

1993

The structure of the holocephalan head and the relationships of the Chondrichthyes

Eileen D. Grogan

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the Chondrichthyes**

Grogan, Eileen D., Ph.D.

The College of William and Mary, 1993

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THE STRUCTURE OF THE HOLOCEPHALAN HEAD AND THE RELATIONSHIPS
OF THE CHONDRICHTHYES

A Dissertation

Presented to

The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of
Doctor of Philosophy


by

Eileen D. Grogan

1993

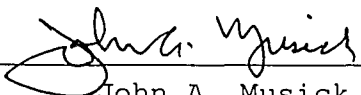
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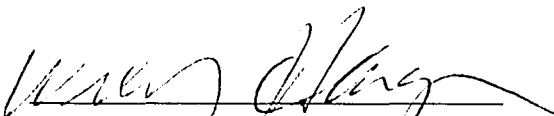


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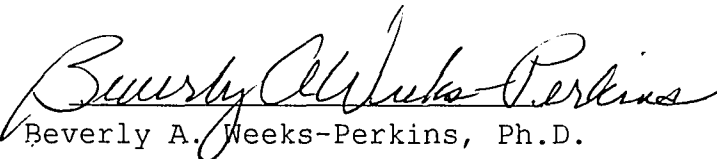
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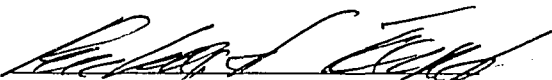
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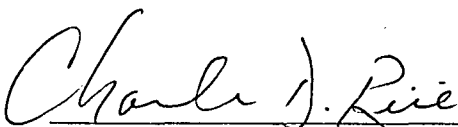
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ABSTRACT

The interrelationship of the chondrichthyan subclasses is evaluated based on divergences in the nature of the suspensorium, the preorbital cranial anatomy, the distribution of major venous sinuses and localization of hematopoietic tissue. The anatomy of representative extant taxa was examined by radiography and/or dissection. Fossil selachians, paraselachians, and holocephalans of the Bear Gulch of Montana, U.S.A. (Mississippian, Namurian E2B) were studied for evidence of vascular pigmentation, suspensorium, and cranial, branchial, and pectoral anatomy. These studies validate the suspensorial condition of autodiastyly and suggest autodiastyly is a fundamental condition involved in the basic radiation of Chondrichthyes. The plesiomorphous condition of all gnathostomes is proposed to be autodiastylic, with the hyoid arch modified for the support of an opercular covering. A precerebral fontanelle is primary within Chondrichthyes, being lost in Holocephali as cranial remodeling induces ethmoid canal formation. The holocephalan pattern of cranial vascularization is based on the more general selachian plan. Thus, given the formulation of a morphocline based on selachian, paraselachian, and holocephalan data, seemingly distinct selachian and holocephalan vascular elements are shown to be analogous. Similarly, the unique patterns of lymphomyeloid tissue distribution identified for each subclass may also be explained on the basis of a general plan which has been subject to relocalization stresses. Finally, both the morphocline and a cladistical analysis of the data support a coeliodont ancestry for extant holocephalans.

THE STRUCTURE OF THE HOLOCEPHALAN HEAD AND THE RELATIONSHIPS
OF THE CHONDRICHTHYES

INTRODUCTION

The Origin and Relationships of Chondrichthyes: A Case of the Disappearing Basal Complex?

The Holocephali and Elasmobranchii are currently held to be sistergroups, principally united by the common character trait of a prismatically calcified cartilaginous endoskeleton. Paleontological evidence of these fish traces the elasmobranch lineage to the Lower Devonian while incontrovertible holocephalans have been traced to the Upper Devonian. The search for a common ancestor for these groups continues today. However, recent paleontological finds from the Pennsylvanian of Indiana (summarized in Zangerl, 1981) and the Mississippian of Montana (Lund 1977a, 1977b, 1982, 1986, 1990) present a clearer and broader view of the difficulties encountered in defining the interrelationships of these groups and identifying the basal members of the chondrichthyan assemblage.

Historically, two schools of thought have prevailed as to the relatedness of Holocephali and Selachii. One holds that these groups are each descendent from Arthrodirian placoderms and subsequently have separate evolutionary lineages (Stensio 1925). Of the arthodiran forms, Orvig advocated a ptyctodont ancestry for chimaerids based on his

description of Ctenurella (1960). Holmgren also supports this association based on the Middle to Upper Devonian Rhamphodopsis (1942). Patterson (1965), in contrast, suggests an association to the primitive rhenanids and stensioellids, albeit indirect. With regard to the selachians, the macropetalichthyidae were interpreted to represent the ancestral stock since these were most reminiscent of an elasmobranch morphotype (Romer, 1966).

Moy-Thomas' and Miles' views are representative of the second school of thought wherein the selachian and holocephalan lineages diverged subsequent to an initial separation of a basal stock into chondrichthyan and placoderm lines (1935, 1971). This interpretation has been supported by the work of Holmgren (1940) and Bendix-Almgren (1968). Yet, confirming this latter theory has proven to be a difficult task. Much controversy has been generated in the attempts to demonstrate a sistergroup status. The major point of confusion may be attributed to the classification schemes originally used to group early sharks and related fishes. These schemes were based upon fragmentary evidence of fin spines, scales, and dentition and often resulted in the identification of fish groups which did little for the understanding of early chondrichthyan affinities. The initial classification of Carboniferous shark and shark-like groups is a case in point. Cladodonts, Xenacanth, Hybodonts, Edestids and Bradyodonts were grouped primarily

according to dentition. It is now understood that of these groupings, the Bradyodonts are the most diverse in body form, dentition, nature of jaw/neurocranial association and cranial dimensions and, as such, are likely to be an unnatural grouping. In keeping with this latter notion, it is important to note that a variety of fossil taxa have been attributed to the Bradyodonts at one point or another. In fact, there have been multiple redefinitions of the group since it was first proposed (Smith-Woodward 1921) as a grouping intermediate to primitive elasmobranchs and chimaeroids. Yet, if one were to seek evidence for a close relationship between selachians and holocephalans then it is most likely to be found within the taxa originally classified as Bradyodont. Moreover, the prospective link between extant and fossil holocephalans may also be found in forms originally classified as bradyodont, i.e. the cochliodonts (Smith-Woodward, 1932; Obrucsev, 1967; Lund, 1986).

My interest in the chondrichthyan sistergroups lies not only in the phylogenetic relationship of fossil forms but in demonstrating how particular points of divergence noted between extant selachians and chimaerids may be explained through the fossil data. These divergences involve characters which have either been extensively examined by few researchers, or are not normally considered in debates on the sistergroup status since they are features of the

soft anatomy. Yet, the finely preserved Bear Gulch material has permitted the unique opportunity to examine these features in fish which give every indication of being involved in the early diversification of the Chondrichthyes.

The four states of departure between the respective selachian and chimaerid conditions which form the focal point of my research are (1) the free versus fused suspensorial state, (2) the presence of a precerebral fontanelle versus formation of an ethmoid canal, (3) the presence versus absence of a hyoid sinus, and (4) the concentration of lymphomyelogenous tissue within or around organs specialized for non-immune related functions versus its concentration within the cartilaginous endoskeleton. I have studied the nature of each of these conditions in recent representatives. The Bear Gulch specimens were concurrently examined to determine if these features also represent points of distinction between the fossil chondrichthyans and, if so, whether or not there is any indication as to the origin of such character divergences. Furthermore, it was anticipated that in answering these two major questions the results would permit a novel approach to answering the sistergroup debate. This dissertation, therefore, presents an analysis of each of these four character divergences and discusses the results of these analyses relative to the prevailing arguments on the

classification of Chondrichthyes as comprised of the subclass Elasmobranchii and the subclass Holocephali.

MATERIALS AND METHODS

The fossils examined for this study are those of the Montana Bear Gulch Limestone (Heath formation, upper Chesterian, Namurian E2b; upper Mississippian). Most of the specimens have yet to be formally described in the hierarchy of a chondrichthyan classification, yet are clearly members of a selachian: paraselachian:holocephalan assemblage which reflect the high diversification characterizing the fish of this early age (ca. 320MYA, Lund, 1990). Fossils examined for this study included both described and undescribed. (The latter are referred to by their code names throughout this text.) The assemblage included;

- a. Cochliodont groups, COCH1 and COCH3
- b. Echinochimaera
- c. ELWEIR
- d. Erismacanthus
- e. Chondrenchelyiformes - Harpagofututor
- f. Harpacanthus
- g. Orodus
- i. Superfish 1 (Sup1)
- j. Heteropetalus elegantulus
- k. Het2
- l. Chomatodus

Specimens are referred to by their field number and/or their

catalogue number corresponding to the appropriate institutional collection. The letter abbreviations and corresponding museum collections are: CM, the Carnegie Museum of Natural History; ROM, the Royal Ontario Museum; and MV, the Vertebrate Section of the Museum of the University of Montana.

All fossils were examined by dissection microscope, employing 70% ethanol when necessary to enhance the visualization of pigments, cartilaginous elements, and soft anatomy. Relevant data for Ornithoprion, Caseodus, Helodus, and Squaloraja were collected from published sketches and writings of other authors.

Extant specimens (obtained through 1990-1992 F.V. Anthony Anne shark long-lining, 1990-1991 R.V. Delaware II, 1991 University of Washington at Seattle and '92 RS Africana cruises) were used for vascular injection procedures and comparative dissections. Radiography carried out on barium injected specimens was performed according to the technique described by Alexander (1990). Thus, cranial as well and abdominal vascularization were surveyed in extant chondrichthyans and compared to the vascular pigment patterns found in the fossil forms. In conjunction with this, features of the suspensorium, rostro-ethmoidal region, branchial position and architecture, and overall cranial dimensions were recorded. Additional characters were noted in extant Holocephali and the Bear Gulch assemblage to

supplement the list of characters that could be used for cladistical analyses. These included relative body proportions, body and fin shape, the distribution of and morphology of cranial and body denticles, shoulder girdle position, development of abdominal organs, etc. The results of all relevant observations and comparisons were used to formulate a clinal transition of the chondrichthyan forms. This transitional series was also used to explain apparent divergences in the vascular, endoskeletal, and immunologic tissue features between selachians and holocephalans. The phylogenetic analysis programs, Hennig '86 and PAUP, were employed to assess the phylogenetic relationships of the members of the morphocline. A total of 77 characters were compiled for these analyses, 25 of which were based on head or head associated features. A character matrix was generated for each of thirteen taxa and run in Hennig '86 as a rooted tree (actinopterygian and acanthodian outgroups) with nonadditive characters. This program was rerun under the same conditions with the exception that the character matrix was limited to head and head associated features. The resulting Hennig '86 cladograms were then compared to those generated by PAUP under identical input constraints.

RESULTS AND OBSERVATIONS

The paraselachians, Superfish1 and Het2, are autodiastylitic chondrichthyans which represent the intermediate forms in a clinal transformation from the selachian morphology to that of the holocephalan. Although the relevant fossil and extant data and results are presented within the context of the appropriate discussions, descriptions of the paraselachian species and other Bear Gulch chondrichthyans are presented here.

Superfish1

Sup 1 exhibits a dramatic foreshortening of the posterior aspect of the neurocranium. This feature occurs in conjunction with the possession of a sole foramen in the lateral/posterior floor of the orbit, i.e. a cranioquadrate passage. Pigmentation and a dorsal orbital foramen indicate the presence of a selachian-type supraorbital vein. As in extant Selachii the Sup1 vessel traverses the supraorbital cartilage to join the orbital sinus. The anterior margin of the orbit is pierced by two foramina. One appears to be the typical orbitonasal foramen, permitting passage of the orbitonasal vein to the nasal capsule. The second foramen lies dorsal to the orbitonasal. The anterior opening to this foramen appears leads to an anteromedially directed bilateral preorbital canal which houses a tributary of the

orbital sinus and carries the vessel to the ethmoidal region.

Cranial Vascularization as indicated by CM41036

The A face of the specimen shows simple forward coursing preorbital vasculature, extending from the orbit to the mandibular symphysis and orbital foramina identified as those for the orbitonasal and supraorbital veins.

Occasional branching can be seen from each preorbital vessel but the counterpart demonstrates these bilateral elements remain independent of each other, and the presence of a well developed orbital sinus. A cranioquadrate passage and associated vasculature are also evident. One branch of the vasculature entering the orbit via this passage appears to arise from the branchial region, the other branch coursing from an anterior palatal region. The lateral head vein can be seen traveling forward along the lateral margin of the shoulder and head region to the strong postorbital wall wherein it traverses the orbital cartilages to enter the orbital sinus.

Cranial Vascularization as indicated by CM35489A

Pigmentation outlines the path of the preorbital canals from orbit to rostrum. The pigments indicating the anterior margin of the orbital sinus extend around the anterior rim of the orbit from the superficial ophthalmic nerve foramen to the orbitonasal foramen. The remaining orbital foramina follow those described for CM46101 and also include the

cranioquadrate passage.

Cranial Vascularization as indicated by CM35488A

The orbital sinus vasculature and its tributaries are clearly indicated, particularly with regard to the lateral head vein, orbitonasal vein , and the preorbital vein tributaries. The pigmentation patterns confirm the observations cited for other specimens and the interpretations of the cranial vascularization plan.

Summary of Salient Superfish1 Features Based on CM41036A+B, CM35489A, CM35488A, MV6175B Specimens.

1. generalized selachian-type body plan
2. deeply seated, immobile first and second dorsal fin spines
3. Derived caudal fin shape: significant epichordal lobe
4. simple, poorly calcified pectoral girdle with unfused right and left halves (Note, however, that all specimens are relatively immature)
5. stout scapular process with high dorsal aspect
6. well developed, calcified claspers on male pelvic girdle
7. sclerotic cartilages which fuse with maturity
8. well developed ceratohyal rays
9. opercular covering
10. branchial basket extending beyond the hind limit of the cranium from a subpostorbital position
11. broad occipital margin the cartilage of which slopes downward posterior to the otic region

12. significant development of axial and cervical vertebral arches
13. simple plesiomorphous lateral line canals
14. separate right and left mandibules
15. dentition evidently extending far back on lower jaw, to the point just anterior to the mandibular articulation
16. moderately broad interorbital orbital span, large eyes, and a stout, prominently displayed postorbital wall
17. palatoquadrate articulations at hind margin of orbit and "ethmoid" or preorbital site.
18. well developed endolymphatic fissure
19. bilateral canals extending from orbit to rostral region

Het2

Certain Het 2 features are reminiscent of those described for Sup 1 although they are more extreme in the morphological shift away from a selachian-type plan. This species possesses a dramatically shortened otico-occipital region which is accompanied by the forwardly placed and nested branchial arches, positioned at a suborbital to subotic level. The shoulder girdle is also placed forward, being situated immediately behind these arches. Just as in Sup1, the hyoid arch is modified to support an opercular covering. Well developed ceratohyals are found and appear to be continuous with hypohyal elements. However, Het 2 is unambiguously distinguished from Sup 1 in the nature of the

mandibular arch. It is placed in an extremely anterior position. The posteriormost portion of the palatoquadrate articulates with the neurocranium at the level of the anterior orbital margin. The anterior articulation is ethmoidal.

