M), nasal (N), parietal (P), palatine (Pal), premaxilla (Pm), parasphenoid (Ps), pterygoid (Pt), squamosal (Sq).

After Carroll.

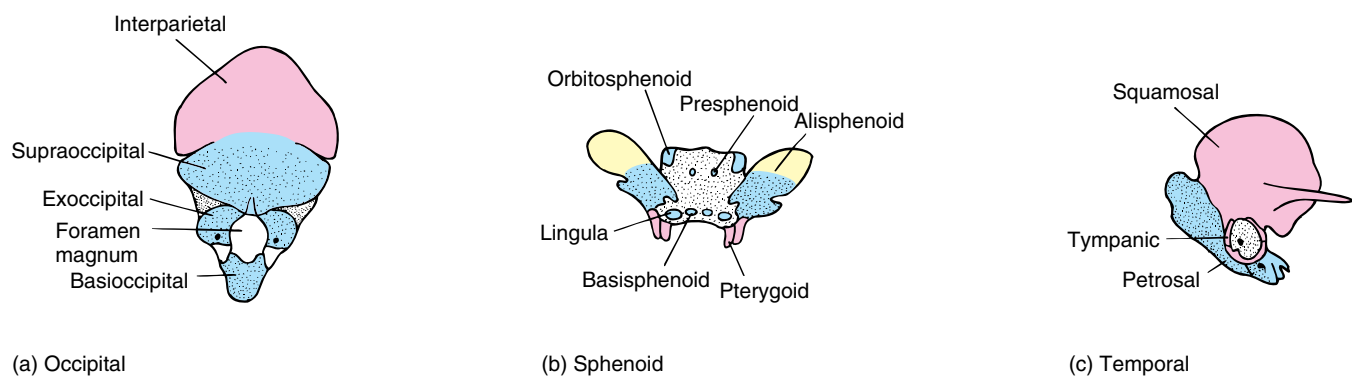


FIGURE 7.52 Composite bones of the placental mammal skull during embryonic development, *Homo sapiens*. (a) Occipital bone has centers of ossification that include the interparietal (postparietal), supraoccipital, paired exoccipital, and the basioccipital. (b) The sphenoid bone is a fusion of the orbitosphenoid, presphenoid, basisphenoid, pterygoid, and alisphenoid (epipterygoid). In many mammals, these fused bones are joined by parts of the pterygoid and lingula. (c) The temporal bone results primarily from the merger of the squamosal, tympanic, and petrosal (prootic plus opisthotic).

After Hyman.

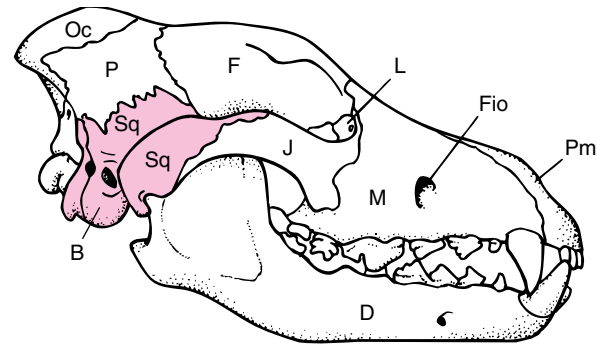
malleus (derived from the articular), incus (derived from the quadrate), and stapes (derived from the hyomandibula). So distinctive is the presence of three middle ear bones, that many anatomists mark the fossil transition to mammals at the point of their acquisition.

Anatomy and function of the ear (p. 696)

Coupled with the derivation of the three middle ear bones are changes in the posterior bones of the mandible. In early synsids (pelycosaurs), the lower jaw includes the tooth-bearing dentary in addition to several postdentary bones (angular, articular, coronoid, prearticular, splenial, surangular) (figure 7.56). In derived synsids (mammals), this set of postdentary bones has been entirely lost from the lower jaw, and the dentary has enlarged to assume the exclusive role of lower jaw function. From pelycosaur to therapsid to mammal, the anatomical details of these changes are well documented in an ordered time sequence by the fossil record. In pelycosaurs, the articular (future malleus) resides at the back of the mandible and establishes lower jaw articulation with the quadrate (future incus). In early to later therapsids, these two bones become reduced, along with the postdentary bones, eventually moving out of the lower jaw and taking up a position in the middle ear. The functional reason for these changes is thought to be related to improved hearing, especially to a wider range of sounds. The phylogenetic reduction in size of these bones would reduce their mass and thus increase their oscillatory responsiveness to airborne vibrations. Their removal from the jaw joint permits their more specialized role in transmitting sound to the inner ear. Alternatively, or along with such changes related to hearing, some morphologists have proposed that changes in feeding style led to changes in the preferred site of insertion of the jaw-closing muscles, specifically a shift forward on the dentary and closer to the teeth. Larger jaw muscles acting close to the tooth row lessen the stresses at the back of the jaw where it articulates with the skull. Loss of postdentary bones then might reflect this shift in forces forward to the tooth row and away from the joint these bones formed.

These changes in the lower jaw were accompanied by changes in the method of food preparation prior to swallowing. Most reptiles bolt their food, swallowing it whole or in large chunks. Mammals typically chew their food before swallowing it, a process termed **mastication**. Mastication also occurs in a few groups of fishes and lizards. But, it is within mammals that feeding strategy is based on mastication of food. If mastication became a more characteristic part of food preparation, then changes in jaw-closing muscles might be expected, with greater emphasis shifting to the dentary.

Secondary Palate and Akinesis In addition to changes in the mammalian lower jaw, the presence of a secondary palate is also related to mastication. The secondary palate includes a **hard palate** of bone and a posterior continuation



Canis dirus

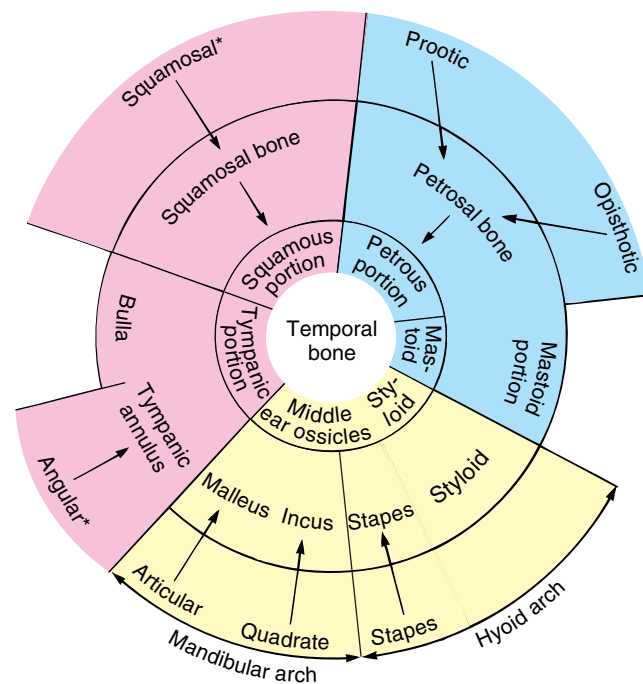


FIGURE 7.53 Mammalian temporal bone. The temporal bone forms phylogenetically from the dermatocranium (angular, squamosal), and chondrocranium (prootic, opisthotic), into which is set contributions from the splanchnocranium (articular, quadrate, stapes, styloid). The separate bony elements in early amniotes (outer circle) contribute to the composite temporal bone of mammals (middle and inner circle). Some of these contributions are dermal bones (*). The otic capsule is buried beneath the surface of the skull, leaving the exposed and often elongated mastoid process. The bulla or auditory bulla forms, at least in part, from the tympanic annulus, itself a phylogenetic derivative of the angular bone. The exposed squamous portion of the temporal bone is illustrated in color on the skull of the Pleistocene wolf *Canis dirus*. Abbreviations: auditory bulla (B), dentary (D), frontal (F), infraorbital foramen (Fio), jugal (J), lacrimal (L), maxilla (M), occipital (Oc), parietal (P), premaxilla (Pm), squamosal (Sq).

