A Comparative Study of Sixteen Vertebrate Skulls

A Thesis
Submitted to the Faculty
Of Saint Meinrad College of Liberal Arts
In Partial Fulfillment of the Requirements
For the Degree of Bachelor of Science

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May, 1973
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ACKNOWLEDGEMENTS

I, David Lee Schuchard, would like to express my appreciation to the Reverend Damian Schmelz, OSB, PhD, for his supervision and critical reading of this comparative study; to Mr. M. Ambre for his production of the photographs of the representative specimens; and to Mr. J. Hoeck for the use of an IBM copier.

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INTRODUCTION

The skull is found in its simplest form in the lowest vertebrates and attains increasing complexity with phylogentic ascension(Montagna,1959). The skull of most vertebrates derives from three separate embryonic components: (1) the chondrocranium, (2) the dermatocranium, (3) the splanchnocranium. The chondrocranium forms as the original floor and sides for the brain and is composed of cartilaginous material which may ossify and be termed neurocranium. The dermatocranium consists of an outer layer of dermal bony plates, arising from the ectoderm of the head, that roofs the chondrocranium and often fuses with it. The splanchnocranium is an element of the visceral skeleton which originally supports the gills and becomes part of the skull of higher vertebrates. Although primitively cartilaginous, some of it becomes sheathed or replaced by membranous bone.

Chondrocranium

The embryonic development of the skull begins soon after the appearance of the central nervous system. During this time the mesenchymal cells that surround the central nervous system differentiate, forming a membranous investing layer that provides the material for the development of the cartilaginous chondrocranium(Weichert,1970). The chondro- is made up of several components(Figure 1).

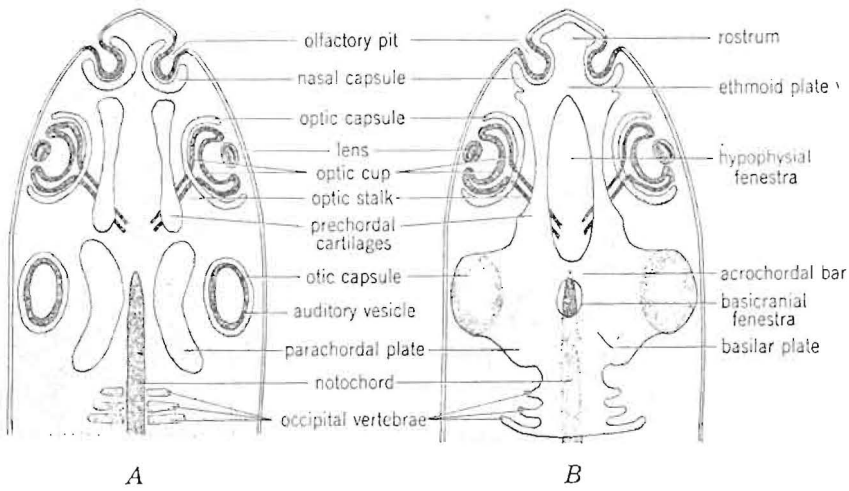
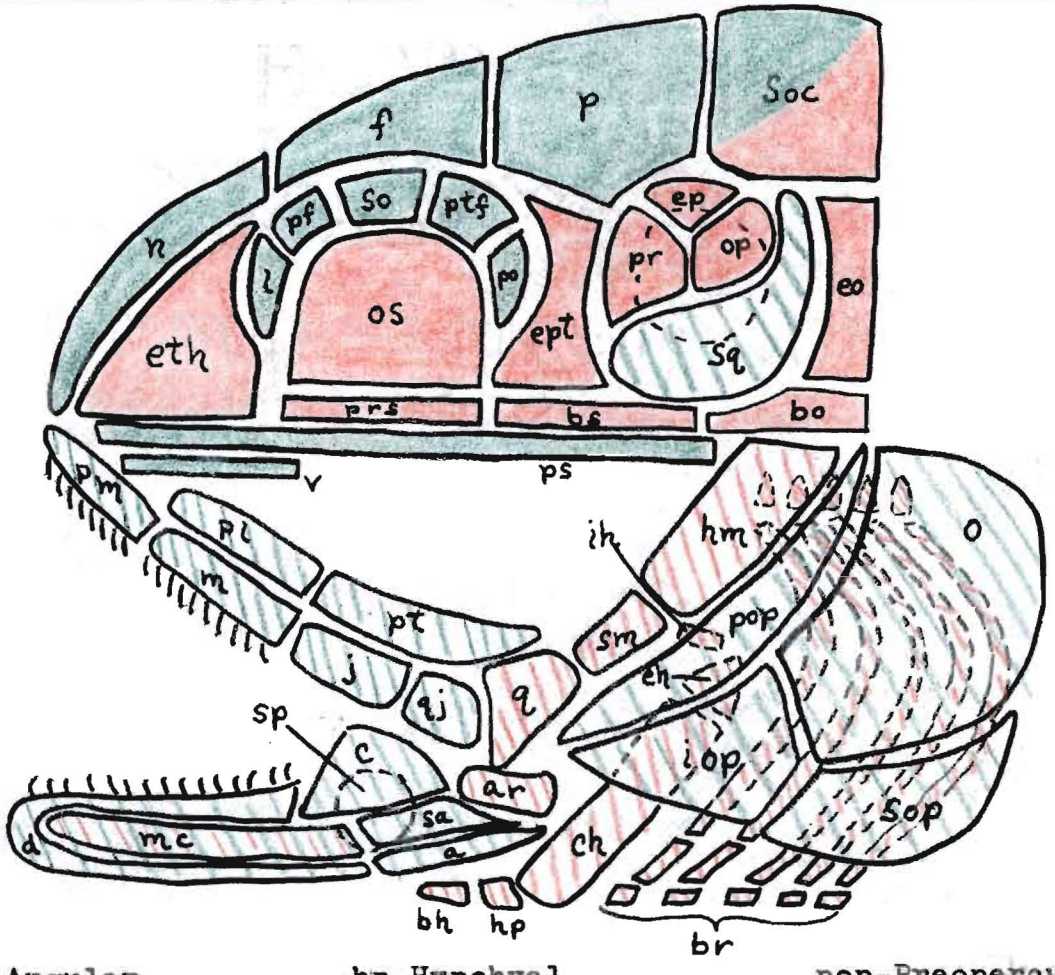


Figure 1 Diagrams illustrating development of the chondrocranium: A, separate chondrocranial cartilages surrounding the sense organs and flanking the notochord and brain; B, all the cartilages except the otic capsules have fused to form the early chondrocranium, (From Weichert, 1970, p. 433).

The parachordals, a pair of flat, curved cartilages, parallel the notochord and extend on either side to the anterior end of the otic capsules. Posteriorly, two to four occipital vertebrae become fused to the parachordals, and the cartilage of this entire region enlarges to enclose the tip of the notochord, becoming the floor of the midbrain and hindbrain. Next, a pair of prechordal cartilages (trabeculae cranii) appear anterior to the parachordals, which enlarge anteriorly until their ends fuse with each other to form an ethmoid plate and posteriorly to fuse with the parachordals (Weichert,1970). While the parachordal and prechordal cartilages are developing, olfactory(nose), optic(eyes), and otic

(ears) vesicles also form. Mesenchyme condenses around these vesicles and forms cartilaginous capsules(Montagna,1959). As a result of the growth of the parachordal and prechordal cartilages, a union occurs with the olfactory and otic capsules(Weichert,1970). The otic capsules, however, remain independent, permitting the unrestricted movement of the eyes. As embryogenesis progresses, the chondrocranium grows dorsally on either side of the brain and in the case of higher vertebrates fuses with the dermatocranium.

Separate ossification centers appear in the trough-like chondrocranium(Figure 2). From the cartilage of the occipital region (parachordal) arise the occipital bones: a large basioccipital on the floor; one lateral exoccipital on either side of the foramen magnum; and one supraoccipital above the foramen magnum, to which bone of dermatocranial origin is added dorsally. Anteriorly, the floor of the chondrocranium consists of a basisphenoid (parachordal) and a presphenoid (prechordal). One alisphenoid develops on each side of the basisphenoid and an orbitosphenoid on each side of the presphenoid. A mesethmoid (prechordal) is formed between the nasal vesicles. Each otic capsule gives rise to an anterior prootic, dorsal epiotic, and posterior opistotic, all located between the alisphenoid and the exoccipital. In fishes, two additional bones from the otic capsule, the sphenotic and the pterotic appear(Weichert,1970).



a-Angular
ar-Articular
bh-Basihyal
bo-Basioccipital
br-Branchial
bs-Basisphenoid
c-Coronoid
ch-Ceratohyal
d-Dentary
eh-Epihyal
eo-Exoccipital
ep-Epiotic
ept-Epipterygoid
eth-Ethmoid
f-Frontal
hm-Hyomandibular
hp-Hypohyal
ih-Interhyal
iop-Interoperculum
j-Jugal
l-Lacrimal
m-Maxillary
mc-Mandibular cart.
n-Nasal
o-Operculum
op-Opisthotic
os-Orbitosphenoid
p-Parietal
pf-Prefrontal
pl-Palatine
pm-Premaxillary
po-Postorbital
pop-Preoperculum
pr-Prootic
prs-Presphenoid
ps-Parasphenoid
pt-Pterygoid
ptf-Prefrontal
q-Quadrate
qj-Quadratojugal
sa-Surangular
sm-Symplectic
so-Supraorbital
soc-Supraoccipital
sop-Suboperculum
sp-Splenial
sq-Squamosal
v-Vomer

Figure 2 A diagrammatic lateral sketch of the vertebrate skull. Chondrocranial bones are solid red; dermatocranial bones are solid green; splanchnocranial bones are red striped(cartilage) and green striped(membrane). (Adapted from Rand,1938, p. 68.)