Bilateral, preorbital canals extend from the anterior and somewhat dorsal margin of the orbit via the superficial ophthalmic nerve/ethmoid foramen. This foramen is located in the anterior mesial margin of the orbit. The extensive pigmentation of this region is anteriorly continuous with that of the nasal capsule. The ventral mid-orbital margin is marked by vascular pigmentation which extends from the orbital floor towards the gills and lower jaw. This pigmentation suggests *Het2* possessed a vessel equivalent to the maxillofacial vein. This interpretation is based on the discovery that the vascular tributaries indicated follow a bifurcation and drainage pattern reminiscent of the holocephalan maxillofacial. As in extant chimaerids this orbital sinus tributary does not pierce any suborbital or basitrabecular cartilage.

At least one other orbital foramen can be found and is located at the dorsoposterior margin of the orbit. There may also be one in the supraorbital crest but this needs to be confirmed in additional specimens. If so, the positioning suggests they convey the superficial ophthalmic nerve and the dorsal cephalic vein.

Vascular and Related Cranial Features of CM46101B

The roof of the ethmoid region merges with the side wall of the cranium and the palatoquadrate cartilage to form a wish bone-shaped structure, one wing of which appears as a vertical and angled lamina at the hind region of the nasal segment. This is interpreted as that portion of the lamina orbitonasalis which separates the nasal capsules from the preorbital canal just forward of the ethmoid articulation. Just medial to this articulation vascular pigmentation suggests that a merging of the two preorbital canals occurred at this anterior point. Otherwise, the canals are separate to the level of the orbit. Three foramina other than that of the preorbital canal are visible. One situated at the dorsal and hind orbital region is interpreted to have transmitted the posterior orbital (jugular) vein. Two foramina, located in the floor of the orbit, are believed to represent the cranioquadrate passage and a more anterior one which has yet to be labeled but may be associated with the branchial arches.

The cartilages of an opercular rim are found, as are opercular rays which are accompanied by extensive vascularization. An articulation is indicated between the posteriormost branchial arch and the right fragment of the shoulder girdle. More dorsally, the shoulder girdle closely abuts against the posterior margin of the cranium. Heavily calcified articulation points are found on the cranial

cartilages corresponding to the palatoquadrate and scapular

Vascular and Related Cranial Features of CM48831B

This specimen offers excellent information on lateral line canals which extend from the rostral tip to the level of the orbital articulation of the palatoquadrate. The path of the preorbital canals follows that of the inner margin of the palatoquadrate element within this span. The three dimensional shape of the neurocranium has also been remarkably maintained. The interorbital region is extremely narrow, with the orbits taking on an oblique orientation to each other. The supraorbital cartilages are stout, flaring slightly in the brow region. The area between the orbit and occipital regions is quickly widened posteriorly over a short distance and the dorsal and ventral occipital margins demonstrate heavily reinforced and calcified articulation zones. The preserved branchial elements are reminiscent in arrangement and form to those of the extant Holocephali in which the shoulder girdle is intricately associated with the branchial skeleton and encases the cardiac region. A count of 5 to 6 branchial arches was estimated.

Vascular and Related Cranial Features of ROM 43173A+B

Details of most of five branchial arches are preserved in this specimen. Opercular rim cartilages are prominent and form a foramen just below the midorbit. A vessel which follows the dorsal limit of the branchial arches is believed to traverse this foramen before entering the orbital sinus.

The pattern of vascularization may be traced for individual arches and, anteriorly, the tributaries of the maxillofacial can be located where the branchial arch skeleton meets the level of the posterior palatoquadrate articulation. As noted for CM48831 the shoulder girdle comes into contact with the branchial basket in this specimen. Heavy calcifications are found at the level of the forward "ethmoid" articulation in A while B also shows the laminae orbitonasalis at this level. Heavy preorbital canal pigmentation is found at the calcifications and extends posteriorly to directly communicate with the orbit.

Vascular and Related Cranial Features of ROM 43174

The shoulder girdle interconnects to the fifth ceratobranchial element. Remnants of the maxillofacial are found at the juncture between the quadrate articulation and anterior limit of the branchial arches. An extensive calcification has also been noted at the level of the anterior palatoquadrate articulation while, in the orbital region, a strong suborbital shelf flares forward to the orbital articulation of the palatoquadrate. Pigmentation within the orbit, branching from a central focal point would support the identification of a cranioquadrate passage in this region.

Summary of Salient Het2 Features Based on CM46101B, CM48831B, ROM 43173A+B, ROM 43174B Specimens.

1. heterocercal tail .

2. well calcified pelvic claspers in males (Note, both mature and immature forms of both sexes have been identified.)
3. pigmentation found at the base of the pelvic girdle indicates a well developed sinus while that found in the abdominal region indicates a gonadal sinus
4. possession of a mobile first dorsal fin spine which exhibits serrations on its posterior margin
5. a dorsal fin continuing caudally as a long, low structure
6. pectoral girdle position immediately posterior to the cranium
7. no synarcuum is present but anteriormost vertebral elements are strengthened
8. a well developed scapulocoracoid; its dorsalmost process articulates with the occipital region and the posteriormost branchial arch
9. the branchial arches are positioned subcranially; occupying a span parallel to the mid-orbital and occipital regions
10. branchial arch architecture is virtually identical to that of extant holocephalans
11. bilateral ethmoid canals interconnect at the level of the ethmoid articulation
12. the cranial lateralis system does not appear to be extensive nor developed in the extant holocephalan fashion

13. each half of the mandibular arch and shoulder girdle remain separate and unfused

Other Bear Gulch Chondrichthyans:

Heteropetalus elegantulus Although originally described as hyostylic by Lund (1977), this research demonstrates the suspensorium is autodiastylic. This paraselachian differs from Het 2 in that the shoulder girdle is placed far behind the neurocranium and the dimensions of the mandibular elements are entirely different from the adult specimens. The "baby" specimen has longer upper and lower jaw elements with articulations occurring at or behind the posterior limit of the orbit. The features of the orbit suggest more of a selachian type jugular. There is an orbital foramen for the jugular with a sulcus in the lateral cranial wall for the posterior transmission of the vessel. This feature agrees with the more posteriorly placed gills which are located primarily behind the neurocranium.

Heavy organic pigmentation extends from the jugular foramen around the lower margins of the orbit towards the anterior orbital foramina. The anteroventral foramen leads to a short orbitonasal canal which remains lateral to the precerebral fontanelle as it extends anteriorly for a short distance. The resident vasculature of the anterodorsal foramen could not be traced but it appeared to lead to the preorbital region.

Three articulation points were noted between the upper

jaw and the neurocranium. A "postorbital" or otic connection (located at or about the posterior orbital margin), a basal articulation (at the anterior margin of the orbit), and an ethmopalatine articulation.

Harpagofututor volsellorhinus. This is a holostylic paraselachian which exhibits selachian type abdominal features including a finely preserved caudal vein, simple digestive tract, and probable fin sinuses of the selachian form. Cranial features, however, are far from selachian morphology. A strong laterally flaring suborbital process accompanies the holostylic condition. The pigmentation of specimen 91-73001 indicate the presence of a well developed orbital sinus. Heavy pigmentation along the mid-dorsal margin suggests the supraorbital communication of a dorsal cranial vein, an interpretation which is substantiated by specimen 91-73004 which shows the corresponding orbital foramen. Ventroposterior pigmentation, which extends backward at an oblique angle appeared to be residual from a jugular vein. Cutaneous segmental vessels and a probable dorsal fin sinus were also indicated by pigmentation. No evidence of vascularization or canals was found in the ethmo-rostral region. The negative evidence may be attributed to the thickened rostro-orbital cartilage. Sexually dimorphic rostral rods were also preserved. Specimen 91-73004 offers the most orbital information. Orbitonasal and "cranioquadrate" foramina have been

observed. **Chomatodus Groups:** Relevant information is recorded to date for group 2 alone. This form possesses a high braincase, short otic region, a supraorbital ridge with extensive ornamentation, widely spaced eyes which face out, a well developed cranial and postcranial lateralis system, an extremely short rostrum, massive holostylic mandibular cartilages with molariform teeth, and a well developed orbital sinus indicated by the extensive eye pigmentation. Specimen CM35494 demonstrates a foramen for the superficial optic nerve and this is confirmed by CM62705 which shows both the anterior and posterior orbital foramen required for transmission of this nerve across the orbit. Specimen CM62716 may possess a cranioquadrate passage.

Harpacanthus fimbriatus: The cranial dimensions of this autodiastylic species most closely approximates that of Helodus and Chomatodus. Prominent rostral "ticklers" or "feelers" are preserved. The sole specimen available suggests there may have been independent bilateral canals extending forward to rostrum from orbit but this note needs to be confirmed in future specimens.

cf. Orodus sp.: This is an autodiastylic paraselachian of the most primitive form. The palatoquadrate is thin anterior to the orbit and linked to the comparatively massive Meckle's cartilage by significant labial cartilages. The overall vascular plan reflects those features of the selachian arrangement. The superficial dorsal vasculature

of the trunk region runs forward to otic region to a point where a tributary (identified as the supraorbital vein) enters the orbital sinus through a foramen. This foramen is found just ahead of the midorbital level. Another orbital foramen is indicated at the level corresponding to that of the superficial ophthalmic nerve but no forward continuation to an ethmoid or preorbital canal evident. These features place Orodus far from a holocephalan vascular plan.

Iniopterygians: The preservation of these fish is too poor to reveal any reliable vascular information. What has been ascertained for the suspensorium suggests there are autodiastylitic forms.

Echinochimaera: E. meltoni (Lund, 1977) demonstrates a well developed orbital sinus. A possible fenestra in specimen 91-72401 was noted at the dorsoanterior, medial angle of the orbit and suggests there may be a medially directed canal associated with it. In the counterpart there is evidence that a canal exists for each orbit for a short length before they meet along the cranial midline and extend anteriorly. E. snyderi (Lund, 1986) also demonstrates these features with the additional note that, despite the communicating tract, each canal continues forward independently towards the tip of the snout where an anterior opening to the canal can be seen. Extensive and continuous pigmentation within the orbit is indicative of a complete orbital sinus. Two foramen are found in the posterior margin of the orbit, the

locations of which are in the approximate vicinity of the posterior superficial ophthalmic and postorbital/jugular vein foramina. A single, relatively large foramen in the ventral margin is homologized with the cranioquadrate passage (orbital artery and post orbital vein foramina).

Cochliodont Group 1 Erismacanthus and Cochliodont sp.:

Cochliodont sp (91-62601, baby) Preservation is in dorsoventral fashion so cranial dimensions are well marked. Interorbital communication is evident at the near-posterior medial margin of the orbits; heavy pigmentation being associated with all components; ie, the orbit, its foramen, and the communicating path. Two orbital tributaries are located at the posterior lateral margins of the orbit (with evident foramina). The more dorsal and posterior of the two swings laterally and backwards for a short distance after emerging from the orbit. Thereafter it proceeds in a more mesially directed path to emerge alongside the vertebral column/notochord. Just posterior to this point there may be a dorsal sinus or haemopoietic aggregate overlying the vertebral column (analogous to the epimyelencephalic organ of select vertebrates). The second more ventral and posterolaterally directed tributary appears to travel towards the gill and possibly the lower jaw region. The observations taken from Cochliodont 1 and Erismacanthus are similar to those made for the species just discussed. They possess a posterior tributary which traverses the

region of the synarcuum. This latter feature is responsible for the support of the stout, anteriorly directed fin spine. A dorsal fin sinus is found here. This region's vascular elements communicate with the more posterior anatomy via the typical posterior cardinal and caudal veins. The abdominal anatomy and its vasculature is of the selachian plan with well developed organs of the digestive system.

At the anterior margin of the orbit two foramina can be found corresponding to an orbitonasal and anterior superficial ophthalmic nerve foramen. Orbital pigmentation can be found in some specimens to continue forward towards the rostral armature but due to the heavy rostral plate the underlying fine anatomy is typically not observable.

Little 2-Spine: This is a hyostylic selachian. The orbit of CM41074 offers evidence of an incomplete orbital sinus. From the anteriormost orbital margin of this specimen a foramen followed by a long canal can be seen. The canal is bilateral, one from each orbit running lateral to the precerebral fontanelle. (the bilateral canals seem to be a primitive feature for rostral-ethmoidal zones)

In the aforementioned specimen and in 82-723001 pigmentation over the vertebral column suggests a probable epimyelencephalic organ. My research notes describe this mass to as a large, oval, and densely pigmented mass found dorsal to the vertebral column and spanning the region bounded by the VIII through XIII vertebral elements. Since

it is completely a homogeneous, dense mass without any sign of tributaries it should be considered as a epimyelencephalic mass rather than a blood sinus. This point is 4 vertebrae anterior to the spine of the first dorsal fin and is distinct from what has been called a dorsal fin sinus in other fish.

Various unidentified small sharks: Little pigmentation prevails in these specimens. The unifying characters appear to be a "blind sac" extending from the anterior margin of the orbit, heavy orbital pigmentations and some posteriorly extending pigmentation in the region of where the jugular vein would be positioned. The "blind sac" is identified as short preorbital canals which carry both the superficial ophthalmic nerves and the preorbital vasculature to the rostroethmoidal region.

Damocles and Falcatus: These Stethacanthid sharks (Lund 1986, 1985) demonstrate heavy orbital pigmentation and a jugular-type extension of pigment from posterior orbital margin.

El Weirdo: This is an autodiastylic paraselachian which possesses many features more typical of an actinopterygian than a chondrichthyan. Its jaw structure is most compatible with what has been described for Orodus, particularly regarding the labial cartilage arrangement and poorly developed palatine region of the upper jaw. The sexually dimorphic rostral rods found in the males of the species

are found in conjunction with the pigmentation of the preorbital region. Two relevant orbital foramina are indicated. The posterior believed to be for the jugular vein and is found anterior to a jugular sulcus or canal of the lateral, posterior neurocranial wall. The second is the cranioquadrate passage.

Other results: The chondrichthyan morphocline constructed based on these data and the results of the cladistical analyses are presented in the appropriate chapters as they relate to the discussion.