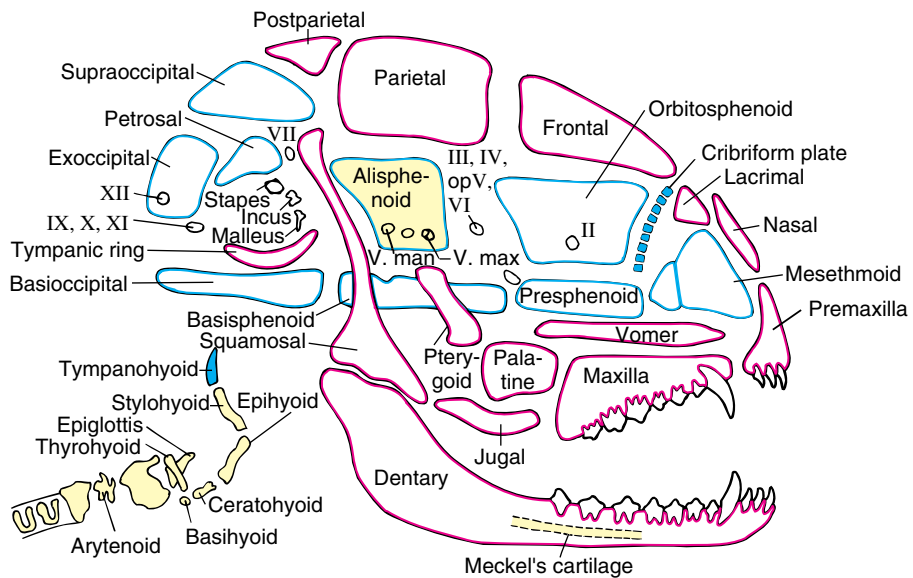


FIGURE 7.54 Diagram of a dog's skull. Sources of the various bones are outlined: dermatocranium (red), chondrocranium (blue), and splanchnocranium (yellow).

After Evans.

of fleshy tissue, the **soft palate** (figure 7.57a,b). The hard palate is formed from the inward growth of bony processes of the premaxilla, maxilla, and palatine that meet at the midline as a bony platform (figure 7.58a–c). This hard palate and its fleshy continuation effectively separate the food chamber below from the respiratory passage above. Some turtles and also crocodilians have a secondary palate, and they benefit from the advantages of separation of routes for food and air. But chewing requires that food stays in the mouth for an extended period of time in mammals; therefore, separation of respiratory and oral passages is especially important. Mastication can proceed without impeding regular breathing. Similarly, the secondary palate completes the firm roof of the food chamber, so that the pumping action of the throat of a suckling infant creates effective negative pressure within the mouth without interfering with the respiratory passage.

Mastication (p. 529)

Mastication in mammals has been accompanied by very precise tooth occlusion to serve the mechanical breakdown of food. Precise, strong occlusion requires a firm skull, so mammals have lost cranial kinesis, leaving them an akinetic skull. The mammalian mandibular condyle fits into a very precise articulation with the squamosal bone. When jaws close about this joint, upper and lower rows of teeth are placed in very precise alignment. This allows specialized teeth to function properly. As a further consequence of precise occlusion, the pattern of tooth eruption in mammals differs from that of most other vertebrates. In lower vertebrates, teeth wear and are replaced continuously (**polyphyodonty**); therefore, the tooth row is always changing. If teeth function primarily to snag prey, this causes little difficulty. However, continuous replacement means that at some location in the jaws, worn teeth are missing or new ones are moving into position. To avoid disruption of occlusion, teeth in most

mammals are not continuously replaced. Mammals exhibit **diphyodonty**. Only two sets of teeth erupt during the lifetime of a mammal, the “milk teeth” of the young and the “permanent” teeth of the adults.

Tooth types and their development (p. 500)

The chain of events leading from mastication to akinesis and to diphyodonty should not be viewed as inevitable. Some fishes chew their food but retain kinetic skulls and polyphyodonty. But evolutionary events that produced the mammalian skull underscore the importance of examining anatomical changes in partnership with functional changes that must accompany phylogenetic modification of vertebrate design. Form and function necessarily go together, an issue to which we next turn.

Overview of Skull Function and Design

The skull performs a variety of functions. It protects and supports the brain and its sensory receptors. It may function to cool the brain during sustained activity or during a rise in environmental temperature. In many active terrestrial mammals, the nasal epithelium lining the nasal passages dissipates excess heat by evaporation as air moves across this moist lining. A similar function has been proposed for the elaborate air passageway in some groups of hadrosaurs, the duck-billed dinosaurs (figure 7.59). Air entering their nostrils would have coursed through intricate passageways formed within premaxilla and nasal bones to provide evaporative cooling. The skull of many animals also supports the voice box and occasionally serves as a sound resonator to deepen or amplify an animal's call. The Weddell seal takes advantage of its jaws to open and maintain its breathing holes in surface ice (figure 7.60).

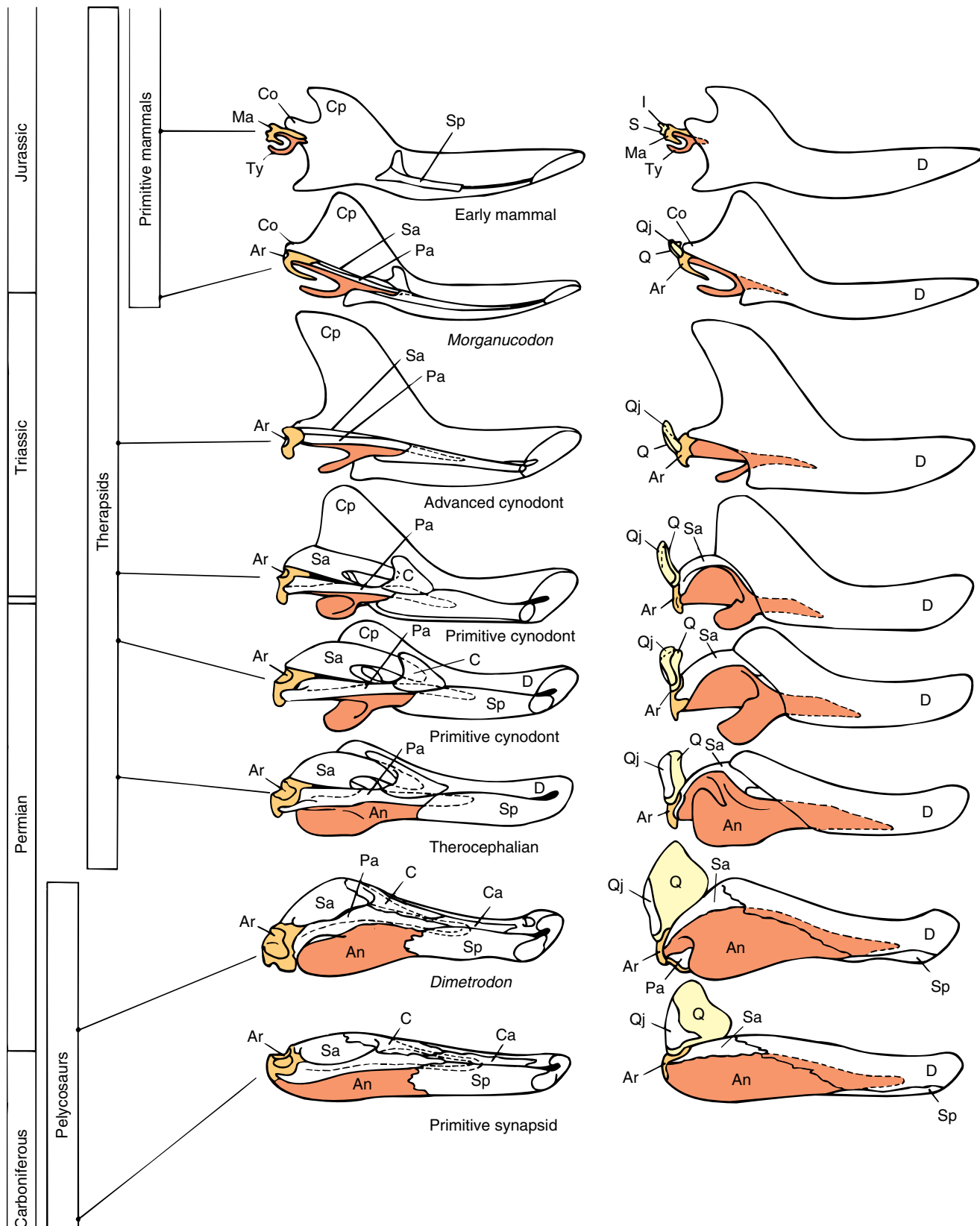


FIGURE 7.55 Evolution of the mammalian middle ear bones. Left column a medial view of the left mandibular ramus; right column lateral view of right mandibular ramus and quadrate. No teeth are shown to make comparisons clear. From primitive pelycosaurs, to therapsids, to the first mammals, changes in the postdentary bones are indicated along with incorporation of the quadrate (incus) and articular (malleus) into the middle ear. The fossil species used to follow these changes are shown in relationship to their occurrence in the geological record. Abbreviations: angular (An), articular (Ar), coronoid (C), anterior coronoid (Ca), condyle of dentary (Co), coronoid process (Cp), dentary (D), incus (I), malleus (Ma), prearticular (Pa), quadrate (Q), quadratojugal (Qj), stapes (S), surangular (Sa), splenial (Sp), tympanic annulus (Ty).

Based on the research of James A. Hopson and Edgar F. Allin.