Dermatocranium

The dermatocranium gives rise to membrane bones, appearing first in the head region of the bony fish as large scales. These gradually sink down into the head and roof over the anterior region of the chondrocranium with which they fuse, thus completing the protective envelope surrounding the brain(Weichert,1970). The roof of the skull anterior to the supraoccipital is formed by the parietals and frontals. In some cases there is an interparietal present between the parietals and the supraoccipital. The latter has a double origin arising also from the chondrocranium. Other membrane bones include the nasals, vomer(s), lacrimals, and parasphenoids. The lateral sides of the skull are completed anteriorly by the maxillaries and posteriorly by large temporal bones, which are splanchnocranial elements.

Splanchnocranium

The splanchnocranial elements of the visceral skeleton, primitively composed of cartilaginous material, tend to be replaced by bone (like chondrocranium) or sheathed with membranous bone (similar to dermatocranium). Thus, this third element gives rise, finally, to bony skeletal structures in two ways.

The first, or mandibular, arch is divided into dorsal (palatopterygoquadrate bar) and ventral (Meckel's cartilage) elements which contribute to the formation of the up-

per and lower jaws(Weichert,1970). The cartilage replacement bone of the dorsal element is the quadrate (incus); and that of the ventral element is the articular (malleus). Membranous bones of the dorsal element are the premaxillary, maxillary, jugal, quadratojugal and squamosal; those of the ventral element are the palatine, ecto- and endopterygoids, dentary, splenial, surangular and coronoid. In bony fishes and in tetrapods, this type of membrane bone takes over the function of the cartilage bone, which disappears or remains merely as a cartilaginous core inside the membranous bones. Finally, one must realize that the first visceral arch becomes reduced and modified as the classes of vertebrates are ascended. In the adult mammal only the ossicles of the middle ear remain as cartilage bone: the incus and malleus, previously mentioned.

The second, or hyomandibular, arch gives rise to several cartilage replacement bones: dorsally to the hyomandibular, symplectic, interhyal and epihyal; ventrally to the ceratohyal, hypohyal and basihyal. The hyomandibular in amphibia, reptiles, and birds forms the columella of the ear and in mammals the stapes; the other elements contribute to the branchial arches or to the hyoid apparatus(Kent,1965).

The rest of the gill arches of the fish form the hypobranchial skeleton of higher vertebrates, contributing to the hyoid apparatus and the cartilages of the larynx(Montagna,1959). Other superficial membrane bones found in bony

fish are the opercular, interopercular, preopercular, subopercular, and branchiostegal rays, which may become associated with the quadratojugal of the higher vertebrates.

Vertebrate Phylogeny

The vertebrates existing today are only part of vast and continuing populations that have inhabited the earth through millions of years. The evolution of vertebrates is important in approaching a comparative study of their skulls. Figure 3 shows the probable relationships of forms, when they first occurred or disappeared, and what other forms did or did not exist at the same time.

No vertebrate remains have been found in the Cambrian rocks. Fossil evidence for the earliest known vertebrates, in the Ordovician period, is very fragmentary, and it is not until the sediments deposited during the Silurian period that fossils are complete enough to give us any idea as to the form and relationships of early vertebrates. Even here the evidence is vague, so it is actually in Devonian rocks that the fossil record of the vertebrates become truly representative, when bony fishes first appeared. However, the perch, an advanced teleost, did not become evident until the Tertiary period(Colbert,1955). Amphibians appear to have arisen from fish during late Devonian, with the Necturus appearing during the Permian period. The reptiles originated from amphibians during the Pennsylvanian period. The turtle made its appearance during the Triassic period. Alligators

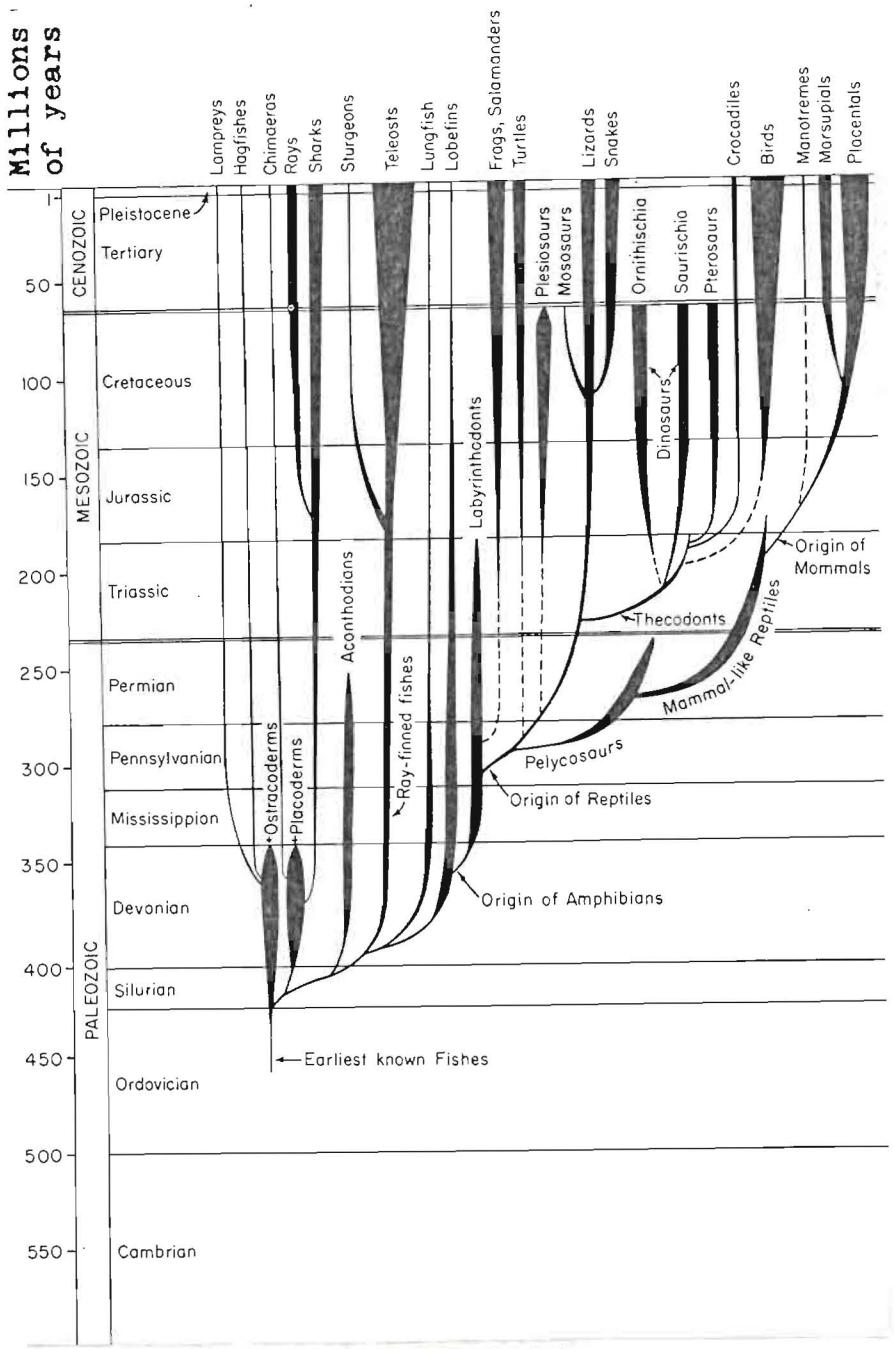


Figure 3 Evolutionary relationships of the major groups of vertebrates. (From Eaton, 1970, p. 185.)

first appeared during the Jurassic and snakes during the Cretaceous period. The birds, bird-like reptiles, first appeared during the Jurassic period. The turtle, alligator, snake and bird evolved to their present forms during the Tertiary period. Mammals originated during the late Triassic from mammal-like reptiles. The Insectivora(mole) and Marsupialia(opossum), first appeared during the Cretaceous period(Figure 4). With the close of the Cretaceous period many of the reptiles disappeared, and mammals became dominant at the beginning of the Tertiary. The Lagomorpha(rabbit), Rodentia(porcupine), Carnivora(cat, fox, bear) and the Primates (monkey and man) first appeared during the Paleocene epoch and developed at varying rates throughout the Tertiary period. The Artiodactyla(deer) first appeared during the Eocene.

The Present Study

In the evolution of the skull from fish to man, there has been a gradual reduction, by deletion or fusion, in the number of bones present. In certain primitive fish as many as one hundred and eighty bones are present, while in man there are only twenty-eight. The purpose of this comparative study is to trace this reduction, using representative specimens of each class of vertebrates.