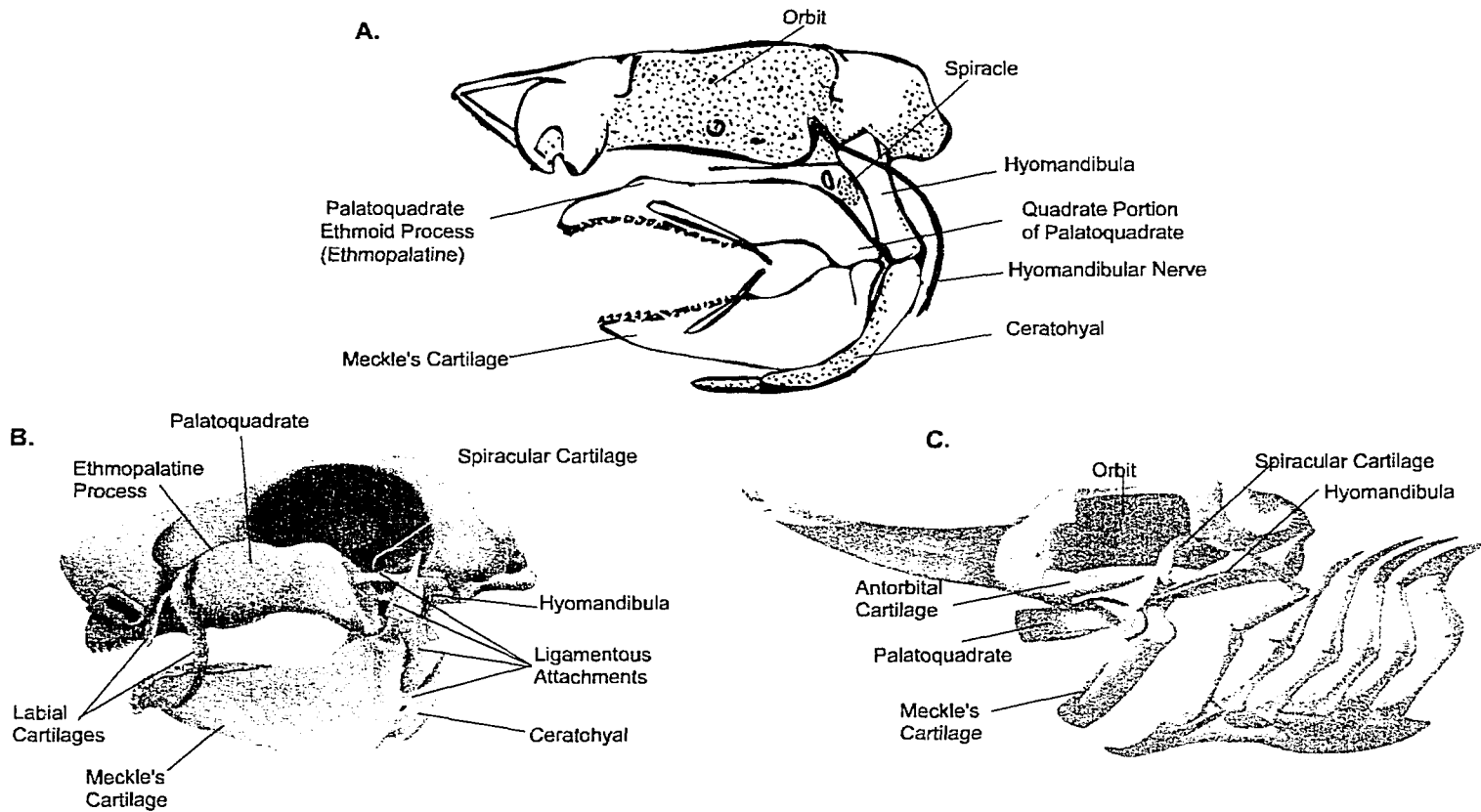
EVOLUTION OF THE JAWED CONDITION

Suspensorium of the extant forms

The relationship of the palatoquadrate to the neurocranium represents a major distinction between the chondrichthyan sistergroups. Elasmobranchii are characterized by a suspensorial palatoquadrate of the hyostylic, modified hyostylic, or amphistylic form (Figures 1 and 2). Of these hyostyly and amphistyly are considered fundamental in the evolution of jaw forms for these are the suspensorial forms of the earliest confirmed selachians. All chondrichthyan suspensoria are principally defined according to the extent of hyoid arch modification wherein the focus is on the development of the hyomandibular element as the primary suspensorial mechanism.

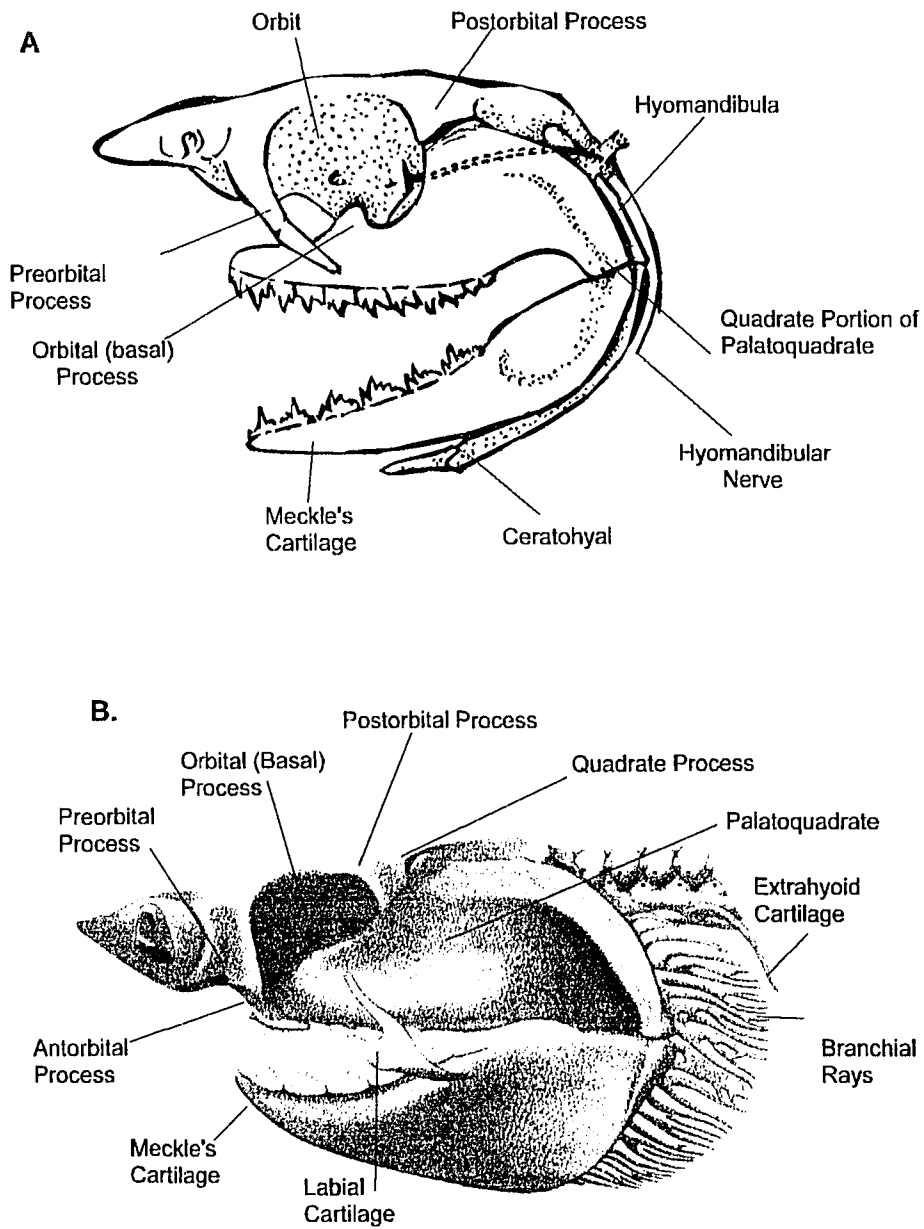
The basic description of hyostyly was formulated by Huxley in 1876 and reiterated by Gregory in 1904. The significantly enlarged hyomandibular is believed to bear the main burden of jaw support. In this state the palatoquadrate is suspended by ligaments from the braincase while the hyomandibular is bound to the posteriormost end of the palatoquadrate. DeBeer (1937) further stipulated the ligamentous attachment of the palatoquadrate to the cranium occurs at the mid region of the palatoquadrate where an

Figure 1: Elasmobranch Hyostyly and Modified Hyostyly



A. Hyostylic *Scyliorhinus* modified from Goodrich, 1958. Relevant features for the hyostylic condition are indicated. B. and C. : Chondrocrania of *Heterodontus* and *Raja*, respectively, from Daniel, 1934. Features of true hyostyly are depicted in B; modified hyostyly in C.

Figure 2.2: Elasmobranch Amphistily



A.: *Heptranchus* cranium and amphistylous suspensorium from Goodrich, 1958.

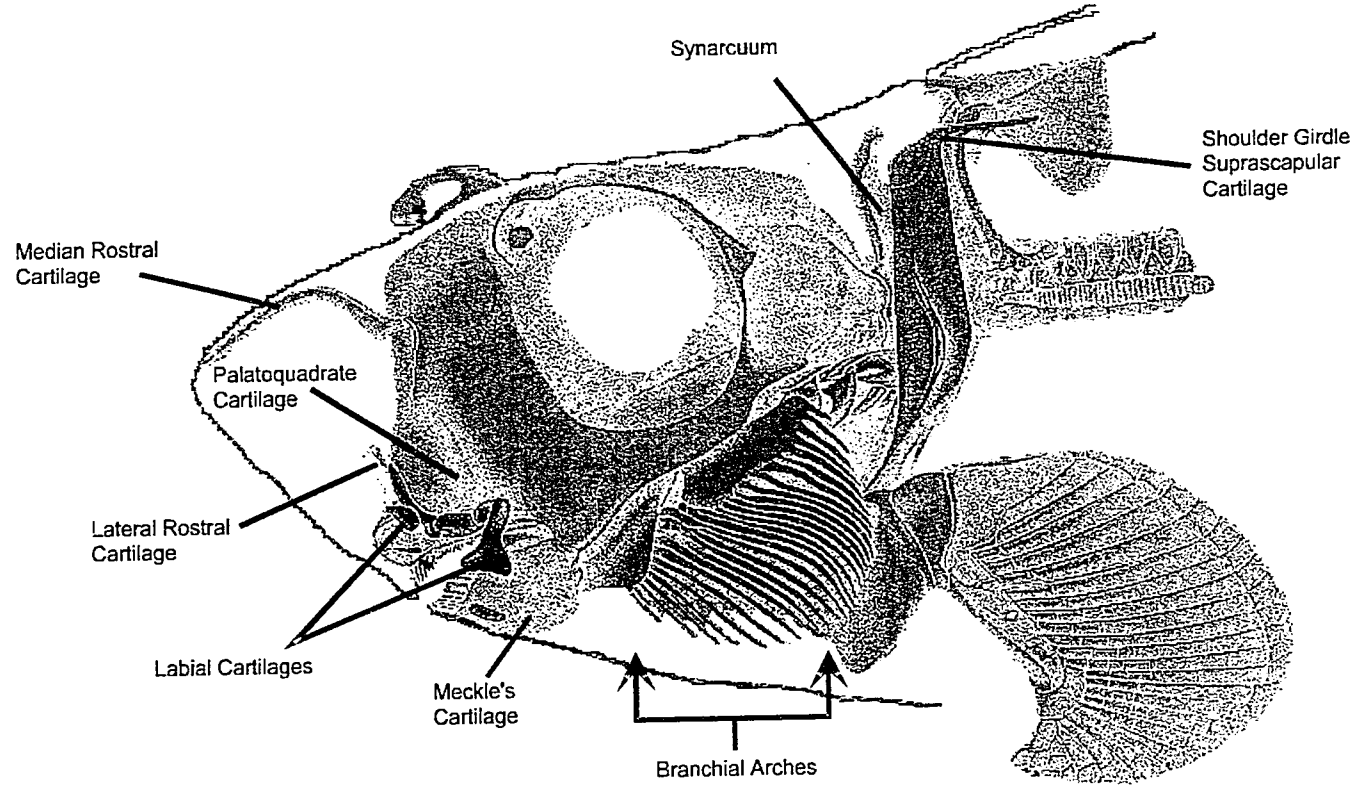
B.: *Heptranchus* cranium and suspensorial elements according to Daniel, 1934

orbital process is found to intercalate with a complimentary region of the basitrabecular cartilage.

Amphistyly was originally described by Huxley (1876) as the condition in which the palatoquadrate is distinct from the rest of the skull and suspended from the braincase either entirely or nearly entirely by its own ligaments. The hyomandibular is said to be "small", contributing little to jaw support. DeBeer (1937) subsequently refined Huxley's definition to specify the possession of (1) a moderately enlarged hyomandibular to prop the jaws against the otic region of the cranium and (2) basal and otic attachments between the cranium and palatoquadrate.

In contrast to the elasmobranch condition, the Holocephali are holostylic, being distinguished within the Chondrichthyes by virtue of the palatoquadrate which is completely fused to the neurocranium (Figure 3). Consequently, the nature of the chondrichthyan suspensorium and possible pathways of transition between the fused and non-fused states have been extensively studied in light of selachian and holocephalan differences and the professed descendance of these groups from an ancestral form with an unfused jaw. The question remains to today; are the Chondrichthyes monophyletic or do they have distinct origins and thereby follow different evolutionary pathways? To answer this, comparative analyses are required of the

Figure 3: Morphology of the Holocephalan Cranium
Cranium of *Chimaera monstrosa* from Garman, 1904



suspensorial forms. Subsequently, the transitional interrelatedness of the forms would take precedence in any debate concerning the appropriateness of the chondrichthyan sistergroup classifications. Thus, this chapter focuses on the development of the jawed condition and examines the possible phylogenetic derivation of suspensoria relative to the selachian and chimaerid conditions.

Analyses of the evolution and transition of jawed states concerns, first, the morphology of the upper jaw. In the description of suspensorial forms if more attention is given to jaw oriented features of the suspensorium rather than emphasizing the nature of the hyomandibular, it becomes apparent that the shape of the elasmobranch palatoquadrate is critical to understanding the suspensorium. The shape of the upper jaw is determined by the regional specializations which result in formation of articulating processes. The articulations between the neurocranium and upper jaw must be a critical variable upon which the formulation of a mechanically sound morphological transition in the evolution of jaws must depend. Furthermore, this variable is, most likely, the key character required to understand the interrelationships of hyostyly, amphistyly and holostyly. Therefore the articular specializations of the palatoquadrate are reviewed here so that the basis of a phylogenetic analyses of jawed conditions can be established.