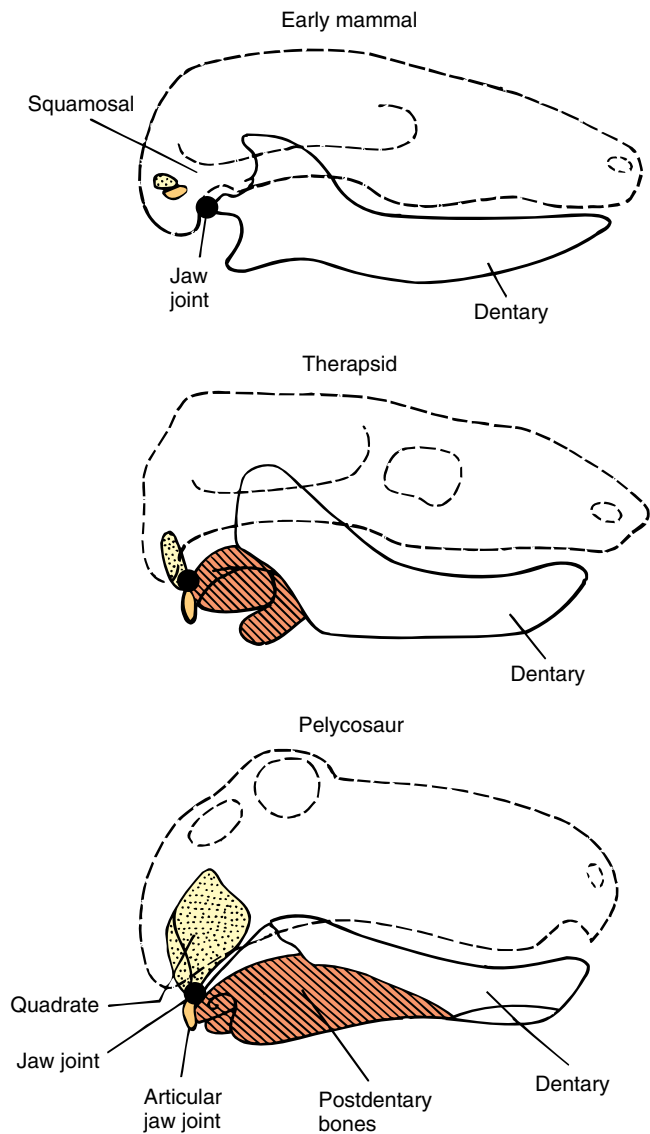


FIGURE 7.56 Changes in jaw articulation during transition from early (pelycosaurs) to late (mammals) synapsids. In mammals, the postdentary bones of the lower jaw are mostly lost and the dentary enlarges. Bones involved in jaw articulation in pelycosaurs, the articular and the quadrate, become reduced and move in to contribute to the inner ear ossicles of mammals. Jaw articulation in mammals is taken over by the dentary and squamosal. The stapes is not shown.

These examples remind us that the skull is a multipurpose “tool” involved in a great variety of functions. Its design reflects and incorporates these multiple roles. Generalizations about skull design and function can be misleading if we ignore its multiple functions. However, if we are cautious, we can understand how skull design reflects fundamental functional problems. The skull primarily functions as part of the feeding system of vertebrates. How it addresses problems of feeding depends largely upon whether feeding occurs in air or in water. Each medium presents different limitations and opportunities. The viscosity of water and the buoyancy of

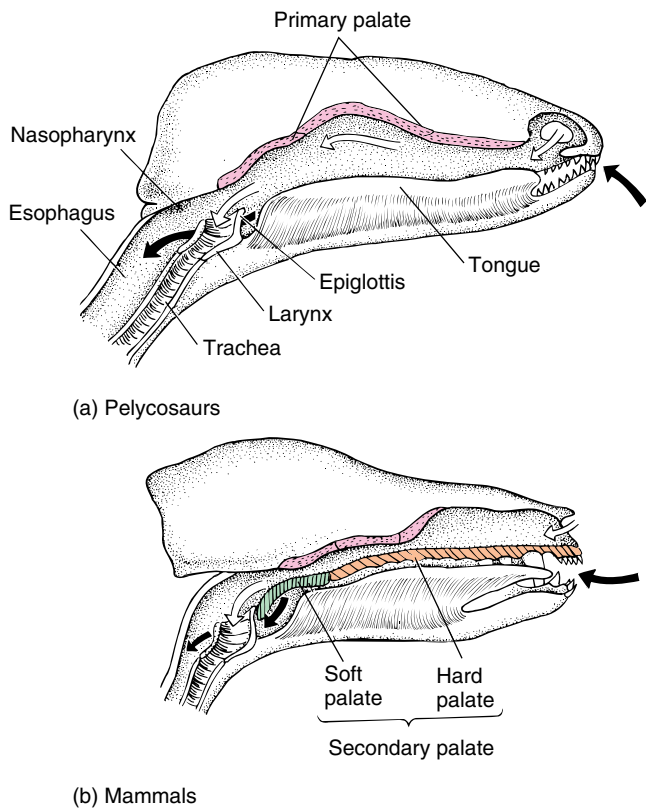


FIGURE 7.57 Secondary palate. (a) In most reptiles, air entering the nostrils and food entering the front of the mouth share a common passage, although each exits differently at the back. Air moves down the trachea, and food travels down the esophagus. (b) In mammals, the routes of air and food are separated from the beginning of their travel by the secondary palate, a structure of bone (hard palate) and soft tissue (soft palate). White arrows indicate the path of air; dark arrows indicate the path of food.

tiny organisms within it mean that water, much more than thin air, contains a richer community of floating planktonic organisms. Suspension feeding and harvesting of these tiny organisms becomes economical, and filter-feeding devices enjoy some adaptive favor. Generally, feeding proceeds in two steps, food capture and then swallowing. We look at each of these in turn.

Prey Capture

Feeding in Water

The first step in feeding is food capture, which depends generally on the medium in which feeding takes place. The higher viscosity of water presents both problems and opportunities for the animal feeding in water. Feeding in water poses a disadvantage in that water easily carries shock or pressure waves (“bow waves”) immediately in front of the predator approaching its food. These pressure waves can arrive an instant before the advancing predator and alert or deflect the intended prey. On the other hand, when a vertebrate quickly

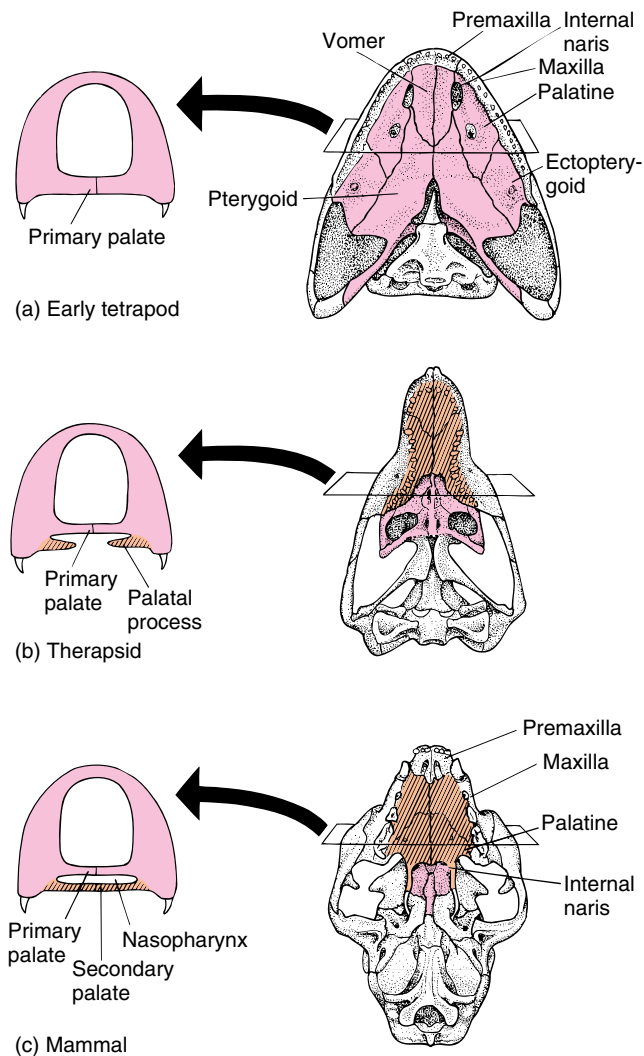


FIGURE 7.58 Evolution of the secondary palate. (a) Early tetrapod with a primary palate in cross section (left) and ventral (right) views. (b) Therapsid with a partial secondary palate formed by the medial extension of the premaxilla and maxilla. (c) Mammal with a secondary palate that, in addition to extensions of the premaxilla and maxilla, includes part of the palatine bone.

After Smith.

gulps water into its mouth, the viscosity of the water drags along the prey as well. This viscosity makes **suction feeding**, used with relatively large prey, possible.

To capture small foods, aquatic animals use **suspension feeding**. The density of water gives it the viscosity to retard the fall of particulate material out of suspension. Compared to air, water holds a floating bounty of tiny organic particles and microorganisms, a rich potential nutritional resource for an organism with the equipment to harvest it. Cilia move and control currents of water (and transport captured food), and sticky mucus snatches suspended food from the current of water as it glides by.