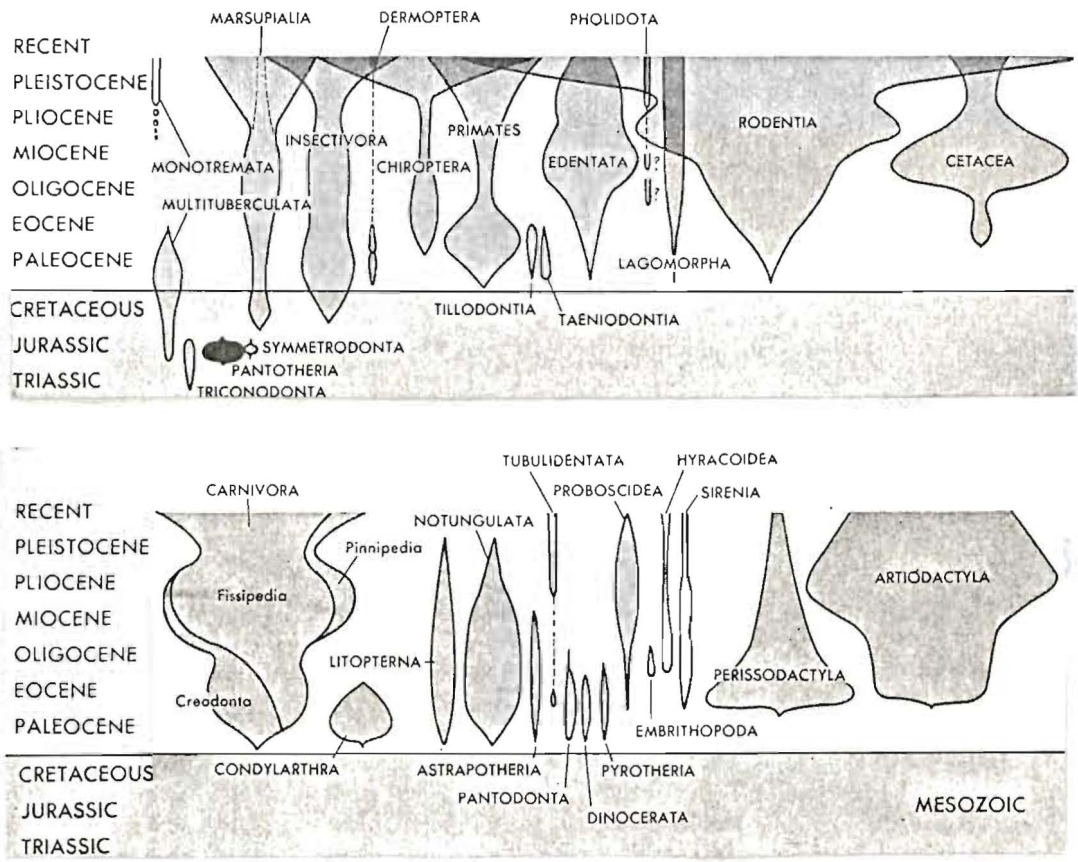


Figure 4 The historical record of the orders of mammals. (From Simpson,1957, pp. 782-3.)

MATERIALS AND METHODS

Sixteen vertebrate skulls used in this comparative study were from the following classes and orders:

Osteichthyes:

Teleostei: Perch (*Cymatogaster aggregatus*)

Amphibia:

Caudata: Necturus (*Necturus maculosus*)

Reptilia:

Crocodilia: Alligator (*Alligator mississippiensis*)

Chelonia: Turtle (*Chelydra serpentina*)

Squamata: Snake (*Ancistrodon piscivorous*)

Aves:

Falconiformes: Hawk (*Buteo borealis*)

Mammalia:

Insectivora: Mole (*Scalopus aquaticus*)

Lagomorpha: Rabbit (*Sylvilagus aquaticus*)

Rodentia: Porcupine (*Erethizon dorsatum*)

Marsupialia: Opossum (*Didelphis marsupialis*)

Carnivora: Cat (*Felis domesticus*)

Fox (*Urocyon cinereargenteus*)

Bear (*Ursus horribilis*)

Artiodactyla: Deer (*Dama virginiana*)

Primates: Monkey (*Saimiri sciurea*)

Man (*Homo sapiens*)

Prepared skulls of the perch, Necturus, and snake were purchased from the Carolina Biological Supply Company. The bear skull, obtained defleshed from the Montana State University, was degreased in the lab. The skulls of the hawk and monkey were prepared from frozen specimens of the lab. The method used for their preparation was by Roberts(1964); however, modifications were made in regards to the length of time for soaking in sodium hydroxide and carbon tetrachloride solutions. The remaining skulls were taken from the lab's collection.

Most of the skulls were sectioned through the medial sagittal plane, with the exception of those skulls possessing very delicate bones or having bones that were clearly evident without sectioning, namely: perch, Necturus, alligator, turtle, snake, and mole. The median sagittal cut was made by using a hacksaw blade (#00006), cutting anteriorly from the occipital region, using medial sutures whenever possible. Individual bones were labelled by symbols(mainly Romer's,1955), using a rapidograph. Photographs were made of the labelled specimens.

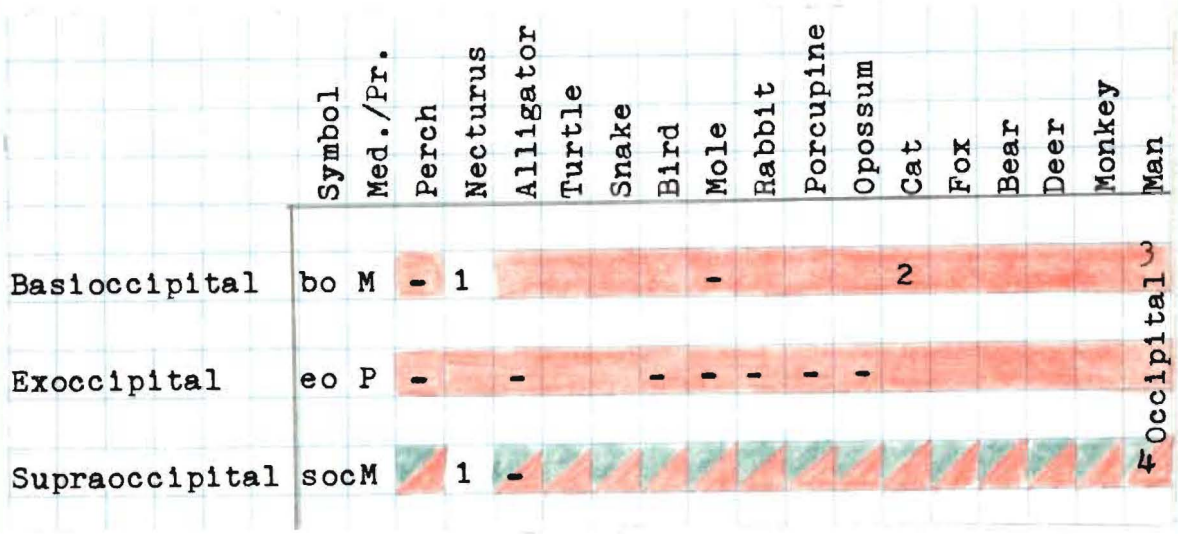
The sixteen vertebrate skulls of this comparative study are in the Biology laboratory of Saint Meinrad College.

OBSERVATIONS AND RESULTS

The sixteen vertebrate skulls have been compared according to occipital, parietal, frontal, otic, orbital, nasal, mandibular, hyoid and opercular regions. Each section begins with a comparative chart of the bones associated with the region. The first column names the particular bone to be traced through the sixteen vertebrate skulls. The second column gives the symbols used in labelling the bones of the individual specimens. The third column describes the particular bone as medial(M), paired(P), or both(M&P). Each of the next sixteen columns represents one of the representative specimens. Colors are used in these columns to illustrate the origin of the bone: solid red = chondrocranial (cartilage replacement bone), solid green = dermatocranial (membrane bone), red striped = splanchnocranial (cartilage replacement bone), green striped = splanchnocranial (membrane bone). A dash (-) appears in a column if the particular bone was not labelled. Some bones could not be positively identified on the actual specimens either due to a high degree of fusion, insufficient and unclear literature and sketches, or the lack of the latter in such cases as the mole, bear, and fox. Others were not labelled due to their position and/or size. The number in a column refers to a statement in the text which explains a particular characteristic of the vertebrate in regards to the particular

bone. Each of the regional charts have been compiled into one concise chart (Appendix A). Photographs of the sixteen labelled specimens, along with diagrams are presented in Appendix B.