How may one explain the morphological transition from the state of the shark upper jaw to that of the chimaerid?

According to DeBeer (1937) up to four processes may develop in any vertebrate as regional specializations for attachment of the upper jaw to the neurocranium. Three of these processes are found in elasmobranchs and are termed the pterygoid (ethmopalatine), basal (orbital), and otic (postorbital) processes. He describes the pterygoid as having formed from the anterior end of the pterygoquadrate and, in elasmobranchs, this process may either establish contact with the ethmoid region of the cranium or may fuse with the corresponding process of the opposite side. The otic process is classically defined as that which is always lateral to the head vein, orbital artery, and the efferent pseudobranchial artery. It is also anterolateral to the hyomandibular branch of the facial nerve. Similarly, the basal process is defined as the result of contact between the pterygoquadrate basal process and the neurocranial basitrabecular process. It is situated antero-dorsal to the palatine nerve, antero-ventral to the orbital artery, and ventral to both the vena capitis lateralis and orbital sinus.

Of the possible articulations, the selachian basal process, which is directed towards the subocular shelf (i.e. complementary to the neurocranial basitrabecular process), is most significant to phylogenetic theory for it is believed to represent the original point of connection

between the braincase and pterygoquadrate (Huxley, 1876) and is one of the most constant features of the jaw/neurocranial association across all vertebrate groups (DeBeer and Moy-Thomas, 1935). Gegenbauer (1872) had originally proposed the otic to be the primary connection and the orbital as secondary but this was debated by Huxley, who argued the contact of the orbital process must be the original point of attachment to the basis cranii. In his reasoning, Huxley considered the basal process to represent the top end of the mandibular arch (i.e. the pharyngomandibular) and cited the hyomandibular attachment as occurring at a corresponding level to the basal attachment. Huxley's argument seemed most logical under the paradigm which advocates derivation of the jawed state from the agnathan condition through specialization of the mandibular and hyoid arches. The widespread acceptance of this approach is exemplified by the subsequent proposal of Suschkin (1910) who also emphasized the primitive nature of this basal connection and introduced protostyly as the hypothetical state of the gnathostome ancestor in which this was the sole connection between the upper jaw and braincase. As a greater argument for the basal being the original attachment, Sewertzoff (1917) reported the existence of an element, defined as the pharyngomandibular, in Mustelus, Squalus, and Scyliorhinus embryos. This element was observed to arise in selachian ontogeny as a separate cartilage, later fusing with the

medial surface of the palatoquadrate basal process. A similar phenomenon was reported by Holmgren (1940) where he cited the development of an embryonic membrane between the selachian palatoquadrate and subotic shelf, and in so doing, contributing to the establishment of the subotic jaw/neurocranial connection. Collectively, these data and interpretations have been taken to indicate, if the contact between the palatoquadrate basal process and neurocranial basitrabecular cartilage generates either a palatobasal articulation or fusion it does so through the more dorsal pharyngomandibular element. Consequently, this is accepted as the most likely site of the original attachment between jaw and cranium, a stage in the progression of mandibular arch remodeling which determines the establishment of any jawed state.

It is apparent these definitions are geared to support or were developed from the notion that (1) the jawed condition arose from an ancestral state in which there was no modification of the anterior visceral arches and (2) the original true-jawed state is best represented by the suspensorial condition of Selachii. Clear, irrefutable evidence which would support either of these assumptions has not been reported to date but these notions have prevailed for all analyses of the jawed condition. They are, in turn, based on the assumed derivation of gnathostomes from agnathans and the idea that the cartilaginous endoskeleton,

as represented by selachians, is the primitive state for vertebrates.

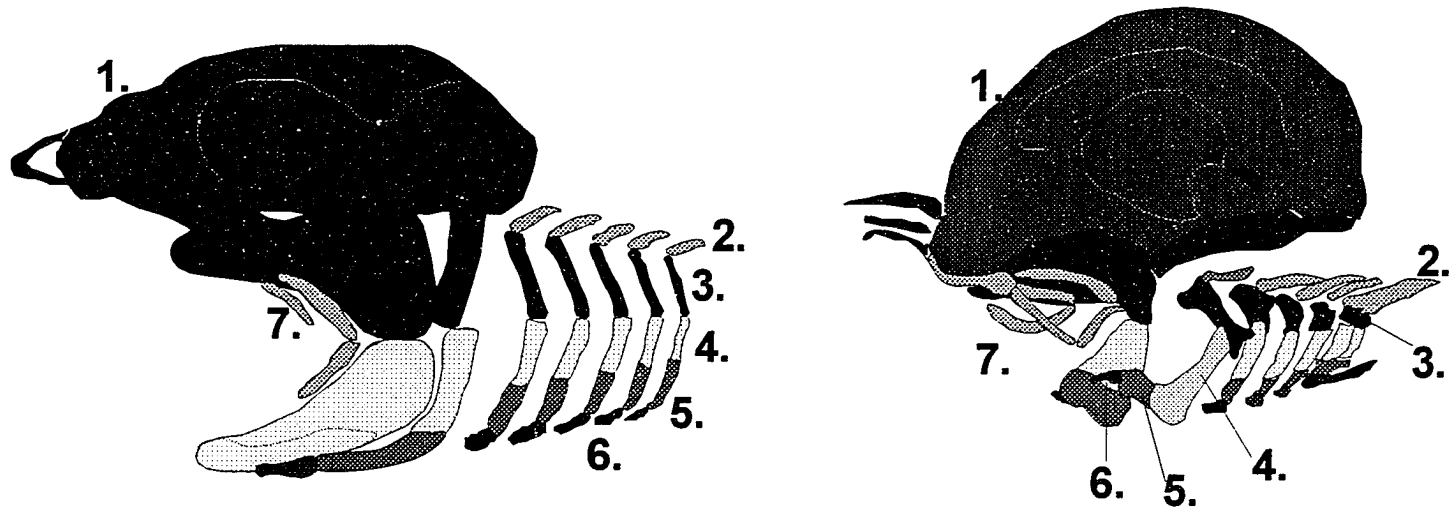
**What is the Origin of Jawed Vertebrates? How Is the
Development of Jaws Explained According to the Fossil
Record?**

The origin of the gnathostome condition is perceived to be rooted in the agnathan condition, for the branchial architecture of the two major vertebrate groups is said to be similar and the earliest vertebrates of the fossil record, the Ordovician ostracoderms, are of the jawless state. In a comparative examination of extant lamprey and shark conditions, DeBeer (1937) and Holmgren (1942) concur with Sewertzoff's (1917) identification of the five arches anterior to the first branchial arch of Petromyzon. These represent, in an anterior to posterior direction, three premandibular arches and the equivalent of mandibular and hyoid archs. As for the nature of the jaws the mandibular and hyoid arch elements of Chondrichthyes are considered to be serially homologous to the branchial arches (Figure 4) and arise as a specialization involved with cephalization (Figure 5). These interpretations and the evidence cited in support of the "primitive nature" of a basal connection have given strength to the assumed derivation of gnathostomes from agnathans.

In a functional approach to explaining the theorized jawed transition the agnathan-type branchial apparatus is

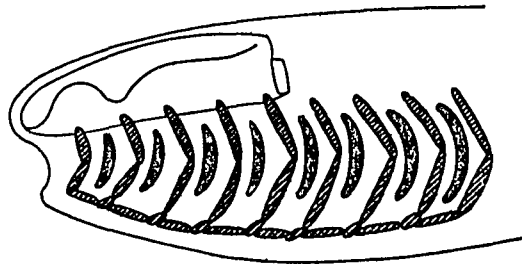
Figure 4. : Comparative Analysis of Visceral Arch Element Homologies

Modified from Dean, 1906

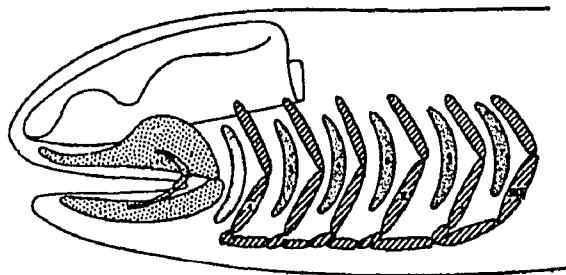


1. CHONDROCRANIUM
2. PHARYNGOBRANCHIALS/PHARYNGOHYAL
3. PALATOQUADRATE AND EPIBRANCHIALS/EPIHYAL
4. MECKLE'S AND CERATOBRANCHIALS/CERATOHYAL
5. HYPOBRANCHIALS AND DERIVATIVES
6. BASIBRANCHIALS/BASIHYAL DERIVATIVES
7. PREMANDIBULAR EXOSKELETAL CARTILAGE DERIVATIVES

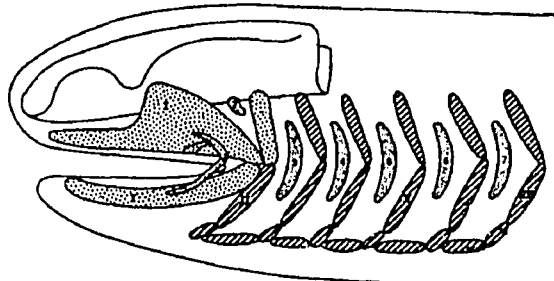
FIGURE 2.5: Model for Jaw Derivation From Archaic Arches
Modified from Smith, 1960



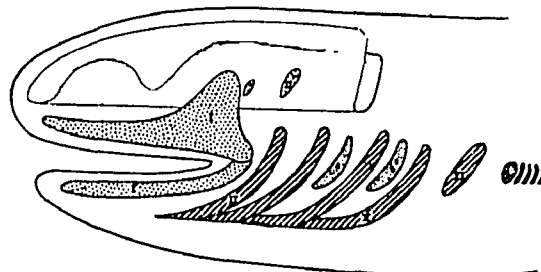
A. Visceral Skeleton of a Theoretical Agnathous Vertebrate



B. Visceral Skeleton of a Gnathostome at an Early Stage of Jaw Development



C. Visceral Skeleton of a Gnathostome at the Second Stage of Jaw Development



D. Visceral Skeleton of a Primitive or Larval Amphibian

believed to be modified such that there is a separation of the basket into feeding and respiratory systems (review by Thompson, 1971). Of the original gill series, the posteriormost arches become strictly respiratory, the anterior orobranchial apparatus (composed of premandibular arches) is lost or incorporated into the gnathostome cranial structure as cephalization transpires, and the two intermediate arches (the mandibular and hyoid) become specialized for the actions of feeding and providing a link between this mechanism and the more posterior respiratory mechanism.

There appears to be a general consensus of agreement regarding the premise of this assumed sequence. This acceptance is reflected in the confluence of this paradigm with the classical descriptions of jaw suspensoria. These descriptions, constructed by various workers, have contributed to the formulation of a transitional paradigm which attempts to unite both the fossil and extant data in a clear sequence. For the earliest stage, Gregory (1904) proposed paleostyly to describe the condition of the gnathostome ancestor, a form in which the visceral arch skeleton is expected to be completely independent of the braincase. Fossil evidence which validates the historical occurrence of this condition remains to be recovered. Later, DeBeer (1937) introduced parautostyly to describe a cyclostome-like arrangement wherein the foremost visceral

arches are fused to the braincase. This condition reflects data like that of Sewertzoff's analysis of the extant Petromyzon but also added the historical evidence of a well known ostracoderm, the Silurian anaspid Jamoytius.

According to the above model the next stage of transition should involve segregation and remodeling of the mandibular and hyoid arches into the true jawed condition. (A qualification of this statement is presented in appended note #1.) This link in the modeled transitional series was provided by Huxley (1876) when he introduced the first classifications of the more complex jaw/neurocranial relationships. The importance of amphistyly and hyostyly pertains to modification of both the cranial articulating mandibular and hyoid arches. The third classification, autostyly would appear intermediate between DeBeer's parautostyly and the more structurally complicated amphistyly and hyostyly. This is emphasized by the specification of the palatoquadrate/neurocranial association. The autostylic palatoquadrate is described to be in direct contact with the cranium at the exits of cranial nerves II (Optic) and V (Trigeminal). A secondary attachment occurs in the form of an otic process, the posterior and dorsal continuation of the upper jaw to the periotic cartilage. Therefore, as the name autostyly implies, the mandibular arch would be attached to the cranium by "that part of its own substance which constitutes

the suspensorium".

At the time Huxley introduced these descriptions and for many years later the fossil evidence indicated the fused state and various unfused states were all well established by the lower Carboniferous. Thus, Huxley's definitions were widely used to describe the condition of the Paleozoic suspensoria. The unfused states of the Devonian to Carboniferous Cladoselache, Xenacanthus, and Mesozoic Hybodus, were sufficiently described by the amphistylic and hyostylic conditions. The third condition of autostyly came to be synonymized with the fused or holostylic state exhibited by extant chimerids, the Carboniferous Paleospinax and Chondrenchelys, and Helodus.

It was this last phenomenon, i.e. the synonymization of the fused upper jaw state with autostyly which led DeBeer in 1931 to question the focal point of Huxley's definition. The central debate was whether the essential feature of autostyly should be non-participation of the hyomandibular or the actual fusion of one or more of the palatoquadrate processes with the neurocranium. This question was important if there is to be a clear understanding of the polarity of suspensorial forms.

DeBeer attempted to highlight the critical feature of Huxley's autostylic condition which would have immediate application to the paleontological record. This regards

specifying the zone of initial contact between mandibular arch and neurocranium. Huxley places this attachment in the proximity of what has come to be identified as the essential and, therefore, universal character in any jawed state; the basal connection. If one accepts the model advocating the derivation of the jawed condition from the agnathan state then the initial contact between mandibular arch elements and the cranium would have to occur in that region. Moreover this connection is required irrespective of the final suspensorial state. Therefore, DeBeer argued this classification mandates, by definition, that autostyly must precede hyostyly and amphistyly in gnathostome evolution.

The paleontological record was assumed to support this analysis to the degree that all three forms of suspensoria, amphistyly, hyostyly, and holostyly were inferred to be widespread in the cartilaginous vertebrates of the Devonian and Carboniferous (The conditions are considered most likely rather than absolutely certain since an unequivocal determination cannot be made without evidence of the complete branchial architecture. In the majority of cases only fragmentary evidence of the post-mandibular branchial elements are sufficiently preserved to permit reconstruction of the arches). Yet, a conflict developed between the theory and application of this classification. Autostyly was originally proposed to represent the primitive condition and to describe the first stages of a jaw/neurocranial

association. Later, it became equated with the fused suspensorium of fossil fish, but, is this synonymization justified? The applied definition of autostyly created confusion with respect to the modeled progression of jawed forms. As a further complication, DeBeer determined from a review of extant suspensorial conditions that a strict interpretation of Huxley's autostyly resulted in the identification of different grades of autostyly covering a variety of extant vertebrates, not just chondrichthyans.