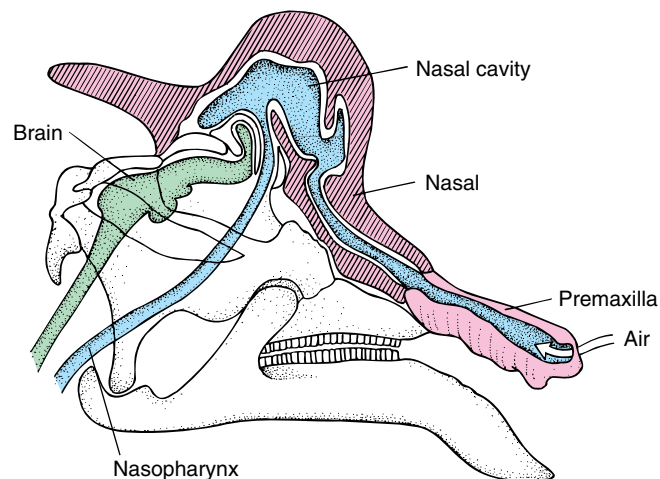


FIGURE 7.59 Air passage of duck-billed dinosaurs.

The air passageway is formed by the premaxillae and nasal bones of the hadrosaur. Air that flowed through the nasal cavity on its way to the lungs cooled the nasal epithelial lining and hence the blood flow through it. Although the vascular system of the hadrosaur is not known, if it were similar to some mammals, then this cooled blood might have circulated in such a fashion as to precool the blood flowing to the brain. In this way, the brain was protected from elevated temperatures. Alternatively or additionally, such an expanded air passage might have been a resonating chamber to amplify vocalizations.

After Wheeler.

Suspension Feeding Suspension feeding is a feeding strategy confined largely, perhaps exclusively, to animals living in water. Some, making an esoteric point, argue that bats “filter” insects “suspended” in air, but this misses the point. Air is too thin to hold suspended food for long. Bats catch or grasp prey, but they do not really use a filtering apparatus nor face the same mechanical problems as aquatic organisms in a viscous medium; so they are not suspension feeders. Most suspension feeders are benthic (bottom-dwelling) organisms or are associated with a herbivorous/detritus feeding style. Respiration and feeding are tightly coupled. Often the same water currents support both activities.

Suspension feeders use several methods to intercept and gather nutrients traveling within streams of water. Captured particles are usually smaller than the pores of the filter. They may collide directly with the filter (figure 7.61a), or because of their inertia, they deviate from the streamlines to collide with the mucus-covered surface of the filter (figure 7.61b). Upon impact, the particles cling to the sticky mucus and are rolled up in mucous cords, and then are passed by cilia into the digestive tract.

Less commonly, a sieve can be used to strain suspended particles larger than the pores of the sieve. As the stream of water passes through the sieve, the particles are held back and then collected from the face of the selective filter (figure 7.61c). This method is rare among animals, perhaps because the relatively large particles filtered tend to

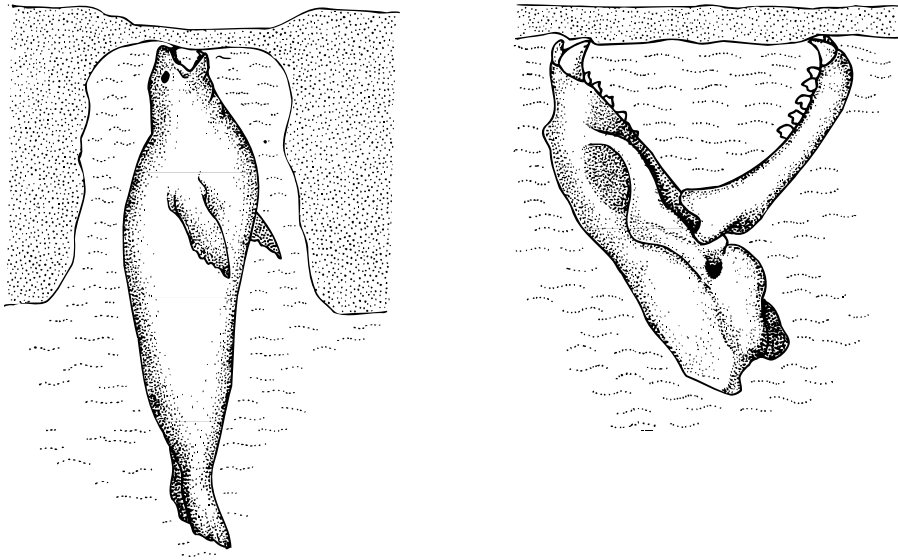


FIGURE 7.60 Weddell seal. In addition to feeding, the jaws of this seal are used to ream away ice to open or reopen a frozen breathing hole.

After Kooyman.

plug and foul the sieve. The buccal cirri of amphioxus intercept large particles, apparently to prevent them from entering the pharynx and clogging the suspension-feeding system. The gill rakers of bony fishes also remove particulate matter. When the filter becomes clogged, these fishes can clear the material by a kind of cough or quick expansion of the gill arches. Larvaceans (urochordates) abandon their filter when it becomes clogged, secrete a new filter, and continue straining microorganisms from the circulating current of water.

In some invertebrates, the mucus is electrically charged. Mild attraction pulls particles out of suspension and into contact with the walls of the filtering device. However, such mechanisms of suspension feeding are unknown in vertebrates and protochordates.

In amphioxus, the endostyle and lining of the pharynx secrete mucus, which is swept upward by the action of cilia also lining the pharynx. The main current, driven by cilia, passes the cirri upon entry into the mouth and pharynx, through the pharyngeal slits, into the atrium, and via the atriopore exits to the outside environment once again. Small suspended particles in the current pass the pharyngeal bars. Some deviate from the stream of water to collide with and become entrapped in the mucous layer. The mucus and its captured particles are gathered dorsally in the epibranchial groove where they are formed into a mucous cord that other cilia sweep into the digestive tract.

In the ammocoetes larvae of lampreys, suspension feeding is similar to that of amphioxus except that a pair of muscular velar flaps, rather than cilia, beat rhythmically to create the current that flows into the pharynx. Mucus, secreted along the sides of the pharynx, is driven upward by cilia into the epibranchial groove. A row of cilia at the base of this groove forms mucus and captured food into a cord that is passed into the digestive tract. The ventral endostyle of ammocoetes adds digestive enzymes to the forming mucous food cord but does not secrete mucus.

Although some envision the ostracoderms as employing new modes of feeding, the absence of strong jaws would have made this unlikely. They seem to have lacked even the muscular tongue of cyclostomes to break up food and place it into suspension. Thus, ostracoderms likely carried forward a suspension-feeding style similar to that of the protochordates before them. Not until gnathostomes do we see a significant tendency away from suspension feeding.

In gnathostomes, suspension feeding is less common. Some actinopterygians use gill rakers like a sieve to filter larger particles from the stream of passing water. The larvae of anurans employ a buccal pump. They draw in a stream of water containing food particles or scrape rock surfaces to enrich the entering stream with these dislodged materials.

The success and efficiency of suspension feeding depends on the size and speed of passing particles. It is most effective with small food particles that neither foul the filter nor escape the sticky mucous lining. To take advantage of large food items, another feeding style evolved, namely, suction feeding.

Suction Feeding Like most fishes, amphibians living in water typically use suction feeding (see figures 7.25 and 7.32). The buccal cavity expands rapidly, pressure drops, and food is aspirated into the mouth. Geometry and enlargement of the buccal cavity are controlled by the muscularized visceral skeleton. Excess water, gulped in with the food, is accommodated in several ways. In salamanders prior to metamorphosis and in fishes, gill slits at the back of the mouth offer an exit for excess water. Flow is unidirectional. In salamanders after metamorphosis, in frogs, and in all other aquatic vertebrates, gill slits are absent, so excess water entering the mouth reverses its direction of flow to exit via the same route. Flow is bidirectional. Turtles possess an expansive esophagus that receives and temporarily holds this excess water until it can be slowly expelled without losing the captured prey.