Occipital Region



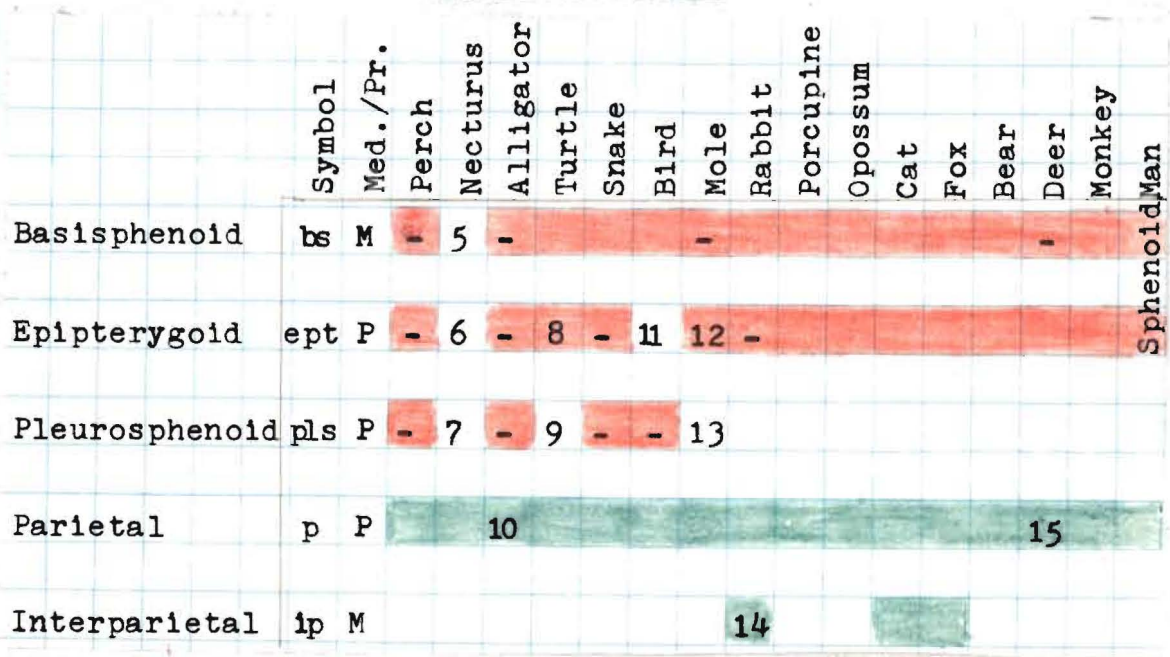
The occipital region is the most posterior portion of the vertebrate skull. It is composed of three cartilage bones: a medial basioccipital, paired exoccipitals and a dorsal supraoccipital, which is peculiar because of its compound origin (cartilaginous and dermal). A mammalian and amphibian characteristic is that the occipital bones bears two occipital condyles derived from the single one of reptiles by the retrogression of the basioccipital contribution; bird and reptiles have a single condyle(Hyman,1947).

The occipital region of the perch, alligator, turtle, snake and bird is composed of all the bones associated

with this region. The supraoccipital and basioccipital bones (1) of the Necturus are absent because they do not ossify (Weichert,1970). The single condyle of reptiles has contributions from the basioccipital and exoccipitals(Weichert,1970). The foramen magnum in the reptiles is surrounded by the basioccipital and exoccipitals, by just the exoccipitals in the Necturus and by all four in the fish and bird.

In the adult mammal, although ossification centers of all four primitive elements are seen in the embryo(Romer, 1955), all four bones of this region are often fused into a single occipital bone. This is the case on the fox, cat, bear, deer and monkey(2). The same is true of man(3); however, on this specimen (because of immaturity or peculiar racial or individual characteristic) the supraoccipital(4) was still very evident.

Parietal Region



The parietal region lies directly anterior to the occipital region. It is composed of five cartilage bones: a ventral basisphenoid, lateral pleurosphenoids and lateral epipterygoids(alisphenoids in mammals); and two dorsal membrane bones roofing this region: the parietals. Also, another membrane bone, the interparietal, may be present.

The parietal region of the perch is composed of all the bones common to this region except the interparietal. The epipterygoids and pleurosphenoids were not positively identified on the specimen.

In the skull of the Necturus the basisphenoid(5) (Neal&Rand,1946) and the epipterygoids(6)(Romer,1955) remain cartilaginous. The literature is unclear concerning the pleurosphenoid(7).

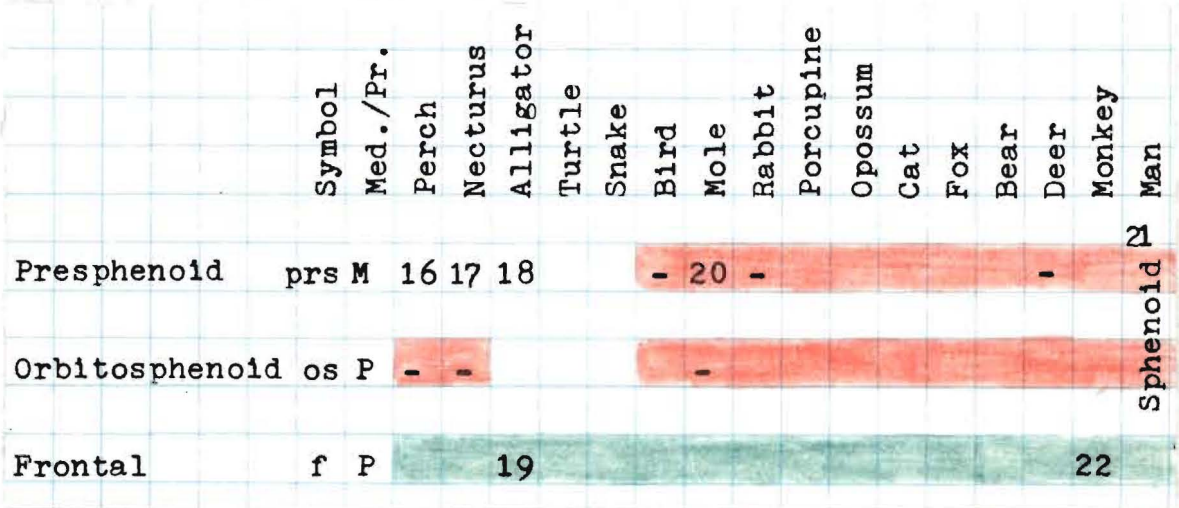
In the alligator and the snake all the bones common to the parietal region are present except the interparietal. The epipterygoids(8) of the turtle have diappeared(Romer,1955). The literature concerning the pleurosphenoids(9) of the turtle is unclear. The parietals(10) of the adult alligator have fused into a single bone. The basisphenoid, epipterygoids and pleurosphenoids of the alligator were not present on the incomplete skull used. The epipterygoids and pleurosphenoids of the snake were not identified on diagrams in the references.

In the bird no epipterygoids(11) develop(Romer,1955). The pleurosphenoid was not identified on the specimen.

The basisphenoid was indistinguishable on the mole

and deer. In mammals there are no pleurosphenoids(13); their place is taken by the epipterygoids which are known as the alisphenoids(12)(Weichert,1970). In the higher vertebrates the cartilage bones fuse into a single sphenoid bone. The parietal is a paired bone in these specimens except the deer (15). An interparietal(14) was present in three specimens: rabbit, cat and fox.

Frontal Region



The frontal region is located directly anterior to the parietal region. It is composed of three cartilage bones: a ventral presphenoid and lateral orbitosphenoids; and two dorsal membrane bones, roofing the region: the frontals.

The frontal region of both the perch and Necturus are composed of four of the five bones associated with the region. A sphenethmoid(16&17), instead of a presphenoid bone

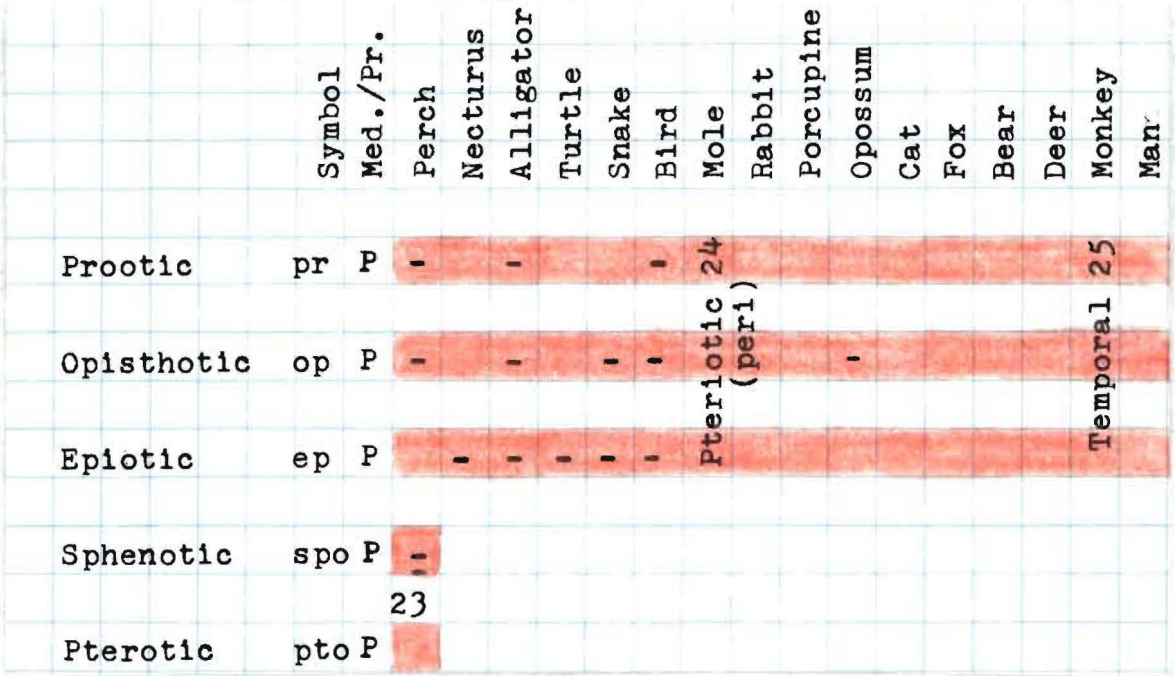
in the lower tetrapods, is present(Romer,1955). The orbitosphenoids of the specimens were not identified on available diagrams.