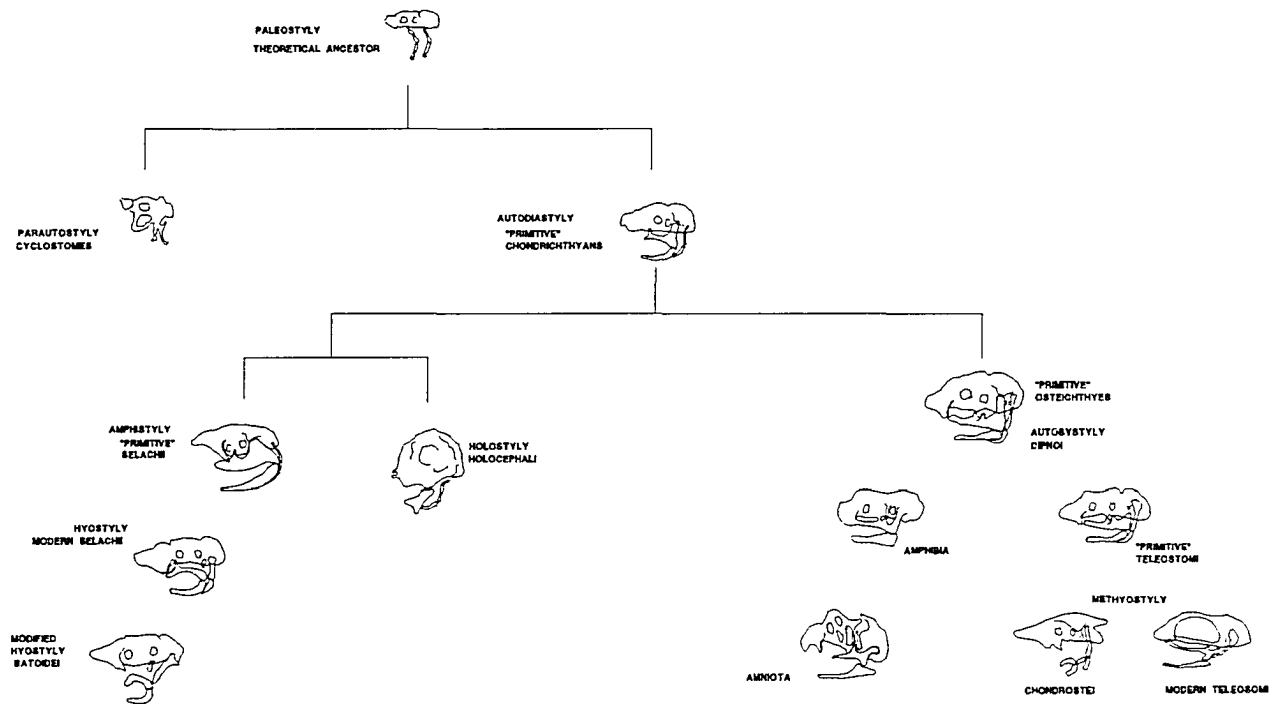
To address these considerations and to avoid the ambiguity of Huxley's definition DeBeer revised the original description of autostyly (1935). His version describes a gnathostome condition in which the hyomandibula plays no suspensorial function whether or not cartilaginous fusions occur between the jaw and the braincase. To distinguish the non-fused version of autostyly from the fused condition he proposed autodiastyly to describe the former state as primitive, and that which is possessed by ancestral fish, Gymnophiona, and Amniota. Autosystyly would describe the latter, as represented by cyclostomes, Holocephali, Dipnoi, Urodela, and Anura. Furthermore, he proposed Gregory's (1904) term holostylic should be used to "denote the peculiar autosystylic condition found in Holocephali." (p.422-423) Under this classification scheme, autostyly is used to describe all gnathostomes which are neither amphistylic nor hyostylic. Furthermore he rationalizes the

subclassification, autodiastyly, to be "more primitive in phylogeny" for "the jaws are merely modified branchial arches, and these are free from the axial skeleton in all forms except the obviously specialized Cyclostomes." In keeping with this interpretation Suschkins's (1910) protostyly would then correspond to an early autodiastylitic form where the basal connection was the only contact between braincase and pterygoquadrate. These tenets are therefore in agreement with the notion that the visceral arch skeleton is phylogenetically older than the cranium and that the "primitive freedom of the jaw is a 'morphological necessity'". (pp 423-424) This conceptual approach to the evolution and systematic classification of jawed forms is represented in DeBeer's working model of cranial transitions presented in Figure 6.

Is there a need to re-examine the concept of autodiastyly and the theorized development of the jawed condition relative to the question of character polarities?

The implications of Huxley's and DeBeer's theoretical constructs are further reaching than what is initially perceived. They are based on the notion of a progressive articulation and subsequent merging of prebranchial arches. Any analysis involving the palatoquadrate and upper jaw must rely on Huxley's stipulation of an initial connection between foramina for the II and V cranial nerves. This zone of contact, however, has become popularly redefined, with questionable justification, to target a more restricted

Figure 6 : DeBeer's (1935) Hierarchical Analysis of Suspensorial Forms



region occupied by the foramina for V and VII. The longstanding value of this criterion of jaw:cranial association is demonstrated in DeBeer's statement that the autodiastylic state, wherein only the basal connection exists, is equivalent to the theorized protostylic state. To verify this view, DeBeer employed Huxley's stipulation that the original point of attachment identified in selachian jaw formation is that which occurs between the orbital process and the trabecular region of the basis cranii.

This path of reasoning may be flawed, however. A conflict arises when the selachian orbital articulation, which most frequently occurs in the region of the foramina for cranial nerves V and VII, is synonymized with the "basal connection" which Huxley originally described in autostyly as the initial cranial:jaw connection between nerves II and V. The confusion generated by this muddled distinction between a basal connection (*sensu stricto*, the theorized initial contact between jaw and cranium) and the assumed nature of the selachian orbital connection has carried over to the identification of palatoquadrate processes in recent and fossil fishes. Moreover, it has biased the early gnathostome link in favor of a form which would reflect suspensorial features of the geologically youngest identified form of selachian suspensorium, amphistyly.

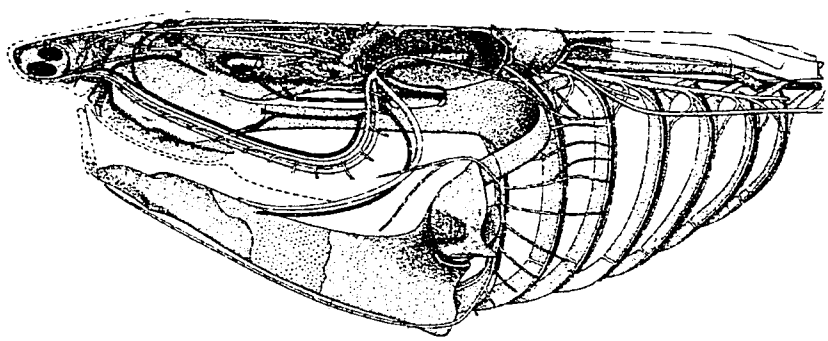
Consequently, these problems immediately carry over to DeBeer and Moy-Thomas' attempt to apply these theories to

the chondrichthyan fossil data. They refer to an autodiastylic condition, involving as the name implies two points of attachment but do not precisely identify where these attachments occur. It is inferred by comparison with amphistily that they employ the reinterpreted descriptives of Huxley; ie basal (intermediate fusion) and otic fusions. Consequently, they interpret autodiastyly as plesiomorphous for the primitive gnathostomes (Chondrichthyes), with hyostily being derived from amphistily through reduction of the otic and basal processes. Chimaerid holostily would be independently derived from primitive autodiastylic Chondrichthyes. As such the application of this theoretical construct still confuses the modeled rise of the jawed state for it is biased to fit the data on selachian suspensoria. The result is to alter the determination of suspensorial character polarities. Ultimately this tends to confuse the interpretations of fossil data and detracts from confidence in any theory of jawed transitions.

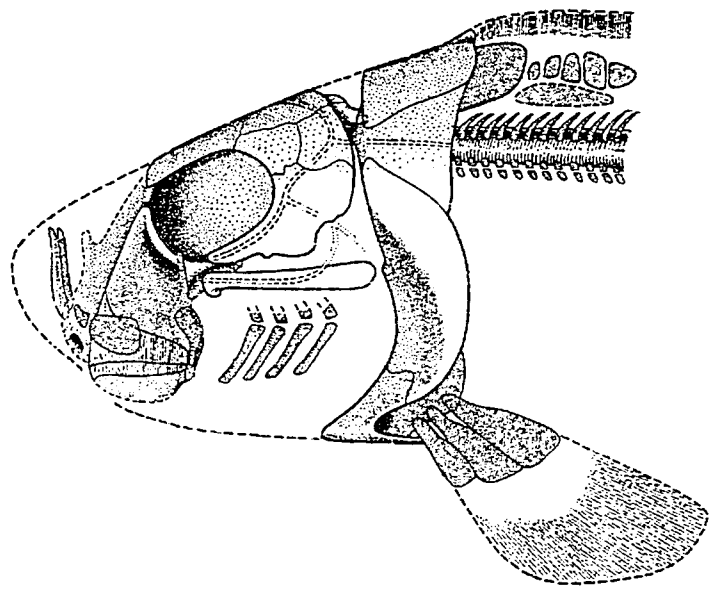
The inconsistencies which develop by forcing the paleontological record to fit theoretical models is further amplified when the condition of the placoderms is considered. Stensio (1963) introduced a description of the Devonian placoderms wherein various modes of "autostily" are propoorted (Figure 7). Some of these tend to resemble selachian amphistily (pareia-autostily of Kujdanowiaspis and Tapinosteus) and others are more reminiscent of chimaeroid

Figure 7: "Autostylic" Placoderms

A.



B.



A. Tapinosteus heintzi from Stensio, 1963
B. Ctenurella gladbachensis from Orvig, 1962

holostyly (tecto-parei-endocranio-autostyly of the pycnodont Rhampodopsis). These are problematical with regard to the theories of jaw formation. These descriptions were confusing for a fully developed hyomandibular was depicted in "autostylic" fish and this, in retrospect, would conflict with the expected hyomandibular-based suspensorium of early gnathostomes; i.e development of the hyomandibular is expected only for the expressed purpose of providing the crucial component of jaw suspension. Yet, it would appear from the placoderms that the hyomandibular was first modified for a nonsuspensorial role and these forms of suspensorium progress from the autodiastylic state. Although Stensio biased his interpretations of the material in view of what is known for the selachian condition, these descriptions are worth noting for it has been confirmed by other authors that the hyomandibular was developed in most of these cases and yet did not have anything to do with the suspensorium. Therefore what was either conveniently ignored in DeBeer's reclassification or was not even considered due to the restricted views of jaw development is shown to be possible and quite apparent at a stage as early as placoderm development. That is, full development of a hyomandibular is possible in the autostylic condition even though this element is classically described as having no involvement in the suspensorium. This query is even more critical to the current study for the condition of the pycnodont placoderms

has been considered as autodiastylic by some authors (Patterson, 1964; Stahl, 1967) and therefore, cited as evidence for an early separation of the chimaerids from the selachians.

Therefore, a reexamination of the early stages of jaw transformation and of autodiastyly, in particular, are required if one is to address the validity of a sistergroup status. This is further advanced if one considers the embryological data on holocephalan cranial development. Studies of chimaerid ontogeny reveal a stage, just prior to complete fusion of the palatoquadrate with the braincase, which may reflect the conditions ascribed to the primitive autodiastylic state.

In summary, the earliest chondrichthyans reported in the fossil record are either hyostylic, amphistylic, or holocephalic. Today, the derivation of amphistyly from hyostyly is firmly established and no irrefutable cases of autodiastyly have been published. With regard to the derivation of holostyly from hyostyly, a morphologic transition has been postulated for extant forms by Holmgren (1942). Yet, up to this point, a clear transition from hyostylic to holocephalic fossil chondrichthyes has not been described in the paleontological record. This lack of evidence has consequently weakened arguments in favor of the sistergroup classification.

The Theoretical Transition from Hyostyly to Holostyly:

A Test of the Sistergroup Status

As previously stated, the Holocephali are distinctive; their fused jaw condition contrasts markedly with the unfused selachian condition (Figure 3). Yet, the general notion has prevailed that chimaerids are derivable from shark-like ancestors. So, if Holocephali are to represent the sistergroup of Elasmobranchii (ie, defined to be more closely related to the Elasmobranchii than to any other group) then one would seek to explain the nature and development of their fused upper jaw in relation to the suspended forms.

A. The Selachian Based Model

Holmgren (1942) has proposed an embryogenic model to describe how the selachian jaw/neurocranial association may set the stage for development of the holocephalan condition. He reports, in selachians, an embryonic membrane which extends from the polar cartilages to the spiracular apparatus and in doing so is responsible for establishing the initial connection between the neurocranial trabecula and the palatoquadrate (refer to Figure 14C). The thick anterior end of the membrane is professed to form the palatoquadrate orbital process while that portion which connects to the trabecula is professed to form a separate cartilage shelf. Later in development this shelf will fuse with the trabecula to form the neurocranial subocular or

basal shelf. That remaining portion of the membrane which is lateral to the subocular shelf retains its connection to the dorsal border of the palatoquadrate and extends caudally to the hyomandibular facet, as the subotic shelf. Now, Holmgren argues, in holocephalans, if one were to envision the subocular shelf chondrification to extend further laterally to reach the palatoquadrate proper an autostylic palatoquadrate would arise. With membrane chondrification the palatine nerves and pseudobranchial artery would be enclosed in such a fashion that the adult palatoquadrate would have the appearance of being pierced by these structures, a condition typical to chimaerids. Consequently, the basal surface of the chimaerid cranium would be of the elasmobranch type wherein the palatoquadrate is fused to the trabecular and polar cartilages while the otic shelf encloses the orbital artery, jugular vein, and palatine and hyomandibular nerves.