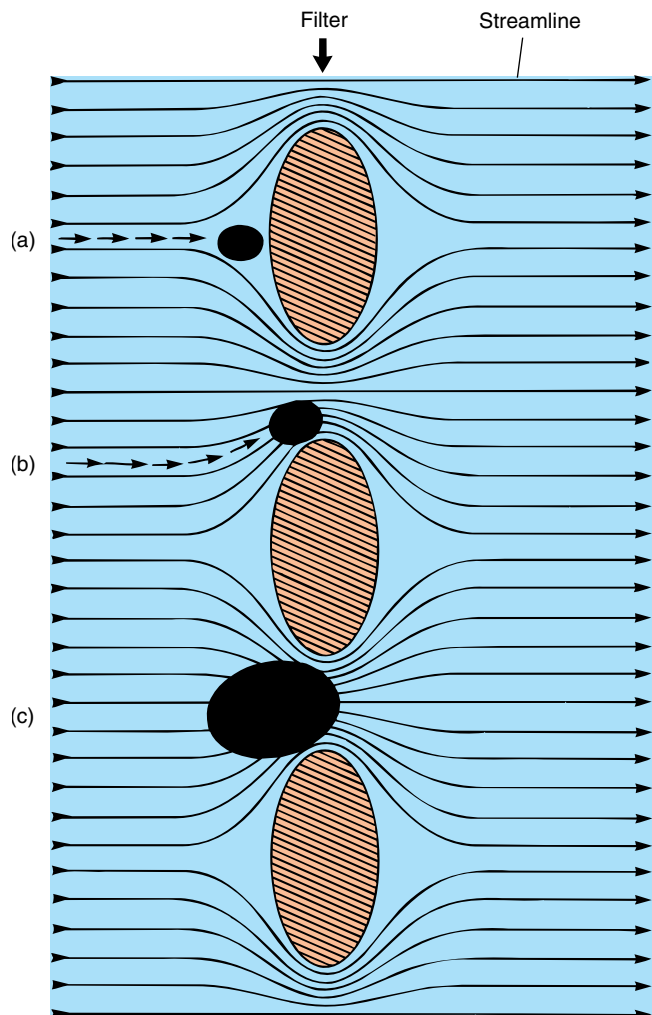


FIGURE 7.61 Suspension feeding: interception of suspended food particles. (a) Direct interception of food particles occurs when particles strike the filtering device. Food is carried in streamlines flowing around bars through openings in the feeding filter. (b) Small, dense particles flow along the streamlines until the fluid is sharply diverted. Particle inertia causes food particles to deviate from the streamlines, collide with the filtering device, and adhere to the mucous coat of the filter. (c) The filtering apparatus can function as a sieve by holding back large particles that fail to pass through the small pores. Cilia drive the food-laden mucus to the digestive tract.

The early stages in vertebrate evolution took place in water, mostly in marine waters, occasionally in fresh water. Adaptations for feeding and respiration took advantage of these conditions. Adaptations for suspension and suction feeding are present in early vertebrates. With the transition of vertebrates to land and air, neither suspension nor suction feeding provided efficient ways to procure or process food. The jaws became specialized for grasping.

Feeding in Air

Terrestrial feeding in most amphibians and many lizards requires a projectile tongue. The term **lingual feeding** recognizes the use of a rapid, projected, and sticky tongue to capture prey (figures 7.62 and 7.41a–d). However, in many other animals, prey is captured by **prehension**, a method by which the animal rapidly grasps the prey with its jaws. In such animals, the jaws are prey traps, designed to snare the unwary.

As a strategy to capture prey, prehension does not always involve the jaws. Birds of prey snatch quarry with their talons, and mammalian predators often use claws to catch and then control intended prey. Jaws are used secondarily to help hold the struggling victim or to deliver a killing bite.

Swallowing

Once an animal has captured and dispatched its prey, it must swallow the prey in order to digest it. In suspension feeders, the food-laden cords of mucus are swept by synchronized ciliary action into the esophagus. Other animals usually swallow prey whole or in large pieces. Suction feeders rapidly expand the buccal cavity repeatedly to work the captured prey backward into the esophagus. Terrestrial vertebrates use the tongue to reposition the food bolus and work it toward the back of the mouth. The highly kinetic skull of snakes allows great freedom of jaw movement. A snake swallows a relatively large animal by stepping the tooth-bearing bones over the dispatched prey (figure 7.63a,b).

Swallowing mechanisms of terrestrial vertebrates (p. 510)

As we have seen in many vertebrates, swallowing involves mastication (the chewing of food). Mastication occurs in a few groups of fishes and lizards. Within mammals, mastication has had a profound influence upon skull design, producing an akinetic skull with precise tooth occlusion and only two replacement sets of teeth, a secondary palate, large jaw-closing musculature, and changes in lower jaw structure.

Overview

Cranial Neural Crest

The cranial neural crest cells leave their initial sites next to the neural tube and form streams of cells contributing to the mesenchyme, which differentiates into bone, cartilage, cranial nerve cells, and various other structures in the head. In particular, note that the hindbrain is segmented into compartments called rhombomeres. Neural crest cells derived from particular rhombomeres migrate into and come to populate particular pharyngeal arches, which in turn give rise to particular cranial structures (figure 7.64). Generally, in tetrapods, neural crest cells from rhombomeres 1 and 2 (and in some taxa, neural crest cells from forebrain and midbrain) migrate into the first pharyngeal (mandibular) arch, producing some of the facial bones, Meckel's cartilage of the lower jaw, and, in mammals, the incus and malleus. Cells of rhombomere 4 enter the second pharyn-

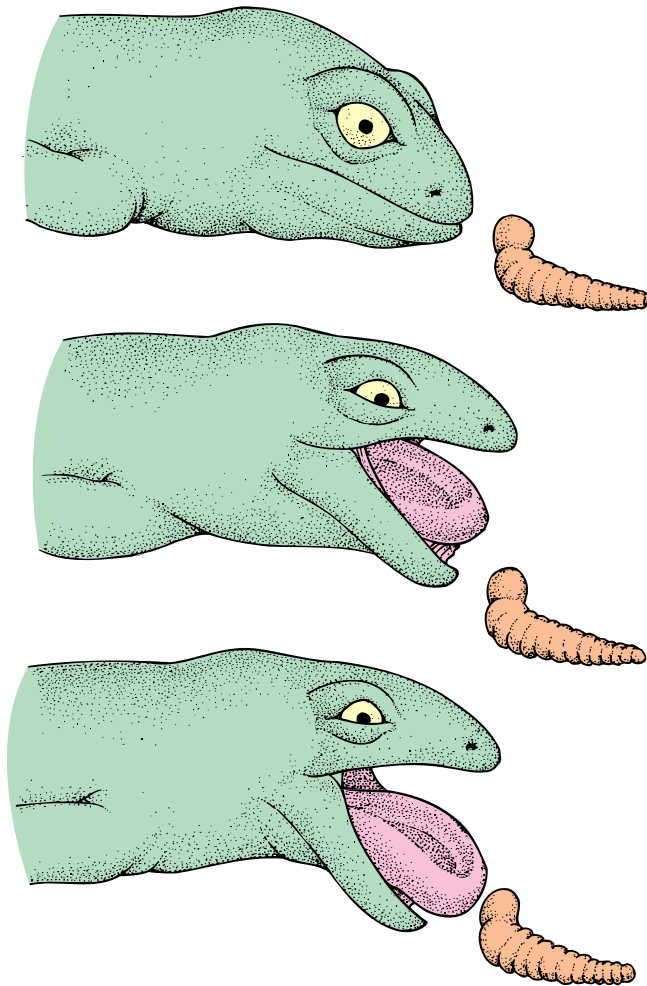


FIGURE 7.62 Terrestrial feeding by a salamander. In this filmed sequence, the salamander's jaws open (top). Its tongue starts to project (middle), approaches (bottom), and then makes contact with the prey.

Based on the research of J. H. Larsen.

geal (hyoid) arch, producing the stapes, styloid process, and a contribution to the hyoid. Rhombomere 6 releases neural crest cells into pharyngeal arches 3 and 4, which contribute to the hyoid and to the thyroid cartilages. Cells from rhombomeres 3 and 5 do not migrate.

Somewhat surprisingly, in at least tetrapods both elements of the mandibular arch, the palatoquadrate and Meckel's cartilages, derive solely from a single condensation of neural crest cells populating the first pharyngeal arch. However, the maxillary arch is not derived from the first pharyngeal arch but instead from several other neural crest sources of the head.

Hox genes expressed in various combinations and regions of the neural crest (figure 7.64) instruct the cells quite early as to which tissues they will form. Although details are still forthcoming, many major evolutionary changes in vertebrate jaws, teeth, and facial bones seem based on changes in the placement or instructed fate of neural crest cells. For example, a *Hox* gene is expressed in the mandibular arch of a

species of lamprey, but not in gnathostomes. This apparent loss of *Hox* gene expression may have been the genetic basis for facilitating the evolution of jaws in gnathostomes.

Neural crest (p. 238)

Emergence of Mammals

Mammals brought many innovations to the vertebrate design; several involved the skull. One change already noted is in the lower jaw. In early amniotes, as in gnathostomes generally, the jaws articulate with the braincase via the articular-quadrate joint. In mammals, this is quite different. The jaws articulate via the dentary-temporal joint. Several postdentary bones become lost during this transition to mammals, and a few move to the middle ear. The dentary expands posteriorly to form a new articulation with the skull, namely, via the dentary-temporal joint. Although the factors favoring these changes are disputed, the reality of these changes is not. Bones located at the back of the primitive amniote lower jaw were either lost or altered in function from jaw articulation to hearing. But this fact raises a new problem. How could bones involved in jaw suspension change function without disrupting the intermediate species? If postdentary bones moved to the middle ear, how could they abandon jaw suspension without producing an individual with no method of supporting the jaw against the skull? G. Cuvier, nineteenth-century French anatomist, would have understood the dilemma. He argued that evolution could not occur for just such a reason, because a change in structure would disrupt function and stop evolution in its tracks before it had begun.