The frontal region of the alligator, turtle and snake has no ossifications in the chondrocranial floor anterior to the basisphenoid(Hyman,1947). In the case of reptiles, both the basal and lateral portions of this region are absent or very imperfectly developed(18)(Kent,1965). The frontals(19) of the alligator have fused to become a single large bone.

All the bones that are common to the basic frontal region are present in the bird. However, the presphenoid was indistinguishable due to its tight fusion with the region.

The sphenethmoid(20) of lower tetrapods persists in mammals, anterior to the basisphenoid, as the presphenoid (Romer,1955). The orbitosphenoid of the mole was not positively identified. The presphenoid and orbitosphenoids in some cases, as in man, combine with the basisphenoid and alisphenoids to form a single sphenoid bone(21). The frontals(22) of the primate group (monkey and man) have fused into a single frontal bone in the adult.

Otic Region



The otic region or the ear capsule, located laterally and anterior to the exoccipitals, consists of three pairs of cartilaginous (chondrocranial) bones: the pro-otic, opisthotic and epiotic.

The perch differs from other vertebrates because two additional pairs of cartilaginous bones, the pterotics and sphenotics(23) have derived from its otic region(Weichert,1970).

The pro-otics and opisthotics of the Necturus are ossified and fused with the exoccipitals(Weichert,1970). The epiotics of the reptiles and bird are fused with the supra-occipital, and the opisthotics are fused with the exoccipitals (Weichert,1970). In the turtle, the opisthotics could still

be detected.

The otic bones of lower tetrapods fuse to form a single bone in mammals called the periotic(24) or petrosal. The periotic, which at first is part of the lateral wall of the chondrocranium, later becomes overgrown by the expanding dermatocranium so that it is relegated to a ventrolateral or even a ventral position(Kent,1965). The periotic(25) of the primate specimens is fused with the squamosal and tympanic and has become the petrous region of the temporal bone(Weichert,1970).

Orbital Region

	Symbol	Med./Pr.	Perch	Necturus	Alligator	Turtle	Snake	Bird	Mole	Rabbit	Porcupine	Opossum	Cat	Fox	Bear	Deer	Monkey	Man
Postorbital	po	P	-	26		28	-	30										
Postfrontal	ptf	P					-											
Supraorbital	so	P	-		-	-	-											
Prefrontal	pf	P		-														
Lacrimal	l	P		27 -		29				-								

The walls of the orbital region are formed by contributions of five pairs of dermatocranial bones: the post-

orbital, postfrontal, supraorbital, prefrontal and lacrimal. The postorbital and postfrontal are posterolateral to the frontal bone. The supraorbital is dorsolateral to the orbit. The prefrontal is anterolateral to the frontal bone, and the lacrimal helps complete the inner wall of the orbit.

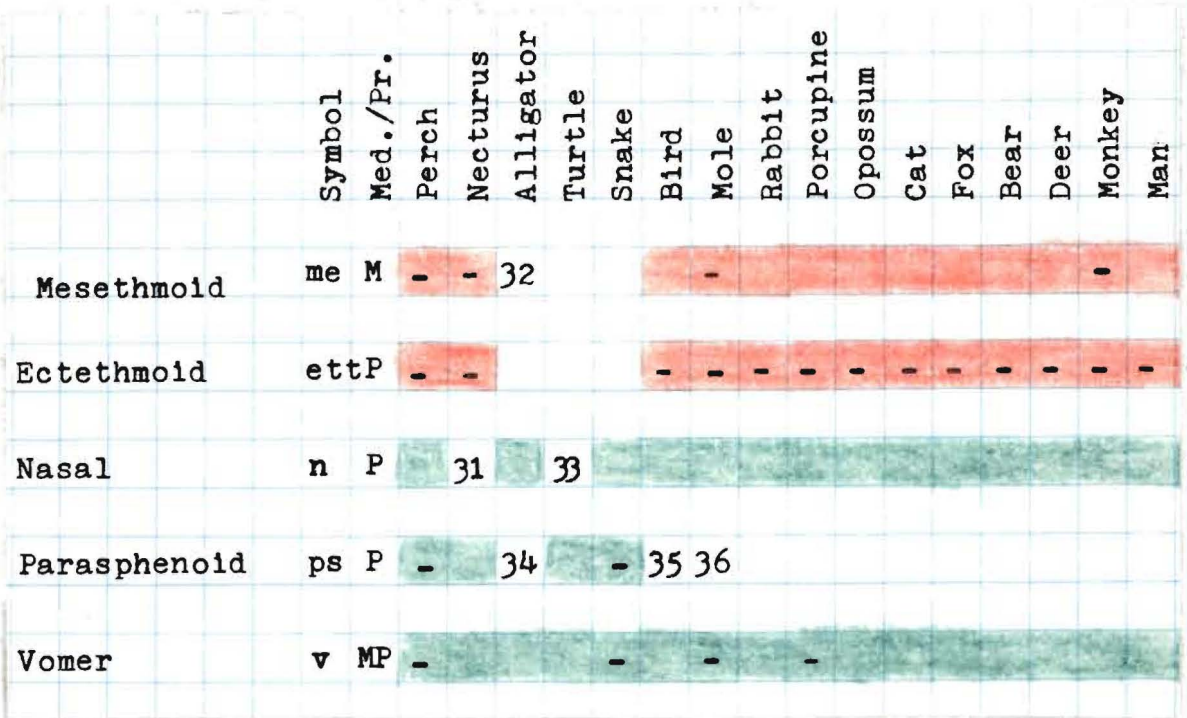
The orbit of the perch consists of all five pairs of dermatocranial bone associated with the region(Weichert,1970).

In the Necturus a reduction of the intramembranous ossification in the roofing area has resulted in the loss of the postorbital(26), postfrontal and supraorbital bones(Kent, 1965). However, there are present on the dorsal side of the cranium prefrontolacrimals(27)(Weichert,1970).

The orbit of the alligator and snake contain the five pairs of bone associated with the region. The postfrontal (28) of the turtle incorporates both the postorbital and post-frontal, and a single bone called the prefrontal(29) takes the place of the nasal, lacrimal and prefrontal(Kent,1965).

All the elements of the orbital region have disappeared in the bird and mammals(30), except the lacrimal. Other bones, such as the maxillary, orbitosphenoid, palatine and sometimes the ethmoid, help form the orbit(Weichert,1970).

Nasal Region



The nasal region lies directly anterior to the cranial cavity. It is composed of three cartilage bones: the ectethmoids and the mesethmoid. The latter is roofed over by a pair of membrane bones: the nasals. Other membrane bones are a pair of vomers (often single) and a ventral parasphenoid.

The nasal region of the perch and Necturus is composed of all the bones associated with the region except the nasals(31) lacking on the Necturus.

The nasal region of the alligator, turtle and snake lack the ectethmoids and mesethmoid(32) because they have retained their primitive cartilaginous character(Weichert,1970). The nasals(33) are lacking on the turtle because they are in-

corporated with the lacrimals and prefrontals, forming the prefrontals(Kent,1965). The parasphenoid(34) is lacking on the alligator and turtle. An unpaired vomer is evident on the turtle(Weichert,1970). The nasal region of the bird is composed of all the bones common to the region and mammals have all except the parasphenoid(36), which has either been lost or incorporated with the vomer(Kent,1965). The ecteth-moid was not positively identified on the available diagrams. The mesethmoid of the mole and monkey due to the interior position and small size, respectively, could not be identi-fied. The anterior part of the parasphenoid(35) of the bird is believed to be homologous with the rostrum, and the pos-terior portion is represented by the basitemporal plate (Weichert,1970). The bird has a paired vomer, while the vomer of mammals is unpaired.

Mandibular Region

	Symbols	Med./Pr.	Perch	Necturus	Alligator	Turtle	Snake	Bird	Mole	Rabbit	Porcupine	Opossum	Cat	Fox	Bear	Deer	Monkey	Man
Squamosal	sq	P							-				48					Temporal
Quadrate	q	P							46									
Endopterygoid	en	P	▲	39	42													(sp)
Ectopterygoid	ec	P	-	40	-	43		45										
Metapterygoid	mp	P	37															
Palatine	pl	P		39														
Quadratojugal	qj	P	38				44		47									
Jugal	j	P							-									
Maxillary	m	P		41				-									Maxillary	49
Premaxillary	pm	P					-	-										

The mandibular region is composed of the upper and lower jaws which surround the mouth cavity and lie ventral to the previously mentioned regions. The upper jaw, to be discussed first, is composed of three pairs of dermatocranial

bones: the endopterygoid, ectopterygoid and palatine; and seven pairs of splanchnocranial bone: the squamosal, quadrate, metapterygoid, quadratojugal, jugal, maxillary and premaxillary.