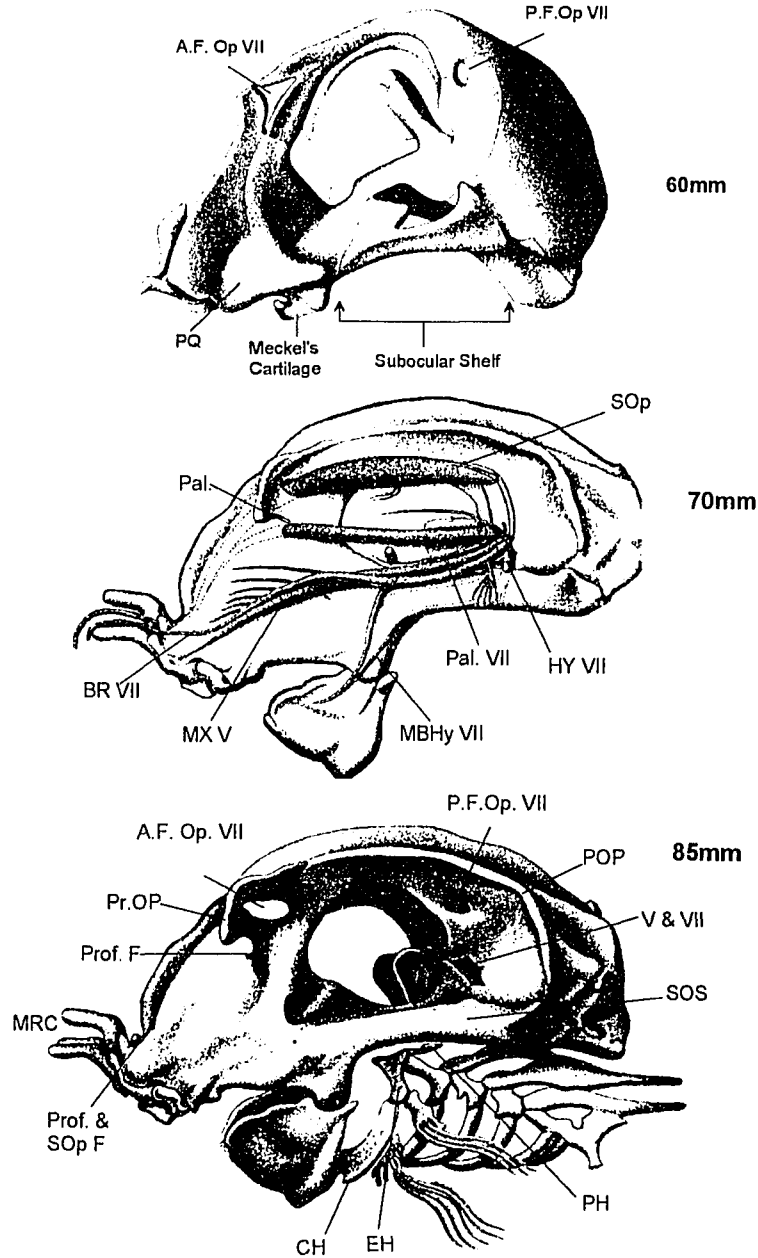
The substance of this embryogenic model can only be assessed through knowledge of the chimaerid plan of development. Unfortunately, studies of this type are limited. Schauinsland (1903), Dean (1906), and DeBeer and Moy-Thomas (1935) have conducted the only published examinations of the early embryonic stages of chimaerid skull development. Through these holocephalan studies some ontogenetic evidence for jaw formation has been uncovered. The observations from these studies have been compiled to

debate the plausibility of holostyly being derived from an initial selachian-type suspensorial state.

B. Holocephalan Based Model

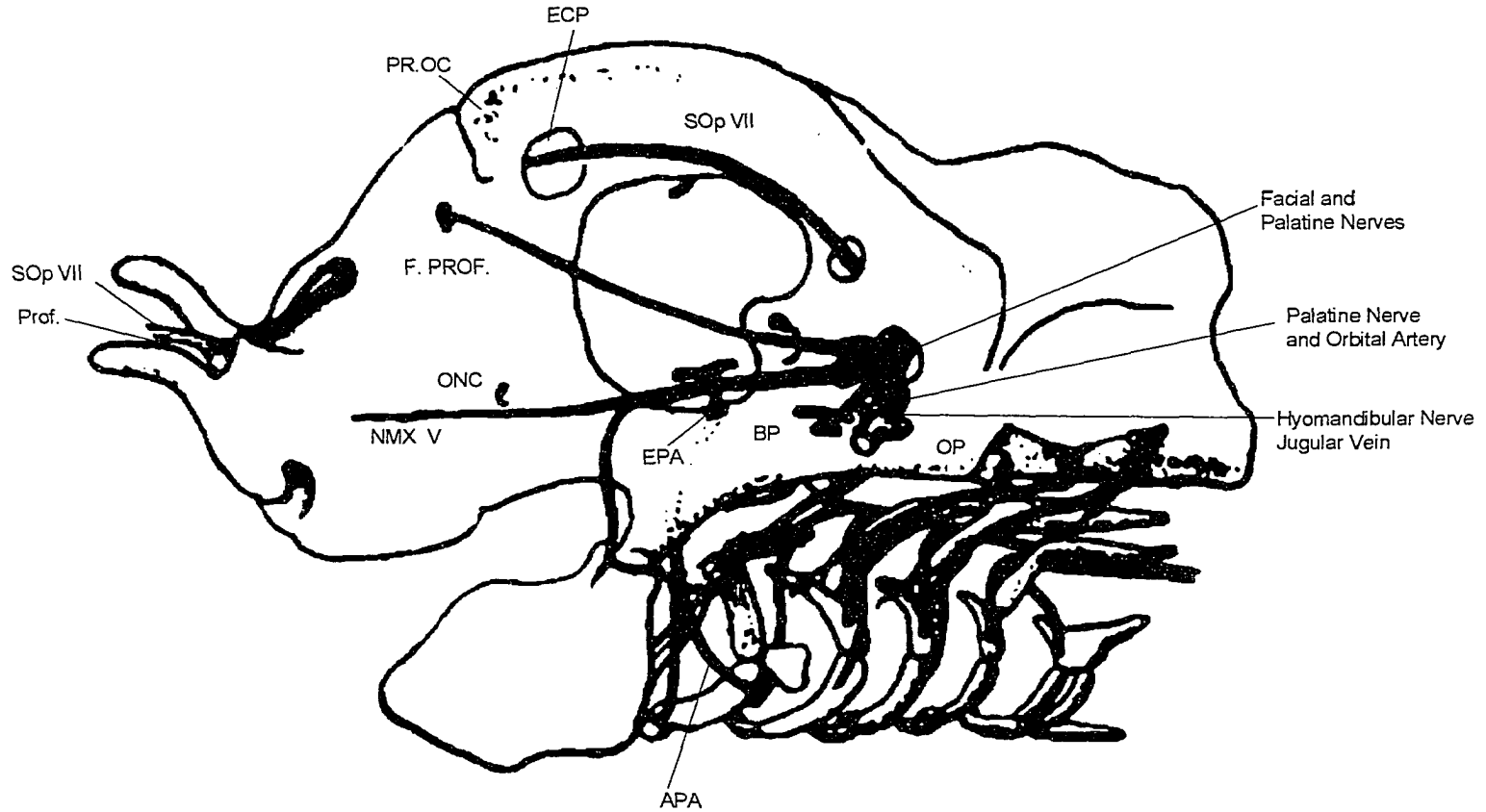
Schauinsland (1903) was the first to provide evidence for an embryological transition in chimaerid development which indicated the recapitulation of an ancestral, unfused state (Figure 8). DeBeer (1935) analyzed Schauinsland's depictions of Callorhynchus antarcticus cranial development in relation to his 95mm embryo of the same species (Figure 9) and concluded an embryological tripartate fusion can be demonstrated between the holocephalan palatoquadrate and neurocranium. DeBeer described this jaw/neurocranial fusion to be generated by an anterior ethmoid fusion (between the ethmoid region of the skull and ethmoid process of the pterygoquadrate), an intermediate basal connexion (between the lateral edge of the trabecular plate and pterygoquadrate), and a posterior otic fusion (fusion of the pterygoquadrate to the otic capsule). In view of the three selachian palatoquadrate specializations which permit articulation with the neurocranium, this tripartate fusion of the holocephalan palatoquadrate would prove to be one of the strongest arguments supporting the derivation of holostyly from hystyly. It will be shown that this analysis in conjunction with the other two embryonic studies represents the cornerstone of analyses on comparative chondrichthyan morphology. They are fundamental not only in

Figure 8. : Schauinsland's Embryonic Callorhynchus Heads



Abbreviations are as follows: A.F.OpVII, P.F.OpVII: Anterior and Posterior Foramina for Superficial Ophthalmic Nerve; BRVII: Buccal Ramus of Facial Nerve; CH: Ceratohyal; EH: Epihyal; HyVII: Hyomandibular branch of the Facial; MBHy VII: Mandibular branch to Hyomandibular Ramus of Facial; MXV Maxillary Branch of Trigeminal; PAL: Palatine Nerve; PAL VII: Palatine Branch of the Facial; PH: Pharyngohyal; POP: Postorbital Process; Prof. F.: Profundus Foramen; Prof. F & SOpF.: Anterior opening of Ethmoid Canal; PR.OP: Preorbital Process; PQ: Palatoquadrate; SOp: Superficial Ophthalmic Nerve; SOS: Suborbital Shelf; V & VII: Trigeminal and Facial Cranial Nerves

Figure 9. : DeBeer's 95mm Callorhynchus embryo with Critical Nerves and Blood Vessels Noted.



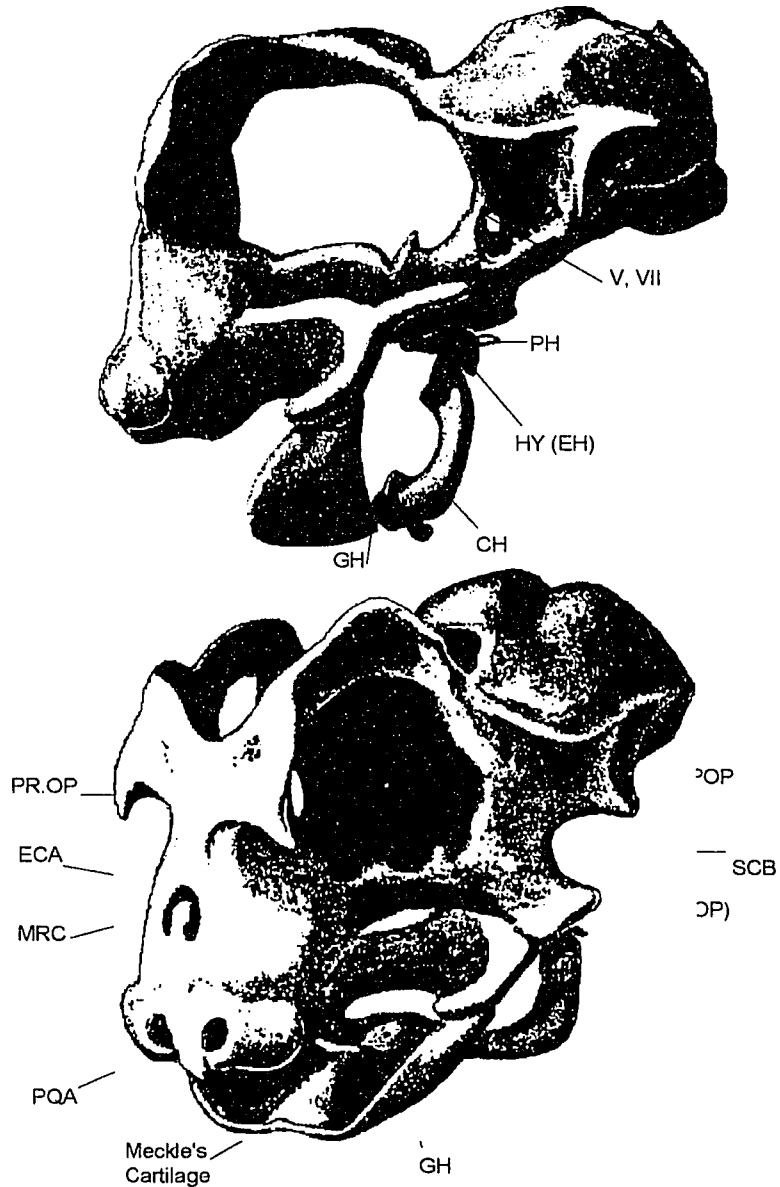
Abbreviations are As Follows: APA: Afferent Pseudobranchial Artery; BP: Basal Process; EPA: Efferent Pseudobranchial Artery; F. Prof. Foramen for Profundus Nerve; NMX V: Nasomaxillary Branch of Cranial Nerve V; ONC: Orbitonasal Canal; OP: Otic Process; PR. Oc: Preorbital Cartilage; Prof.: Profundus Nerve; SOp VII: Superficial Ophthalmic Branch of Cranial Nerve VII.

the identification of chondrichthyan mandibular arch cartilages but also in the identification of (1) cranial foramina, (2) the structures traversing these foramina, and (3) corresponding features of fossilized material. It is through the identification of these features that we may accurately assess the theories proposed for the structural shift from hyostyly to holostyly.

**Is There Correspondence and Agreement Between the
Ontogenetic and Theoretical Analyses Defining a Suspensorial
Transition?**

In establishing the plausibility of a selachian to holocephalan suspensorial shift one would, minimally, need to define the extent of the palatoquadrate element and its processes of articulation, and demonstrate the remodeling or fusion of these features as transformation proceeds from the free to the fused state. DeBeer's description of fusions between embryonic chimaerid palatoquadrate and neurocranial cartilages provided the critical basis to test and critique such a theory. However, data obtained from early stages (60,70,85,95mm) of Callorhynchus development (Schauinsland 1903, DeBeer and Moy-Thomas, 1935) and the temporally incompatible early stage of Chimaera (51mm) development (Dean, 1906) did not preclude distinct descriptions of the palatoquadrate element by different researchers (Figures 8-10). In particular, the nature of the shelf of cartilage at the base of the skull has been interpreted as neurocranial

Figure 10. : Dean's Embryonic Chimaera Cranium



Labels indicate Dean's and Holmgren's identifications of elements. Those in parentheses are the identifications of DeBeer and Moy-Thomas. Abbreviations are as follows: BTP (OP): Basitrabecular Cartilage (Otic Process); CH: Ceratohyal; ECA: Anterior opening of the Ethmoid Canal; GH: Glossohyal; HY (EH): Hyomandibula (Epihyal); MRC: Median Rostral Cartilage; POP: Postorbital Process; PH: Pharyngohyal; PR.OP: Preorbital Process; PQA: Anterior fusion between the palatoquadrate and neurocranium; PQB: Posterior fusion between the palatoquadrate and neurocranium; PQF: Palatoquadrate Fissure; SCB: Subcranial Bay.; V, VII: Foramen for Cranial Nerves V and VII

by one school of thought and as a derivative of the original palatoquadrate element in another. Each interpretation supports and is based on a hyostyly/holostyly transitional paradigm but the controversy seems to arise with regard to the identification of the palatoquadrate element itself and secondarily concerns the points of jaw/neurocranial fusion.