Diarthrognathus, a late cynodont close to primitive mammals, suggests an answer. Its name means two (di-) sites of articulation (arthro-) of the jaw (gnathus). In addition to the articular-quadrate joint inherited from reptiles, a dentary-squamosal joint was apparently present. We do not know the feeding style of *Diarthrognathus*, so we cannot be sure of the biological role played by this second articulation.

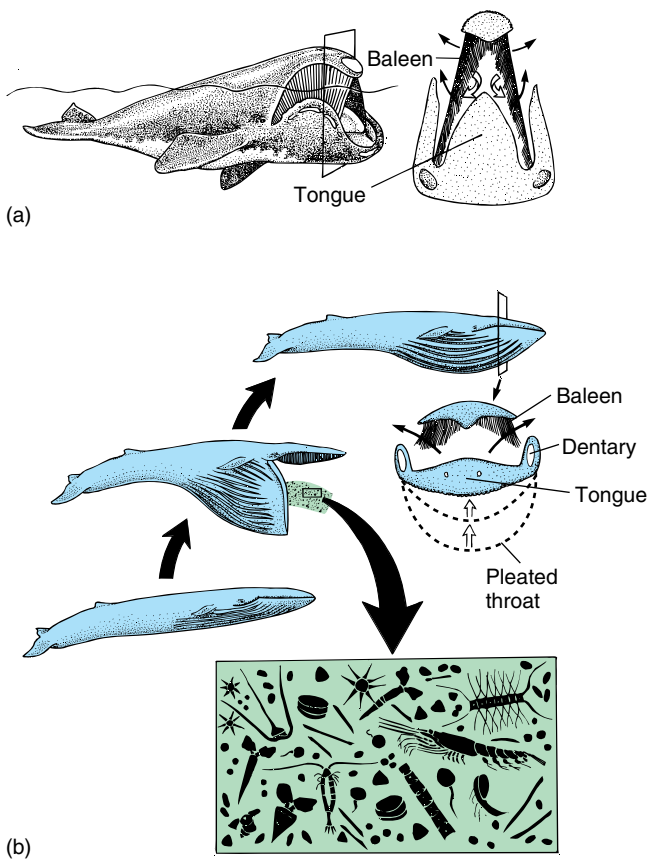
What do living vertebrates suggest? Some birds, such as the skimmer, for example, feed by holding their lower jaw just below the water's surface and flying swiftly along until they strike a fish. Then the jaws snap shut to snatch the fish. A secondary articulation seems to strengthen the lower jaw and help prevent its dislocation as it collides with the fish. *Diarthrognathus* did not feed on fish, but it may have wrestled with struggling prey or fought with competitors. A second jaw articulation would make the jaw stronger. Whatever its advantages, a dentary-squamosal joint was established before the postdentary bones departed from the lower jaw; therefore, when the quadrate and articular bones departed, an alternative method of lower jaw-skull articulation was already in place. This is significant because loss or movement of these bones to support hearing did not disrupt the function they abandoned,

BOX ESSAY 7.4

The largest animal alive today is the blue whale. It makes its living as a filter feeder. The filtering device is the baleen, a brush-like specialization of the oral epithelium occupying the site where teeth might otherwise be expected in the upper jaw. “Whalebone” is a misnomer for baleen. The term is inaccurate because no bone occurs within the baleen. Because baleen is frayed, it acts like a strainer to hold back food from the stream of water passed through it. Food preference depends a little on species, but most baleen whales strain small fishes or shrimplike crustaceans called “krill,” which school or gather in dense swarms. Food collected in the baleen is licked free by the tongue and swallowed.

Blue and humpback whales represent one subgroup of baleen whales called fin whales, or rorquals. Right whales are the other subgroup. In both groups, the teeth are absent, the baleen is present, and the skull is long and arched to hold the filter-feeding equipment.

To feed, right whales part their jaws slightly and swim through swarms of krill. The stream of water enters the front of the mouth and passes out the lateral suspended wall of baleen. Here the krill become entangled in the frilly baleen and are licked up and swallowed (box figure 1a). The blue whale feeds differently. As it approaches a school of fishes or krill, it opens its mouth wide to swim over and engulf the concentrated prey and accompanying water. Pleated furrows along its neck and belly allow the throat to inflate like a pouch and fill with this huge mass of water (box figure 1b). Up to 70 tons of water are temporarily held in the



BOX FIGURE 1 Whales feeding. (a) The right whale has long plates of baleen suspended from its upper jaw, and it feeds by swimming through plankton with its mouth parted. Water enters, passes along the sides of the tongue, and then departs through the curtain of baleen, leaving the plankton entangled in the baleen. (b) As a fin whale approaches a concentration of planktonic organisms, usually krill, it opens its mouth and engulfs these organisms together with the water in which they reside. Its pleated throat allows for considerable expansion of the mouth in order to accommodate the plankton-filled water. The whale lifts its throat to force water out through its baleen, which holds back the food but allows excess water to filter out. Its tongue licks this food from the baleen

jaw suspension. The existing dentary-squamosal articulation was in a sense “ready to serve,” preadapted for a new or expanded function.

Preadaptation (p. 18)

Probainognathus, another late cynodont, like *Diarthrog-nathus* exhibits a posterior extension of the dentary to establish a secondary point of jaw articulation with the skull (figure 7.65). *Probainognathus*, *Diarthrog-nathus*, and several other late cynodonts with similar transitional double jaw articulations suggest how a harmonious transition in form and function might have occurred. They remind us again that a series of anatomical changes alone are an incomplete

statement about evolutionary events. They must be coupled with hypotheses about the accompanying functional series of changes. Form and function go together, and both must receive attention if we are to bring some understanding to the process of evolutionary change.

Evolutionary Modifications of Immature Forms: Akinesis in Mammals

We sometimes forget that an evolutionary modification can debut in an embryonic or infant stage and later become incorporated or expanded in the adult. Such may have been the case with akinesis in mammals. In all mammals, infants suckle milk from their mothers. Suckling requires a pump

expanded throat. The whale then contracts the swollen pouch, forcing water through the baleen where the food is strained, collected up by the tongue, and swallowed.

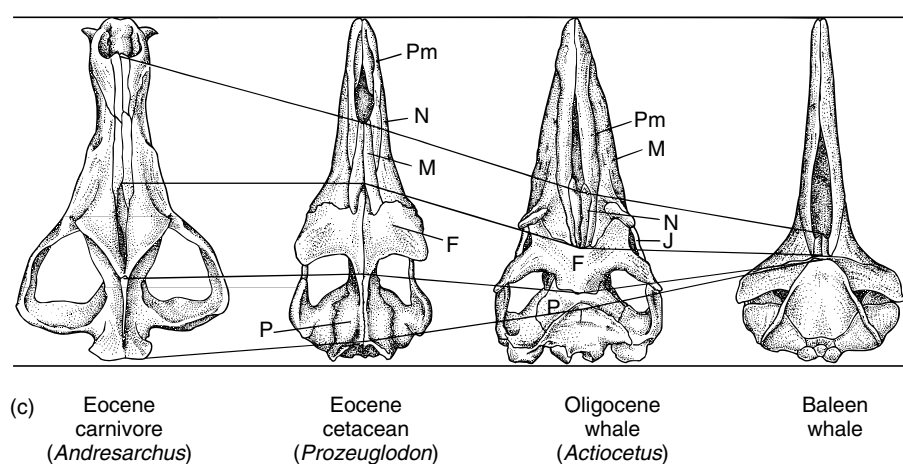
Humpback whales have been observed to release air bubbles while circling a school of prey swimming above them. As the air bubbles rise, they form a “bubble cloud” that may corral or drive the school up to the surface ahead of the whale. The

bubble cloud may also immobilize or confuse schools of prey, causing them to clump together, or it may disguise the whale as it surges upward with its mouth open through the center of the bubble cloud. Some humpbacks begin feeding at the surface by lopping or slapping their tail against the water as they dive. Just as the tail flukes are about to reenter the water, a whale flexes its tail so that the flukes hit the

water, leaving a bubbling effervescence at the surface. This is thought to startle prey and stimulate them to clump tightly together in a school. The whale then releases a bubble cloud as it dives, which it follows by a feeding lunge back up through the bubble cloud to collect the prey in its mouth.

The oldest fossil whales come from the Oligocene and bear unmistakable resemblances to primitive terrestrial mammals. Distinct incisor, canine, premolar, and molar teeth were present. From these earliest whales, two major modern lines soon arose. One is the baleen whales, formally called the mysticetes. The other major line of whales is the toothed whales, or the odontocetes, including sperm, killer, and other whales with teeth.