The endopterygoids and ectopterygoids of the perch were indistinguishable. A palatopterygoid exists in the Necturus and is composed of the endopterygoid and palatine (39). The ectopterygoid(40) of the Necturus is absent(Weichert, 1970). The metapterygoid(37) is present only in the teleosts (Kent,1965). The quadratojugal and jugal(38) of the perch seem to be absent and are definitely absent on the Necturus. The maxillary(41) of the Necturus is lacking.

The squamosal, quite evident on the reptiles and bird, is indistinguishable on the mole and has become fused with the temporal(48) on the cat, fox, bear, deer, monkey and man. The quadrate(46) of mammals, due to developmental history, has become the incus of the middle ear(Weichert,1970). The endopterygoid remains and is referred to as the pterygoid (42), which in man fuses with the sphenoid bone(sp). The ectopterygoid is present on the snake, indistinguishable on the alligator and absent on the turtle(43), bird and mammals(45). The jugal and quadratojugal are absent on the snake(44), and the latter is also absent on mammals(47). The maxillary and premaxillary(49) of the primates have fused to become a single bone called the maxillary.

The lower jaw of the mandibular region is composed

	Symbol	Med./Pr.	Perch	Necturus	Alligator	Turtle	Snake	Bird	Mole	Rabbit	Porcupine	Opossum	Cat	Fox	Bear	Deer	Monkey	Man
Articular	ar	P		-			-		52									
Dentary	d	P						-	53									
Splenial	sp	P	50	-			-	-										
Coronoid	c	P		51		-	-	-										
Surangular	sa	P					-	-										
Angular	a	P	-						54									55

of six pairs of splanchnocranial bones: the articular, dentary, splenial, coronoid, surangular and angular.

The splenial, coronoid and surangular(50) of the perch are lacking due to a reduction of the bones of the lower jaw(Weichert,1970). The latter two bones(51) are also lacking on the Necturus. The angular of the perch and the articular of the Necturus were indistinguishable.

All bones common to the lower jaw are represented on the reptiles and bird; however, many of them are indistinguishable. The articular(52) of mammals has become the malleus of the middle ear. The dentary, splenial, coronoid and surangular(53) have fused to form a single bone called

the mandible. The angular of mammals becomes the tympanic(54) which in man fuses with the temporal(55).

Hyoid Region

	Symbol	Med./Pr.	Perch	Necturus	Alligator	Turtle	Snake	Bird	Mole	Rabbit	Porcupine	Opossum	Cat	Fox	Bear	Deer	Monkey	Man
Hyomandibular	hm	P		56	-	-	-	-	57	-	-	-	-	-	-	-	-	-
Symplectic	sm	P																
Interhyal	ih	P	-															
Epihyal	eh	P	-															
Ceratohyal	ch	P		58														
Hypohyal	hp	P	-															
Basihyal	bh	M	-															
Urohyal	uh	P																

The hyoid, or second visceral arch, does not become so highly modified as the mandibular arch during its evolutionary development. It consists of seven pairs of splanchnocranial bones: hyomandibular, symplectic, interhyal, epihyal, ceratohyal, hypohyal and urohyal; and a medial basihyal.

The bones common to this region are present on the

perch. The interhyal, epihyal, hypohyal and basihyal were indistinguishable.

The hyomandibular is called the columella(56) in the amphibian, reptiles and bird. In mammals it is called the stapes(57) of the middle ear. In most species, the parts of the original hyoid apparatus are lost except for an occasional remnant(Weichert,1970). The ceratohyal, hypohyal, basihyal and urohyal(58) have a variable number of hyoid elements.

Opercular Region of Fishes

	Symbol	Med./Pr.	Perch	Necturus	Alligator	Turtle	Snake	Bird	Mole	Rabbit	Porcupine	Opossum	Cat	Fox	Bear	Deer	Monkey	Man
Operculum	o	P	59															
Preoperculum	pop	P																
Interoperculum	iop	P																
Suboperculum	sop	P																
Branchiostegal Rays	br	MP	60															

The operculum is a flap of tissue that arises as an outgrowth of the hyoid arch and extends backward over the gill slits(Kent,1965). It consists of four pairs of dermal bone: a large operculum, smaller preoperculum, suboperculum and

interoperculum. Associated with this region is a medial and and paired branchiostegal rays. No homologues of the opercular bones(59) or branchiostegal rays(60) are found to be in tetrapods(Weichert,1970).

DISCUSSION

There are more individual bones in the skull of teleosts, such as the perch, than in that of any higher vertebrate. However, the exact homologies of these bones are unclear(Montagna,1959). The perch has a well ossified skull, although in many places the bones are loosely fused. Each sense organ is surrounded by a series of small bones, for example the eye, which provide protection and permit some movement and freedom of growth. The skull is closely joined to the vertebrate column which results in the fish's inability to move its head. Small teeth are present on the premaxillary, maxillary, dentary, palatine and branchial arches. These arches serve as support for the gills, which are covered by opercular not represented in adult vertebrates above the fish. The cranial cavity extends anteriorly.

The number of bones in the skull of the amphibian is reduced either by fusion or elimination. This reduction corresponds to the shift from total aquatic to a partial terrestrial life which has left many of the fish's structures, such as the gills, without a function. Also, in the case of the Necturus, the supraoccipital and basioccipital of the chondrocranium are not ossified. The area around the sense organs have been simplified by loss of many small bony elements. A large parasphenoid makes up most of the ventral side

of the skull. Small teeth are present and located on the dentary, premaxillary, maxillary, vomer, splenial and palatopterygoid. The entire skull is flattened dorsoventrally, shortened and widened, and articulates with the first vertebra by means of a pair of occipital condyles. The cranial cavity extends anteriorly.

Reptilian skulls show a further increase in the degree of ossification. Within the group there are many variations corresponding to different habitats and food habits. The alligator has a heavily roofed skull with tightly fused bones, a long snout and teeth, which are large and of various lengths and sizes. The skull of the turtle is exceptionally large in comparison to the enclosed brain, and very heavy with pronounced fusion of the various bones. The jaws lack teeth, but have cornified layers which crush the food. The skull of the snake is light and very delicate. It is not tightly fused, enabling bones to move on one another. All the bones of the skull are moveable except for the brain case. The bones of the jaw apparatus are highly modified, enabling the snake to swallow prey much larger in diameter than itself. Thus, the snake neither chews nor tears its food, but swallows it whole. The teeth, located on the dentary, premaxillary, maxillary and pterygoids, have a backward slant that enables the snake to hold food while it is being swallowed. Also, poisinous snakes have a pair of specialized teeth, or fangs, that conduct venom used to kill their prey. The movement of the head in reptiles

is freer because the skull articulates with an improved cervical vertebra by means of a single, medial occipital condyle. The cranial cavity does not extend as far anteriorly.

The bird has a domed skull that is larger and more spherical than that of reptiles. Every bit of bone that could be spared has been eliminated from its skull; the bones are thin and light in weight, however, quite strong. The bones have fused so tightly in the adult that the sutures have become obliterated. Its chief peculiarity is the large size of the orbits which are out of proportion to the rest of the skull. The enormous size of the eyes have resulted in the cranial cavity of the expanded brain assuming a more posterior position, accommodating the correspondingly enlarged occipital lobe for vision. The facial bones are elongated to form a horny beak for feeding, instead of teeth, resembling the turtle. As in the reptile, the skull articulates on a single occipital condyle; however, the condyle has taken a more ventral position for the bird's semi-erect posture.

The mammalian skull is proportionally larger than that of any other vertebrates because of its increased cranial capacity, which accommodates the expanded cerebral hemispheres. Except in primates, there is usually a long snout in which the olfactory sense is highly developed. The number of bones again has been progressively reduced by fusion of adjacent elements to form single-bone complexes, such as the occipital, sphenoid and temporal. In all forms below mammals the lower jaw articu-

lates with the skull at the quadrate, whereas in mammals, it articulates with the squamosal. In the ear region there are now three ossicles, the incus, malleus and stapes, homologous to the quadrate, articular and hyomandibular, respectively, which have assumed a new function as a result of modification of form and a shifting of position. The eyes of mammals, as in the lower vertebrates, are located on the lateral sides of the skull in order to permit the animal to watch on both sides for enemies. However, the eyes of primates are directed anteriorly to provide a binocular vision. The marsupials, such as the opossum, have a fenestrated palate, and the brain capacity is comparatively small to that of placental mammals. As the cranial process progressively expands to accommodate the increased size of the brain in the placentals, there is a reduction in the size of the facial elements until in the primates the brain case makes up most of the skull and extends over the facial elements in such a way that they are ventral to the cranium rather than anterior to it. The mammal can move its head to a greater degree than lower vertebrates because of two occipital condyles articulating with the first vertebra, the atlas, in association with the second vertebra, the axis. The condyles also have assumed a more ventral position ascending the mammals until in primates, especially man, the posture is very erect. The teeth of mammals are located only on the premaxillary, maxillary and mandible. Comparatively, the teeth become proportionally larger and are quite sharp for shearing

piercing in flesh eaters.