DeBeer (1935) maintains the essential feature of the holocephalan pterygoquadrate is its "completeness"; being fused with the neurocranial nasal capsule and ethmoid region anteriorly, the lateral edge of the trabecular plate intermediately, and the otic capsule posteriorly. Along with his 1935 co-author, Moy-Thomas, and Goodrich (1930), DeBeer has maintained, if the upper jaw were to fuse with the basis cranii in a transition from the selachian to holocephalan state then the palatoquadrate would contribute extensively to formation of the lateral wall and floor of the orbit. Thus, in Schauinsland's 95mm Callorhynchus, a cartilage which extends backwards in a horizontal fashion from the orbital to otic region is interpreted by DeBeer and Moy-Thomas as part of the palatoquadrate proper (Labeled SOS and OP in Figures 8 and 9 respectively). These researchers argue this cartilage fulfills the definition for the otic process of vertebrates (Appendix note 2) and, therefore, is appropriately deemed the otic process of the holocephalan pterygoquadrate. Moreover, they conclude this structure is, at least, analogous to the selachian processus oticus

since the position of the process is the same in the holocephalan condition as it is in the selachian.

The interpretations of DeBeer and Moy-Thomas appear to be in continuity with Holmgren's morphological transition described earlier. Yet Holmgren (1942) offers a very different interpretation of the cranial cartilages based on Schauinsland's illustrations. He identifies the palatoquadrate as an anterior cartilage; an element much shorter than what either DeBeer or Dean envision (Labeled PQ in 60mm stage of Figure 8; that cartilage extending between PQA and PQB of Figure 10). Behind this, he describes a shelf-like cartilage which is principally unchondrified and encloses the jugular vein, orbital artery and the hyomandibular and palatine nerves in one wide fenestra. Holmgren identifies this shelf as the neurocranial subocular shelf, not as an otic process as DeBeer would have (Figure 8).

Holmgren argues this cannot be a palatoquadrate otic process given that the cartilage in question (1) develops later than what he identifies as the palatoquadrate proper and (2) is evident as a shelf, distinct from the palatoquadrate. Rather, Holmgren describes this shelf as a combination of basitrabecular cartilage (delimiting the posterior margin of the palatoquadrate) and a subocular process. This latter process would arise if holocephalan cephalic development were to follow the selachian mode. In

the latter mode of development, Holmgren professes, "The subotical shelf develops from a separate rodlike rudiment, possibly a palatoquadrate branchial ray, which in Scyllium develops outside the orbital artery and fuses on to the basiotic lamina anteriorly and posteriorly to the artery." (1942, p.194) Thus, he emphasizes, if there were to be an otic process in holocephalans then only that portion of the shelf lateral to the fenestra may be considered as a "processus oticus" if the features here are to correspond with the development of selachian internal and external otic processes. (Holmgren's description of these are given in appendix note 3).

Yet, in reference to the 60mm C. antarcticus (Figure 8) Holmgren (1942) admits there may be some evidence to support DeBeer's interpretation but does not consider it compelling. The central point to his argument against DeBeer's interpretation regards the discontinuity evident in the earliest embryonic stages of Callorhynchus and Chimaera between DeBeer's "otic process" and the postorbital process (SCB in Figure 10). In describing the conditions of this subcranial gap Holmgren observes, "The 'processus oticus' joins the auditory capsule below the level of the postorbital process and only secondarily, in older stages, does it become connected with the postorbital process by means of a ridge..." (p.189) In selachii, however, when the processus oticus externus "...reaches the auditory capsule,

it joins the latter by means of the postorbital process, which is not a part of the capsule but a separate structure (a primary postorbital process) or a continuation of the supraorbital crest secondarily fused on to the auditory capsule. Thus a processus oticus externus may not be directly connected with the auditory capsule, as it is in the 60 and 85mm Callorhynchus embryo. This evidence at once makes the "processus oticus" in Holocephali somewhat doubtful.."

Having refused the otic process argument, Holmgren argues that the nature of this region can be explained in relation to his observations on the trabecula/palatoquadrate association in selachian embryogenesis. He theorizes it is after formation of the palatoquadrate that the holocephalan subcranial bay is occluded by a cartilaginous lamella which is thought to be the equivalent of the selachian connecting membrane. This lamella first appears in the space anterior to the ventrolateral process of the otic capsule. Later, the only remnant of the original gap between the palatoquadrate and neurocranial otic region is a single fenestra permitting passage of the (a) hyomandibular, internal mandibular, and palatine nerves and the (b) jugular vein and orbital artery (labeled PQF in Figure 10). Within this model, then, he argues the subocular process only secondarily connects to the otic region by the 85mm stage where, "the adult condition is

attained" and not directly as the selachian otic process does. Therefore, at this latter stage the impression is given of a palatoquadrate extension linking to the auditory capsule but the nature of this cartilage is actually neurocranial.

Limiting oneself to the evidence presented here there are certain points in these arguments which strengthen the legitimacy of one theory over the other. DeBeer's depiction of the holocephalan embryonic condition is the only one of the three studies which depicts the information from the vascular and nervous system plans. His figure demonstrates exactly what he has described, the position of the jugular (lateral head) vein and hyomandibular nerve relative to the cartilage in question correspond to those positional criteria Goodrich has defined for the otic process in any vertebrate group. Holmgren even concedes this point and the logic behind DeBeer's interpretation in his statement, "The strongest reason why the 'processus oticus' is considered to be a processus oticus is its relation to the jugular vein and the hyomandibular nerve both lying on its inside."

(p.190,1942) Moreover, it is important to note Holmgren's analyses are biased to the degree that he has not considered the extent to which, in early ontogeny, regressive development is possible and that the effect of such a phenomenon is to alter the appearance of those elements which are subject to remodeling in phylogenesis. Thus, given

the brief appearance of the spiracle in early chimaerid embryos and lack of detailed, early data on chimaerid mandibular arch transformation to date, one cannot determine with any degree of certainty the ontogenetic fate of those cartilages which may correspond to those generating the selachian internal and external otic processes. This, of course, does not even address the appropriateness of Holmgren's assumption that the holocephalan state is derived from the selachian form. Therefore, the most parsimonious interpretation is that DeBeer was most likely correct in his interpretation, i.e. the cartilage must represent the otic process and should not be considered as the subocular process of the basis cranii.

C: A Paraselachian Based Model.

The tripartite fusion of jaw and neurocranium evident in chimaerid ontogeny and the degree of similarity shared by this phase and features of jaw development in selachian ontogeny lend credence to the basic theories of (a) jaw development involving an autodiastylic ancestor and (b) a close relationship between selachians and holocephalans. An independent approach to determining the correctness of the selachian/holocephalan jawed transition and resolving the DeBeer -v- Holmgren debate is possible by addressing the validity of autodiastily. This approach is justified, because, if autodiastily did exist then it must be a central character in determining the validity of the sistergroup

status. That is to say, if autodiastyly is primitive then identifying an autodiastylic form is critical to any phylogenetic analysis of the base of the gnathostome radiation. Furthermore, if autodiastyly did exist, it was primitive relative to autosystyly. Thus, if autodiastyly can be demonstrated, its utility as a central character can be accepted and employed in a phylogenetic context.

This study does not represent the first attempt to verify the existence of an autodiastylic condition in the earliest cartilaginous fishes. Jaekel (1927) first reported autodiastyly in acanthodians, basing his determination on what he believed to be an unmodified hyoid arch. This was later shown not to be the case. The only other reported interpretation of autodiastyly in the fossil record I have found was that by Patterson and it may have been influenced by the popular synonymization of holostyly with autostyly. In searching for a holocephalan ancestor in the placoderms (and targeting forms with a reduced otic process, based on Holmgren's analysis) references were made to the autodiastylic Rhamphodopsis and Ctenurella. I believe the suspensorial condition of these fish does not comply *sensu stricto* with the description of autodiastyly. In these mid to upper Devonian placoderms, the palatoquadrate is said to have three articulations between the autopalatine and the neurocranium (Orvig 1962, Stensio 1962, Moy-Thomas and Miles 1971). However, an additional

association with the exoskeleton via the postsuborbital plate is probable, particularly in consideration of the condition of brachythoracid placoderms noted previously. In an evolutionary analysis, then, the ptyctodont state can only be considered as either (a) a condition antecedent to a truly autodiastylic fish where the exoskeleton plays no significant role in establishing the suspensorium or (b) as representing a distinct lineage which arose after divergence from a paleostylic ancestor. In either case, the ptyctodont arthrodires most likely represent a highly specialized lineage arising from brachythoracids and quite distinct from any lineage giving rise to the holocephalans.

Because the Mississippian chondrichthyans are known to exhibit considerable variation in the jaw/neurocranial association these fish were examined for evidence of autodiastily and other possible stages of early jaw transition. In particular, those specimens currently classified as paraselachian were targeted for their unusual combination of physical characters. The grouping Paraselachiomorpha was introduced by Lund in 1977 with the intention of alleviating some of the confusion generated by the Bradyodonti classification and to emphasize the evidence for a tremendously diverse assemblage of Carboniferous chondrichthyan fishes, most of which do not fit into a strictly selachian or chimaerid classification. These include specimens, such as Orodontiformes, edestids, and

iniopterygians, which were originally placed in the Bradyodonti despite the possession of a selachian plan dentition, a condition of which is often heterodont in these fish. The assemblage is made up of forms ranging from specimens with a fused palatoquadrate (holocephaly) to those with an articular association to the cranium and, within these latter forms, the articulations may vary. In the holocephalic forms no line of demarcation can be found to distinguish the palatoquadrate contribution from the remainder of the skull. Nor is there any evidence of a precerebral fontanelle in those forms with a well developed rostrum.

This brief synopsis of paraselachian conditions highlights the types of "uniquely" holocephalan and "uniquely" selachian characters which occur in various combinations in the paraselachian grouping. It is therefore appropriate to consider the Paraselachians of the early Carboniferous as the unique and appropriate group to answer the questions regarding (a) the model of transformation to the jawed state, (b) the validity of an autodiastylic condition and (c) the implications of the autodiastylic condition on the interrelationship of Selachii and Holocephali. The Bear Gulch collection was examined to address the question of autodiastyly first and, then, in terms of a morphocline which reflects changes in the jawed state. This was carried out with the additional expectation

that, due to the uniqueness of the specimens and character combinations, a morphocline analysis would shed some light on the question of selachian versus holocephalan derivation.

Select paraselachians were designated to form the core morphotypes for a clinal analysis. The selection was based on the combination of cranial, branchial, and pectoral characters which affect overall morphology and best represent the paraselachian assemblage. These specimens were evaluated according to those characters listed in Table 1. The resultant grouping of fossils, based on a structural grade analysis are;

1. Orodus with El Weirido as the outgroup
2. Heteropetalus elegantulus (Edestids are specialized offshoots of this morphotype.)
3. (A) Ctenacanth, Dabasacanthus, Chondrenchelys,
Harpagofututor, Cladoselache, Stethacanthidae
(B) Superfish 1
4. Het 2
5. Erismacanthus, Cochliodonts, Menaspis.

A more detailed morphocline is presented in Figure 11 and the body types for a corresponding subset of these are similarly presented in Figure 12. It must be emphasized that this classification scheme is meant to be a morphocline generated with primary emphasis on the nature of the suspensorium, and, given sufficient preservation, also on the hyoid and branchial arches.

Table 1: Features considered in the morphocline:

- 1. Nature and dimensions of the palatoquadrate.**
 - a. fused or articulated
 - b. long or short relative to the total length of the braincase.
 - c. for the long palatoquadrate, the position of its posterior limit relative to the orbit (anterior, mid-, or posterior level of the orbit)
 - d. processes forward of the hind articulation: presence of a process at the mid to anterior orbital level; presence of a preorbital process; presence of an anterior symphysis.
 - e. ventral quadratic articulation: the position relative to the length of the orbit; the position relative to the length of the palatoquadrate.
- 2. Features of the branchial basket and hyoid arch.**
 - a. presence or absence of an opercular covering.
 - b. degree of epihyal development.
 - c. orientation of arches relative to the mandibular arch elements: High, lateral position just behind the mandibular arch and extending past the posterior cranial margin, or obliquely angled behind the mandibular arch and extending partly behind the cranium, or subcranial, nested arrangement.
- 3. Girdles.**
 - a. position of the pectoral girdle relative to the head: abutting against the occipital region (forward), positioning at or about the anterior one third of the body length (posterior), or at an anterior position less than one third of the total body length (intermediate).
 - b. evidence of a link between the branchial basket and the shoulder girdle.
 - c. development of girdle cartilage(s) into high dorsal elements.
- 4. Cranium.**
 - a. interorbital dimensions.
 - b. length of preorbital region relative to total head length.
 - c. length of otico-occipital region relative to the total head length.
 - d. position of nasal capsules.
 - e. presence or absence of preorbital canals.
 - f. presence and placement of articular condyles at the

posterior and posteriolateral margins of the cranium.

5. **Orbit.**

- a. size relative to total head length.
- b. presence of sclerotics and ontogenetic fusion of original sclerotic elements.

6. **Presence or evidence of a synarcuum.**

7. **Body Characters.**

- a. overall shape
- b. fins: types, shapes, placement along body
- c. fin spines: presence or absence according to fin type; evidence of spine ornamentation.
- d. body and cranial denticulation patterns.