In both baleen and toothed whales, the skull is telescoped. Some bones are pushed together and even overlap, yet a long snout persists (box figure 1c). In the odontocetes, the backward lengthening of the facial bones creates the snout. In the mysticetes, the occipital bones are pushed forward. Although achieved differently, the result is the same—to reposition the nostrils to a more central and dorsal position. When a whale surfaces to breathe, this position of the nostrils allows easy venting of the lungs and drawing in of fresh air without the whale having to tip its entire head out of water.



and swallows it. (c) Skulls of whales have been highly modified during their evolution, especially the design of the face and the position of the nostrils. *Andresarchus*, a terrestrial carnivore from the Eocene, may have belonged to a group from which early cetaceans arose. For comparison, Eocene (*Prozeuglodon*), Oligocene (*Actiocetus*), and a modern baleen whale are illustrated. Although not on a direct evolutionary line with each other, these comparisons show the changes in cetacean skull design, especially in the facial region. Abbreviations: frontal (F), jugal (J), maxilla (M), nasal (N), parietal (P), premaxilla (Pm).

(a,b) After Pivovarov; (c) after Olsen; Romer.

and a seal. Fleishy lips provide the seal around the teat of the mammary gland, the mouth is the chamber that receives the milk, and the up-and-down action of the tongue pumps the milk from the mother to the infant's mouth and esophagus. If respiration and feeding shared a common chamber, as in most reptiles, the infant would have to interrupt nursing and release its attachment to the nipple in order to breathe. A secondary palate makes this inefficient interruption in feeding unnecessary. It separates feeding from breathing by separating the mouth from the nasal chambers. But a secondary palate that separates the mouth from the nasal passages also fuses left and right halves of the skull, thus preventing any movement within or across the braincase. The result is an akinetic skull.

Further changes in the adult evolved later. With loss of kinesis, the skull is firm and ready to serve strong jaw-closing muscles. Mastication, development of specialized teeth to serve chewing (accurately occlusal tooth rows), and a muscular tongue (to move food into position between tooth rows) might then find adaptive favor. Certainly there are other ways to chew food. Some fishes with kinetic skulls and teeth that are continuously replaced chew their food. In mammals, the conditions seem especially favorable for mastication, and we find this adaptation in almost all mammalian species, including its appearance in some late therapsids. Analysis of evolutionary events often centers on adult stages, yet understanding of these events must come from a knowledge of the entire life history of species.

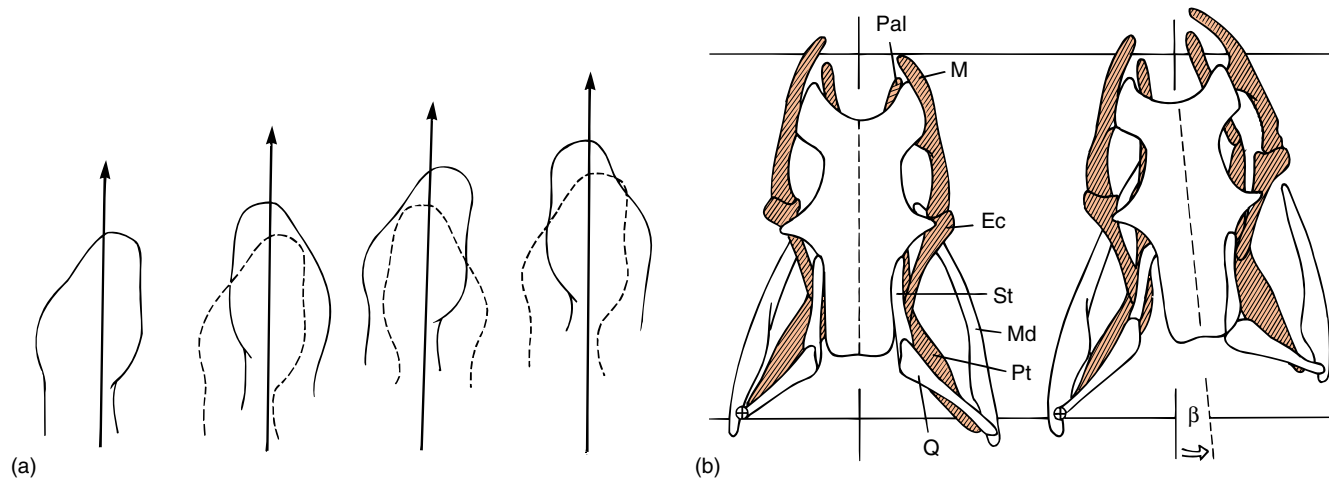


FIGURE 7.63 Swallowing by a rat snake, *Elaphe*, as seen in dorsal view. (a) Outline of snake's head during successive swallowing motions, left to right. Previous head position is indicated by the dotted outline. With alternating left and right advances, the jaws walk over the prey along a line of progress, the axis of swallowing, until the jaws pass over the entire prey. These jaw-walking displacements place the prey at the back of the throat where contractions of neck muscles move the prey along to the stomach. (b) Movable bones of the skull (shaded) on one side swing outward from the prey and advance farther forward where they come to rest momentarily on the surface of the prey at a new position. Movable bones of the opposite side now take their turn. By such reciprocating motion, jaws walk along the prey. In addition to jaw displacement, the skull itself swings outward from the swallowing axis (arrow) through an angle (β) in the direction of the advancing bones to place them farther along the prey. Abbreviations: ectopterygoid (Ec), maxilla (M), mandible (Md), palatine (Pal), pterygoid (Pt), quadrate (Q), supratemporal (St).

After Kardong.

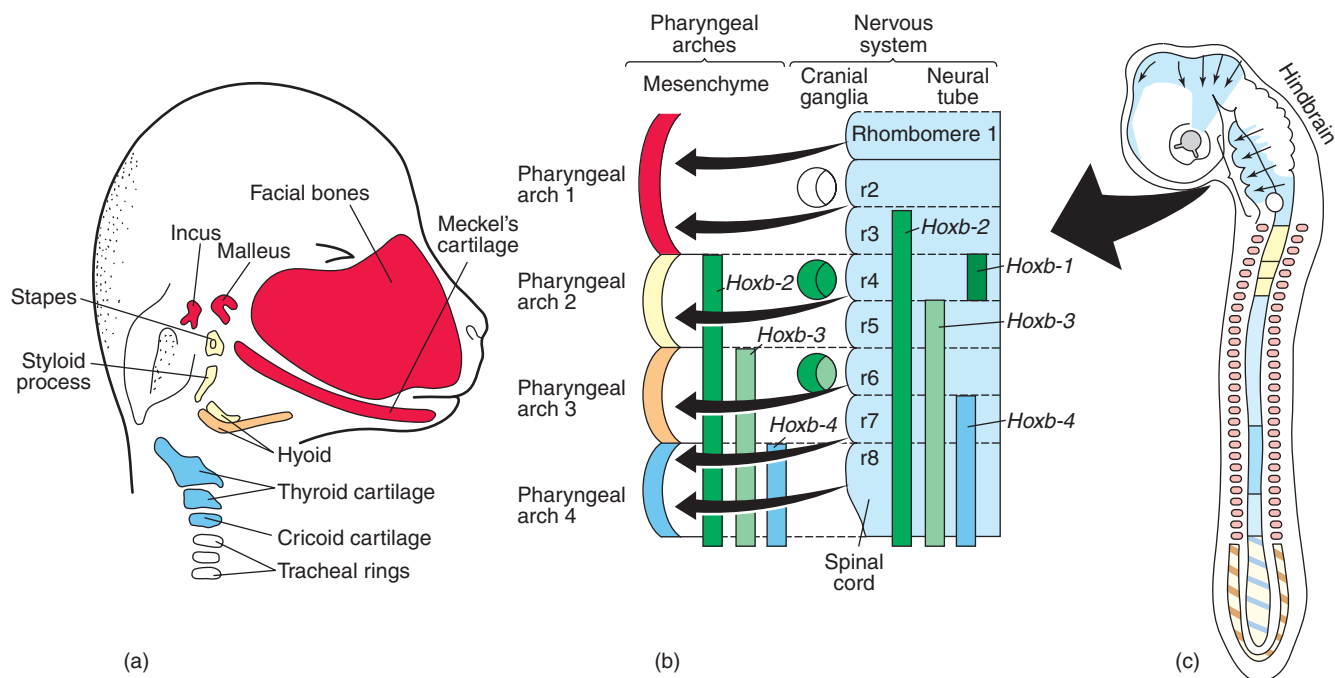


FIGURE 7.64 Cranial neural crest migration and *Hox* genes, generalized tetrapod. (a) Various cranial structures derived from particular pharyngeal arches. (b) In turn, these pharyngeal arches are themselves populated by neural crest migrating (arrows) out of the rhombomeres of the hindbrain. (c) Embryo showing location of pharyngeal arches and hindbrain. *Hox* expression patterns in the neural crest show the boundaries of these gene domains. Key to abbreviations: r2–r8, rhombomeres 2–8.

After McGinnis and Krumlauf; Carlson.