SUMMARY

The vertebrate skull originates from three separate embryonic components: chondrocranium (cartilage replacement), dermatocranium (membrane) and splanchnocranium (cartilage replacement and membrane). The vertebrate skull undergoes a gradual reduction of the number of bones with phylogenic ascension. Reduction in number results from fusion, elimination, or remaining unossified. The shape of the skull varies according to the habits, environment, degree of development of a particular sense and size of the brain of the vertebrate. As the vertebrate group is ascended, there is an increased degree of ossification and also, an increase in the cranial capacity. Most bony elements of the vertebrate skull are homologous, deriving from the basic pattern of development and arrangement of these elements.

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APPENDIX A

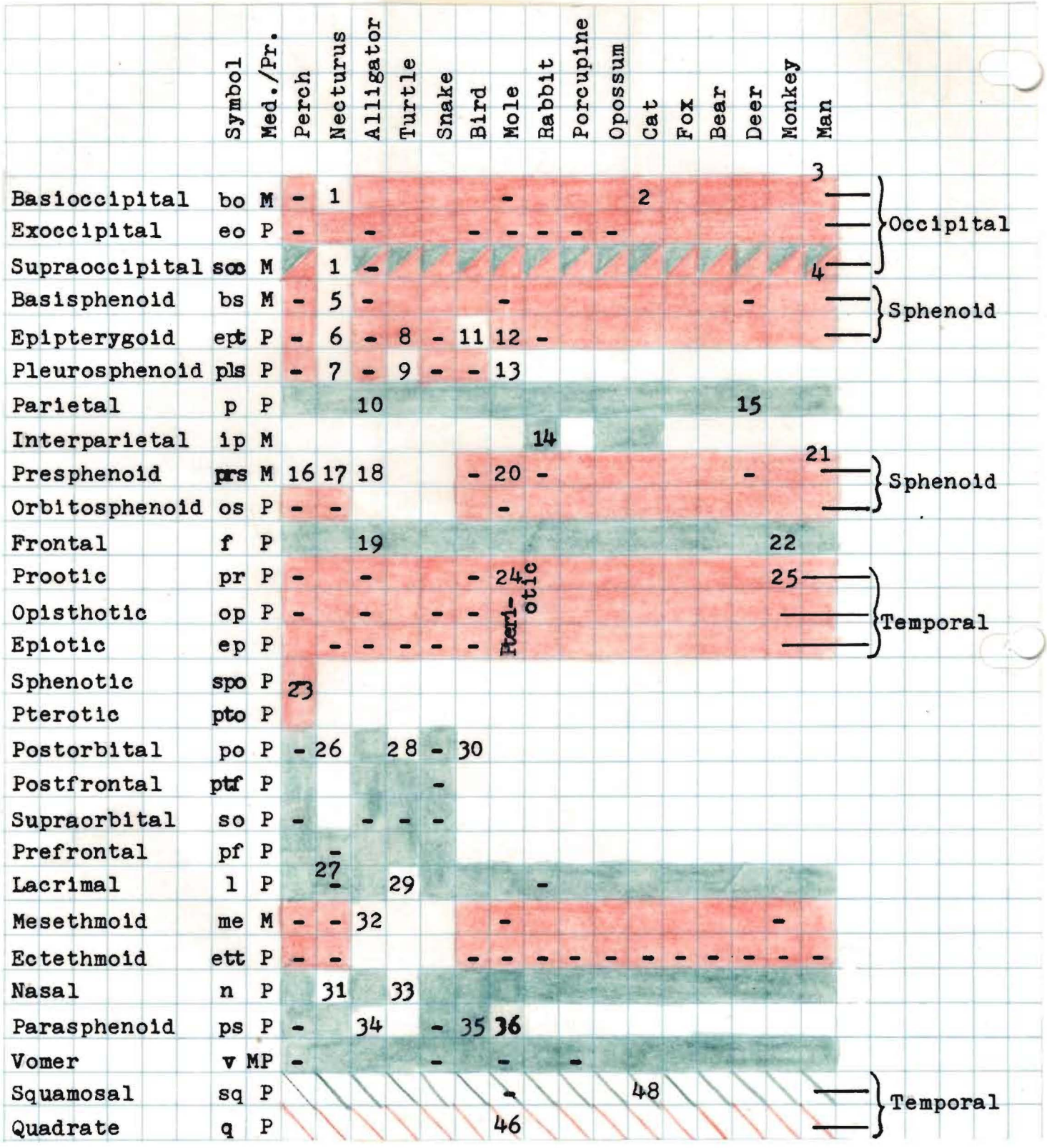

Figure 5 A comparative chart of sixteen representative vertrbrate specimens. First column names particular bone; second gives its symbol; third describes bone as medial, paired, or both; next sixteen names representatives. Colors represent origin: solid red=chondrocranium(cartilage replacement bone); solid green=dermatocranium(membrane bone); red striped=

	Symbol	Med./Pr.	Perch	Necturus	Alligator	Turtle	Snake	Bird	Mole	Rabbit	Porcupine	Opossum	Cat	Fox	Bear	Deer	Monkey	Man
Endopterygoid	en	P	-	39	42													(sp)
Ectopterygoid	ec	P	-	40	-	43		45										
Metapterygoid	mp	P	37															
Palatine	pl	P		39														
Quadratojugal	qj	P	38				44		47									
Jugal	j	P							-									
Maxillary	m	P		41				-									49	} Maxillary
Premaxillary	pm	P					-	-										
Articular	ar	P		-			-		52									
Dentary	d	P						-	53									
Splenial	sp	P	50	-			-	-										
Coronoid	c	P		51		-	-	-										
Surangular	sa	P					-	-										
Angular	a	P	-						54									55
Hyomandibular	hm	P		56	-	-	-	-	57	-	-	-	-	-	-	-	-	-
Symplectic	sm	P																
Interhyal	ih	P	-															
Epihyal	eh	P	-															
Ceratohyal	ch	P		58														
Hypohyal	hp	P	-															
Basihyal	bh	M	-															
Urohyal	uh	P																
Operculum	o	P		59														
Preoperculum	pop	P																
Interoperculum	iop	P																
Suboperculum	sop	P																
Branchiostegal Rays	br	MP		60														

splanchnocranium(cartilage replacement bone); and green striped=splanchnocranium(membrane bone). A dash (-) appears in a column if the bone was not labelled on the particular specimen. The number in a column refers to a statement in the text which explains a particular characteristic of the vertebrate in regards to the particular bone.

APPENDIX B


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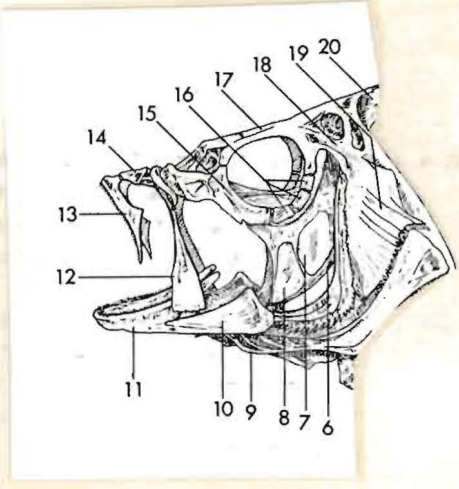
Figure 6 Lateral view of the skull of the Perch (Cymatogaster aggregatus).

Figure 7 Diagrammatic drawing of the lateral view of the perch. Numbers refer to the following: 6-Symplectic, 7-Metapterygoid, 8-Quadrate, 9-Branchiostegal rays, 10-Articular, 11-Dentary, 12-Maxilla, 13-Premaxilla, 14-Nasal, 15-Lacrimal, 16-Orbitals, 17-Frontal, 18-Parietal, 19-Operculum, 20-Supraoccipital(From Carolina Biological Supply Company, Review Sheet 119).

Figure 8 Diagrammatic drawing of the lateral view of the perch. Symbols refer to the following: A'(ar)Articular, BS(br)Branchiostegal rays, CH(ch)Ceratohyal, D"(d) Dentary, E(eth)Ethmoid, EPO(ep)Epiotic, FR(f)Frontal, HM(hm)Hyomandibular, IO (iop)Interoperculum, MX(m)Maxilla, O(o) Operculum, PA(p)Parietal, PF(pf)Prefrontal, PMX(pm)Premaxilla, PO(pop)Preoperculum, PTF(ptf)Postfrontal, PTO(pto) Pterotic, Q(q)Quadrate, SM(sm)Symplectic, SO(sop)Suboperculum, SOC(soc)Supraoccipital, SQ(sq)Squamosal, UH(uh)Urohyal (From Romer,1955).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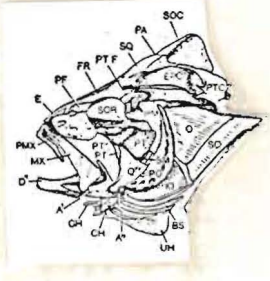
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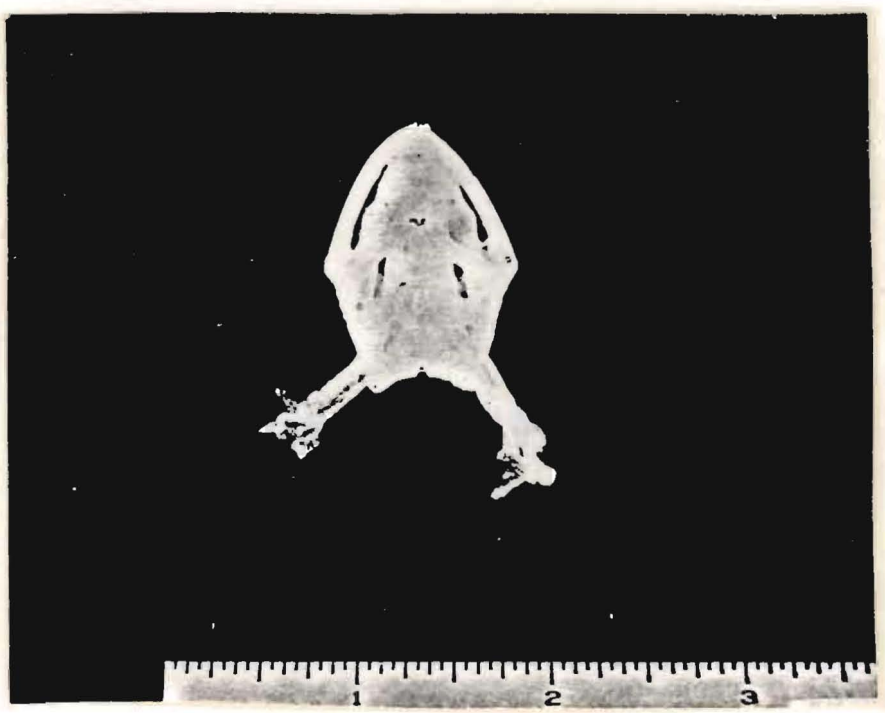
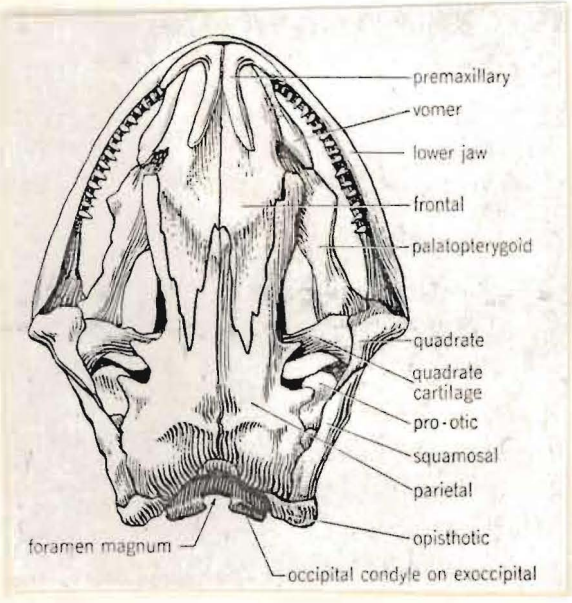


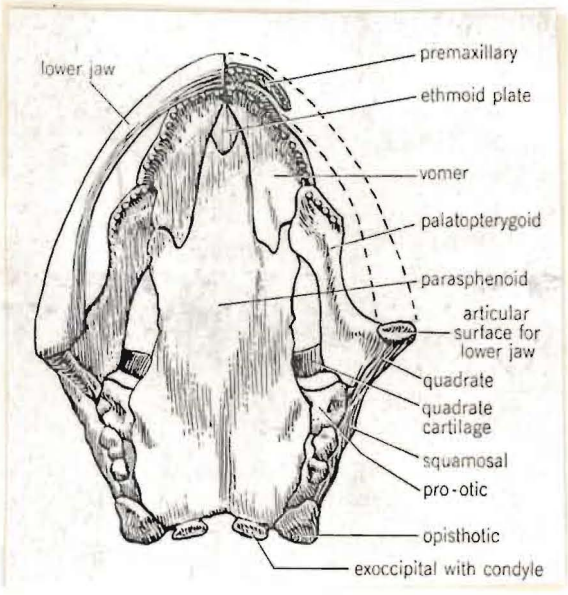
Figure 9 Dorsolateral view of the skull of the Necturus (Necturus maculosus).

Figure 10 Ventral view of the skull of the Necturus.

Figure 11 Diagrammatic dorsal view of the skull of the Necturus(From Weichert,1970).

Figure 12 Diagrammatic ventral view of the skull of the Necturus(Weichert,1970).


premaxillary
vomer
lower jaw
frontal
palatopterygoid
quadrate
quadrate cartilage
pro-otic
squamosal
parietal
opisthotic
foramen magnum
occipital condyle on exoccipital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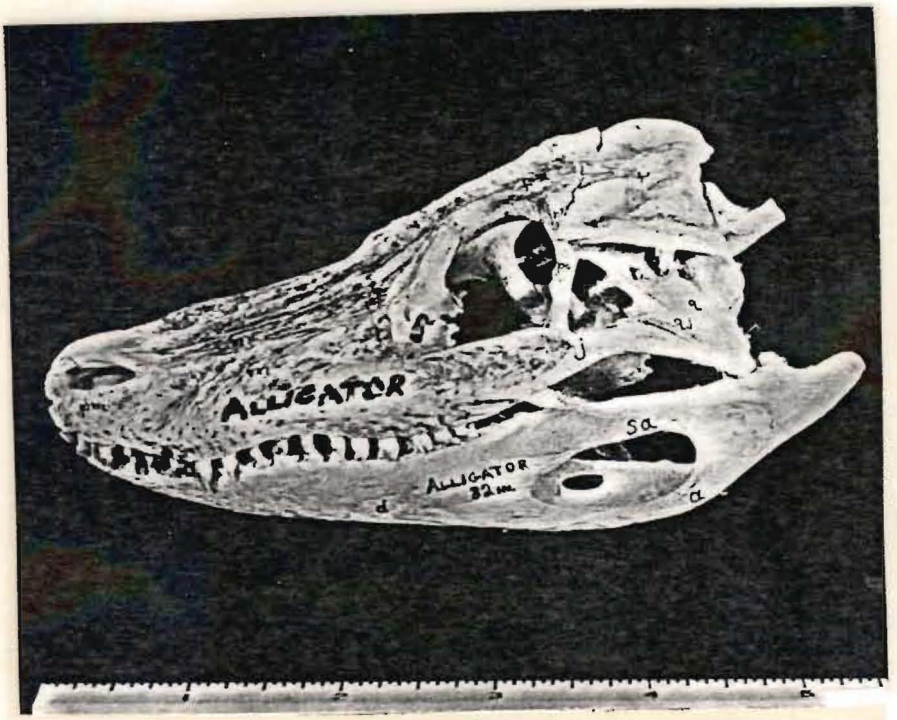
premaxillary
ethmoid plate
vomer
palatopterygoid
parasphenoid
articular surface for lower jaw
quadrate
quadrate cartilage
squamosal
pro-otic
opisthotic
exoccipital with condyle


ALLIGATOR
ALLIGATOR
32 mm.

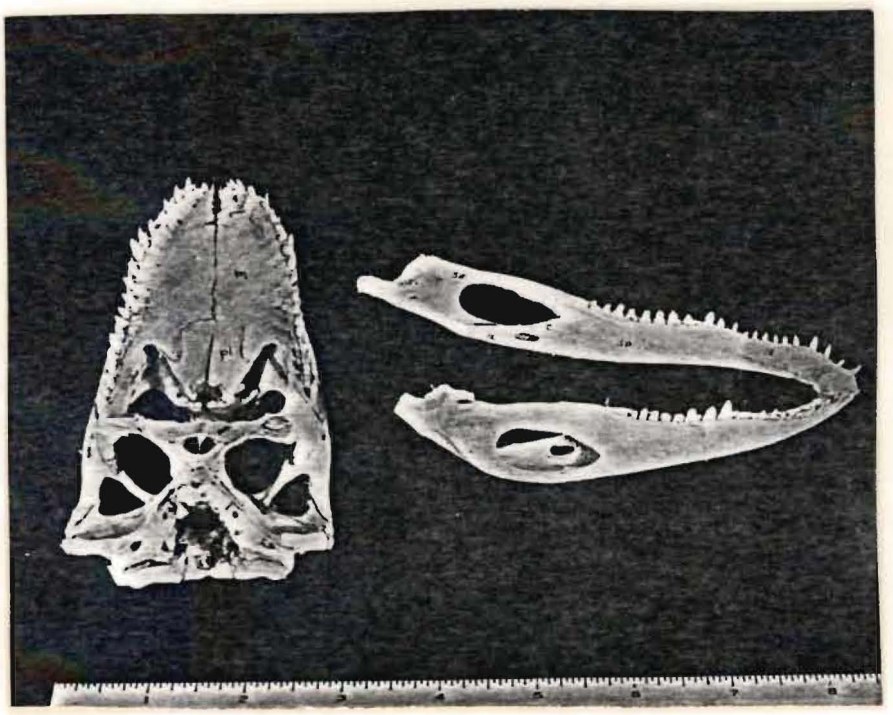


Figure 13 Dorsolateral view of the skull of the alligator(*Alligator mississippiensis*).

Figure 14 Ventral view of the skull of the alligator along with its mandible.

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