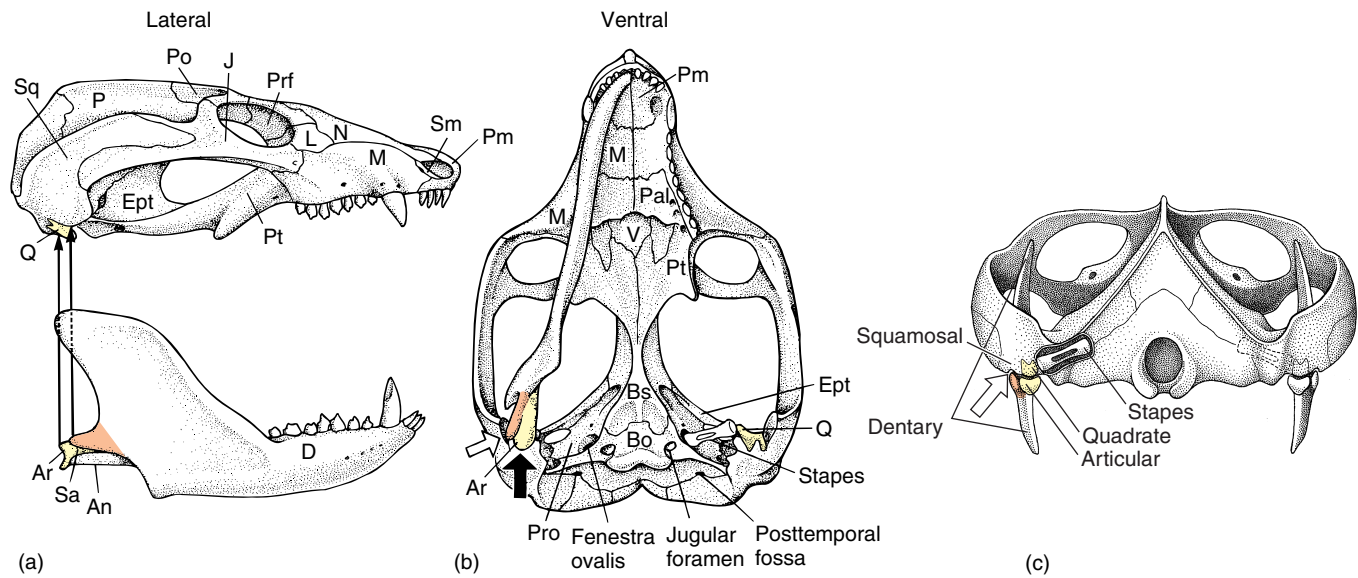


FIGURE 7.65 Double jaw articulation. Skull of *Probatognathus*, a late cynodont (therapsid). Shown in lateral (a) and ventral (b) views, double jaw articulation occurs between the quadrate and articular (solid arrow), the primitive condition, and another articulation occurs between dentary and temporal (squamosal) (open arrow) that came to predominate in later mammals. (c) Posterior view, with window cut to show the stapes and its contact with the reduced quadrate. The new articulation, dentary-temporal (via squamosal), open arrow, as well as the primitive jaw articulation, quadrate-articular, are present. Abbreviations: angular (An), articular (Ar), basioccipital (Bo), basisphenoid (Bs), dentary (D), epityergoid (Ept), jugal (J), lacrimal (L), maxilla (M), nasal (N), parietal (P), prefrontal (Prf), premaxilla (Pm), prootic (Pro), postorbital (Po), pterygoid (Pt), quadrate (Q), surangular (Sa), septomaxilla (Sm), squamosal (Sq), vomer (V).

After Carroll; after Romer.

Composite Skull

Dermatocranium, chondrocranium, and visceral cranium contribute to the skull. Although their phylogenetic backgrounds are different, parts of each combine into a functional unit, the skull. If species were stamped out one at a time, each being a unique creation, then there would be little reason to expect a composite skull. Yet, clearly the skull is a combination from different phylogenetic sources. In Darwin's day as now, we can point to this as evidence that supports evolution, not special creation. Evolution is behind the origin of new structures and the species that display them.

The skull also illustrates a point made earlier. Evolution proceeds by remodeling, seldom by new construction. Consider the splanchnocranium. From fishes to mammals, it

is variously modified to serve the adaptive demands of the organism of the moment, first as support for gill slits, and then as the source of jaws, as support for the tongue, and in mammals as part of the ear (figure 7.66). In this series of transformations seen in retrospect, we have no reason to believe that the splanchnocranium of the first fish anticipates its eventual contribution to the hearing devices of mammals. Evolution does not look ahead. The sequences or trends we see are apparent only after the fact, after evolution has taken place. There is no evolutionary arrow anticipating the future. We have seen that changes in the splanchnocranium, chondrocranium, and dermatocranium serve biological roles of the moment. They are not predestined changes preparing for the future.

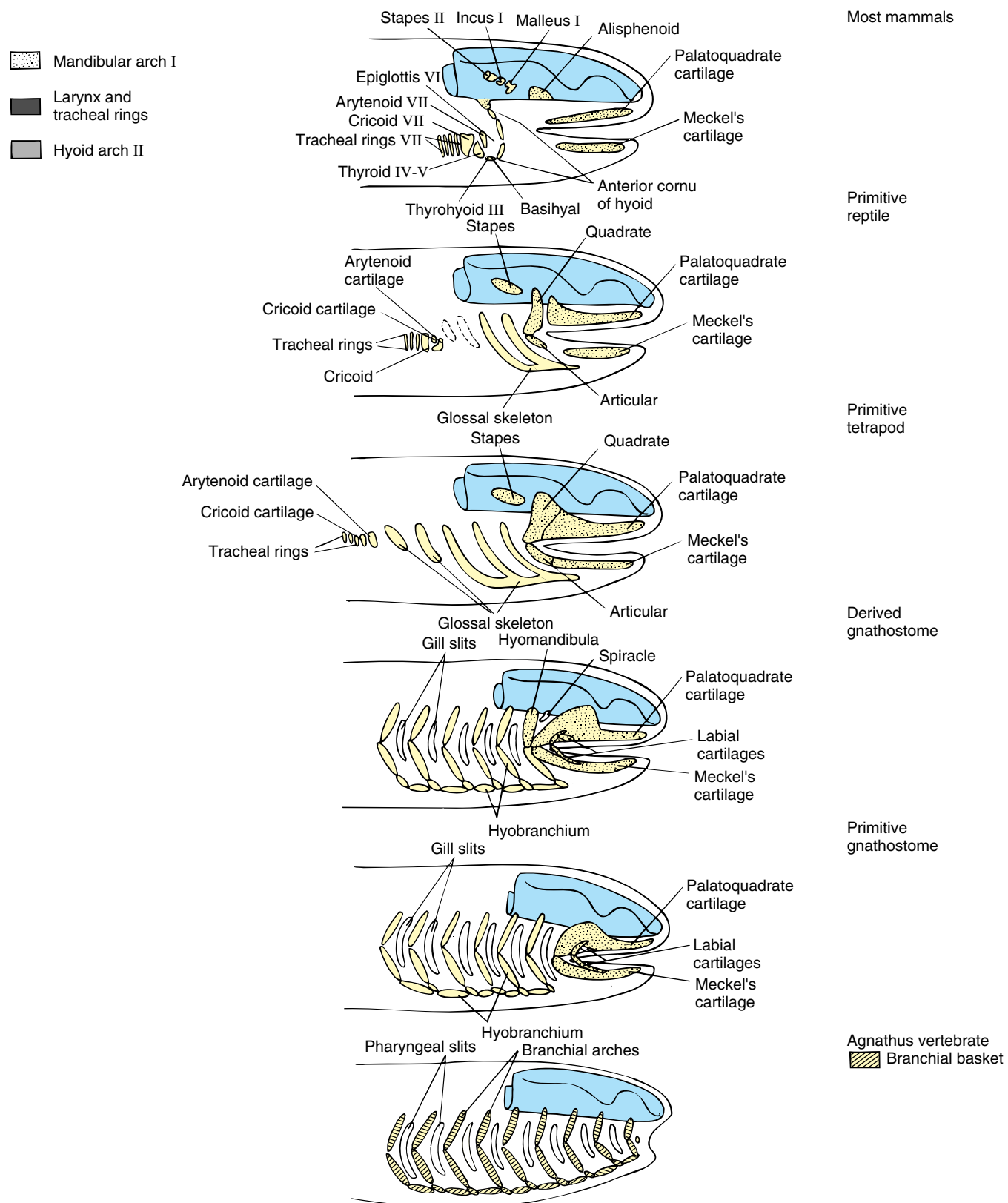


FIGURE 7.66 Phylogeny of the splanchnocranium. Notice how the branchial arches are remodeled to serve various functions within each succeeding group. Parts of the branchial basket become the jaws, tracheal cartilages, tongue supports, components of the neurocranium, and ear ossicles. Roman numerals indicate branchial arch number.

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