Figure 11 : A Morphoclinal Analysis of Bear Gulch and Bear Gulch Related Suspensoria

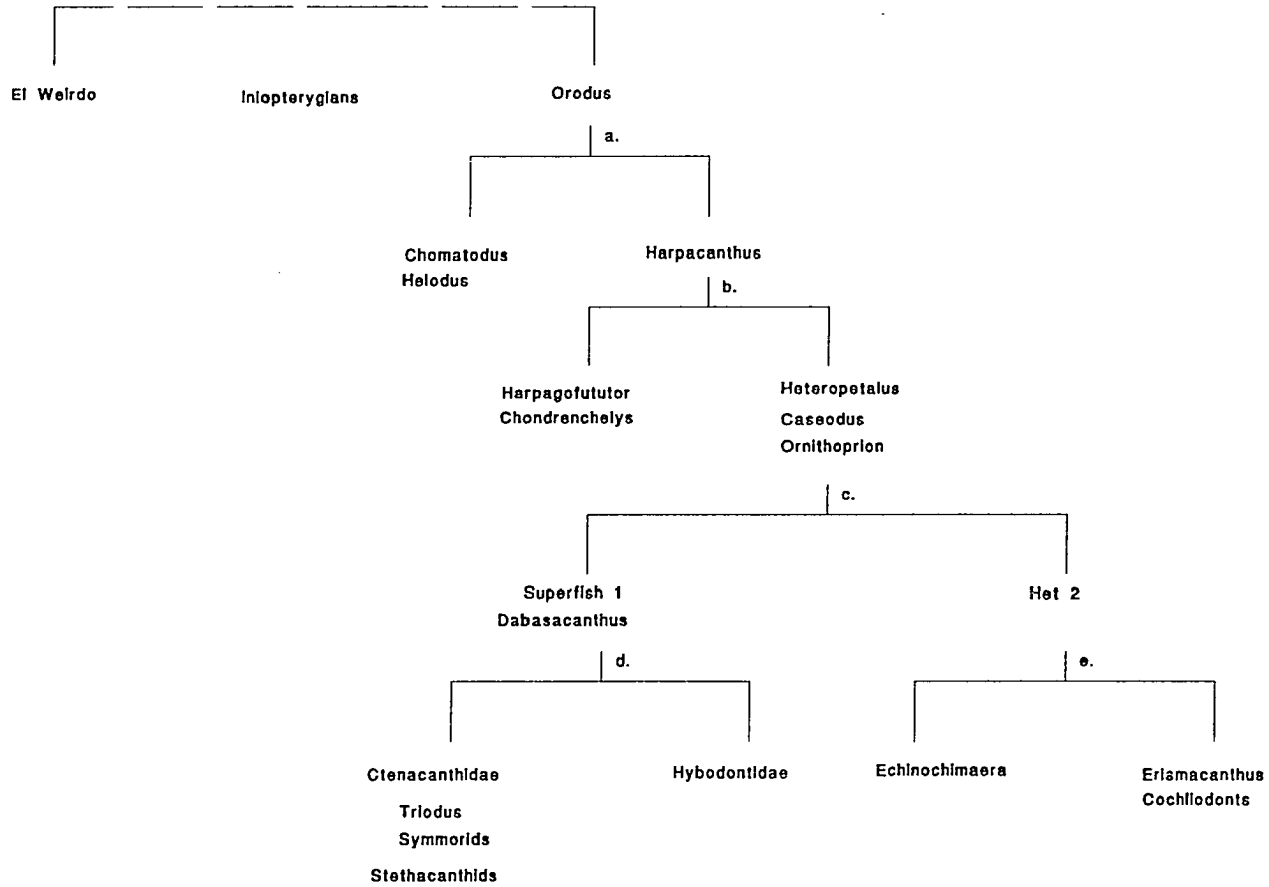
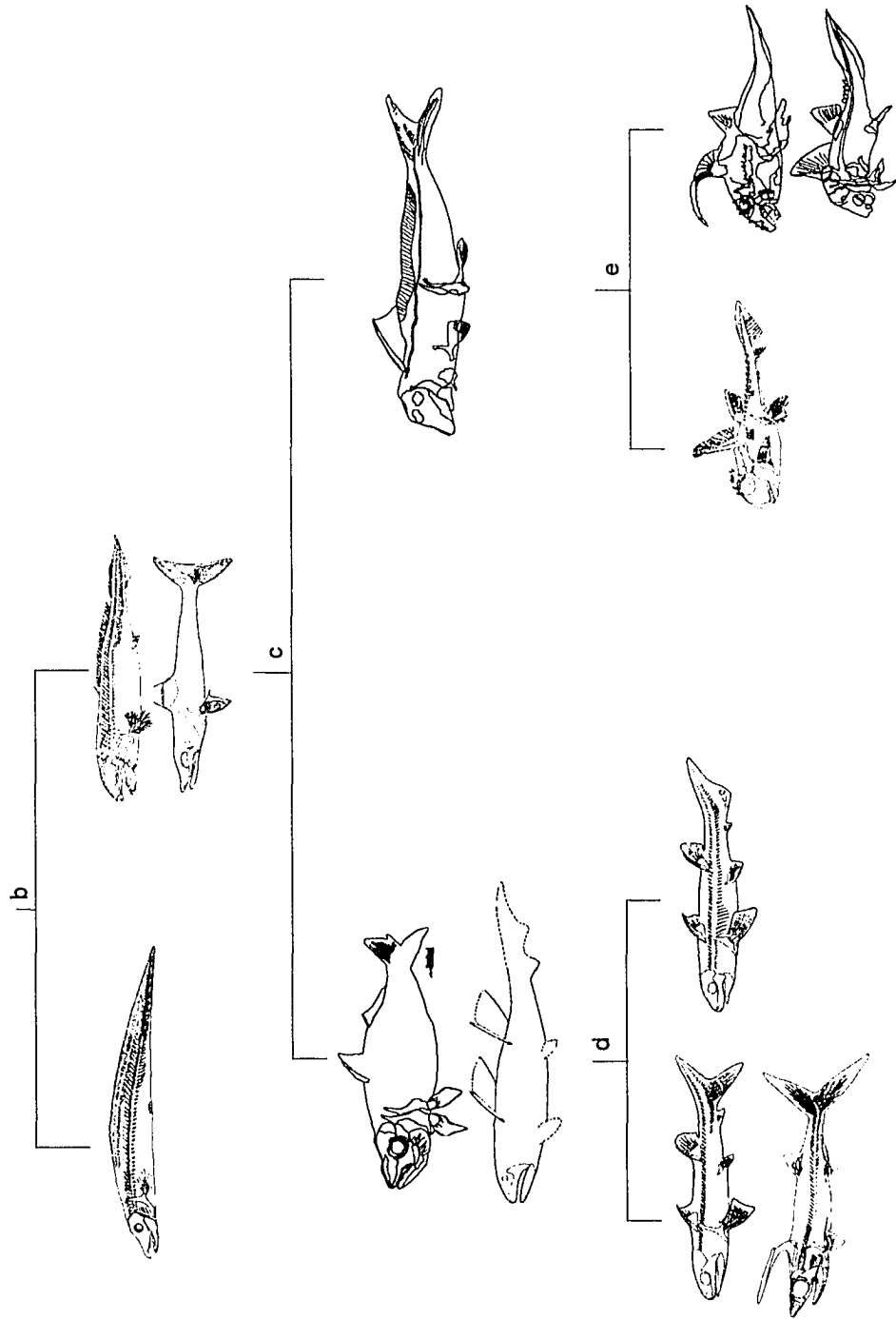


Figure 12. : The Major Body Types Reflected in the Morphoclinal Analysis Based on Suspensoria



The proposed morphocline reflects a transitional analysis of suspensorial forms which is in agreement with the classical transition discussed earlier. There is, however, a vital conceptual difference. The distinction is that the hyoid arch is postulated as being initially modified, not for the purpose of mandibular arch suspension, but for the support of a hyoid opercular valve. Thus, the palatoquadrate is initially autodiastylitic, relying on additional suspensorial assistance from labial cartilages alone. In this study the primitive nature of both the gnathostome labial cartilages and the opercular covering are argued to be based on their derivation from ancestral extrabranial arch elements.

**A Transition Analysis of Suspensorial Forms Based on the
Morphocline of Bear Gulch Chondrichthyans.**

The Bear Gulch paraselachian morphocline features a progression from the autodiastylitic condition to either a holocephalic or hyostylic, and secondarily amphistylitic, state. This suspensorial transition is accompanied by shifts in features of the hyoid arch, the branchial series, and the pectoral girdle. A detailed description of this morphologic transition series is presented to highlight the overall trends noted for critical paraselachian features.

The transitional analysis from autodiastylity to hyostyly and holostyly is based on evidence that the earliest vertebrates exhibit features which correspond to the stage

of jaw formation described in step B of the classical model of jaw formation (Figure 5). This is the phase wherein the mandibular arch has undergone that remodeling necessary to achieve some form of upper and lower jaw elements. The fossil evidence suggests the suspensorium is autodiastylitic at this stage and involves an upper jaw element which has a poorly developed anterior palatine portion. A well developed posterior quadratic portion is found to articulate with a similarly developed Meckel's cartilage. Premandibular arches and probable exoskeletal elements are interpreted to have been redesigned for incorporation into the cranium proper and as accessory suspensorial elements, respectively. The accessory elements of suspension are critical to establishing the rim of the mouth by providing the rigid or fixed stability required in primary stages of feeding and respiration while also allowing the flexibility required in subsequent phases of these actions. The hyoid arch also undergoes some modification but the changes concern, at most, slight changes in the ceratohyal and more ventral elements. The basi- and hypohyal elements are developed to form the floor of the mouth. An increase in the mass or girth of the epihyal occurs for the purpose of supporting the opercular covering generated from original exoskeletal arch elements. The closer proximity of the hyoid arch to the mandibular (in comparison to the relative placement of the first branchial arch, a condition which is retained from

the agnathan state) suggests a high probability of contact between these two arches. If so, the effect is most likely to link the mechanical stresses and strains of respiratory activity to the hyoid and mandibular arches, thereby creating an integration of otherwise independent systems. Thus the main interaction between hyoid and mandibular elements is seen at the level of the cerato/hypo- and basi-elements since the function of these hyoid elements is to contribute to opercular support and respiratory action and to link these with the lower jaw. The fossil Orodus, by virtue of its suspensorial condition and position of the operculated gill arches most clearly represents this stage of the model.

The next phase of the transition would revolve around subsequent specializations of the upper jaw which secondarily influence the nature of both the hyoid arch and the mandible/branchial arch association. The relative dimensions of the upper jaw morphology are altered as the palatine segment undergoes more significant development. This anterior development probably occurs in conjunction with that cranial remodeling resulting in the enhancement of the rostral-ethmoidal or rostral-orbital region. Posteriorly, the palatoquadrate otic segment establishes more of an intimate association with the orbit. This change would be expected to account for an overall increase in upper jaw dimensions and, as such, establishes a strong,

mechanically stabilizing association between the orbital region and upper jaw. Those changes in upper jaw dimensions which occur up to this point do not dramatically alter the features of the hyoid arch but any subsequent modifications would affect its architecture, and concurrently, the features of the lower jaw, the position and arrangement of the branchial arches, and the placement and relation of the shoulder girdle to the respiratory apparatus. The Bear Gulch "bradyodont", Heteropetalus elegantulus best typifies the conditions of this phase while Superfish 1, Het 2, and Erismacanthus exemplify, respectively, the clinal states 2, 3B, 4, and 5 where changes in the latter features are evident (Figure 13).

Figure 13 depicts the further development of the palatoquadrate element which is correlated with a progressively intimate association between upper jaw and neurocranium. The form of association, as determined by the regionally select palatoquadrate remodeling, also influences the relative placement of the lower jaw quadratic articulation. Depending upon the stresses associated with feeding and respiration the condition described up to this point may subsequently transform to either of two conditions (A or B) in stage 3 of jaw formation (Figure 12). Transformation "A" shows an enhancement of the epihyal element in the event that the main bracing and stabilization

of the jaw is principally focused at the orbital level while permitting increased flexibility to the jaw mechanics. In application, this arrangement would result in a hyostylic suspensorium and permit subsequent formation of amphistyly. Compared to the conditions of both stages 1 and 2 the branchial basket is permitted to expand posteriorly (as indicated by the arrow), and may do so to accommodate the increased range of motions in the feeding mechanism.

Transformation "B" involves placing the mechanical emphasis along the length of the upper jaw and would require a more structurally significant association between the palatine and ethmoidal zones of the palatoquadrate and braincase respectively. This is achieved by development of an anterior orbital articulation. The posterior articulation is also significantly reinforced by development of a postorbital process. Within this mechanism the position of the quadratic articulation would have to acquire a more of a suborbital position to facilitate the dispersal of feeding stresses along the upper jaw. The elements of the hyoid arch would undergo moderate realignment in response to the lower jaw shift. The ventral hyoid arch elements would retain their association with the lower jaw as the latter "migrates" forward while the more dorsal epal segment becomes more obliquely oriented just behind the posterior margin of the upper jaw. This realignment would force the anteriormost pharyngobranchial elements into a closer

arrangement and result in a "nesting" of the branchial arches with forward migration of the shoulder girdle. The forward displacement of the shoulder girdle is anticipated if it is to assist in supporting a respiratory system which is superficially, and possibly functionally, distinct from that favored by the trends in pathway "A". Therefore, an articular connection would be found between the girdle and branchial system.

The pathway to stages 4 and 5 involves an intensification of those trends initiated in 3B. In 4 the forward position of the palatoquadrate signifies an intense specialization of this element and obviously is correlated with changes in the positioning of the shoulder girdle and branchial arches. The final condition of stage 5 depicts the consequence of the trend towards a progressively closer association between upper jaw and cranium, i.e. the holostylic state, but, as indicated in the morphocline of Figures 11 and 12, the conditions outlined here need not be the only mechanism by which holostyly is achieved.

The Bear Gulch chondrichthyan fossils used in this study demonstrate irrefutable evidence of the autodiastylic condition. This suspensorial state is found in those paraselachians which exhibit both holocephalan and selachian features. Therefore, these fish are believed to have been involved in the basic radiation of Chondrichthyes.

Consequently, this research indicates the chondrichthyan sistergroup status is determined, if not solely then to a large degree, by the autodiastylic state.

The data also indicate holostyly and hyostyly have arisen a number of times in the extensive basal radiation of Chondrichthyes. The multiple development of this condition should be viewed as ecotypically driven. However, there is some variability in the gross appearance of the holocephalic Bear Gulch specimens which corresponds to a parallel variation in overall cranial dimensions. A comparative examination of Harpagofututor and Echinochimaera best demonstrate this observation. This phenomenon is interpreted to stem from the distinct nature of the autodiastylic palatoquadrate in the direct ancestor of one form (long) versus that of the other (short). Thus, the correlation of the palatoquadrate dimensions in the early autodiastylic forms with overall cranial dimensions generates a character set which segregates the holocephalic forms in a clinal analysis. Additionally, the construction of a morphoclinical analysis on the basis of suspensoria yields a similar pattern of segregations or groupings according to body form. The resultant subgrouping of the paraselachian assemblage provides a clearer interpretation of the likely interrelationships between selachians and holocephalans.

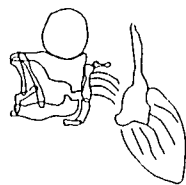
How The Clinal Transition of Jawed Forms Affects Various Features of the Cranium

The clinal grades of my transition model are based on observations which infer much about the trends in chondrocranial remodeling. Consequently that information generated from the morphocline has been used to assess the more apparent controversies regarding the interrelationship of the selachian and holocephalan conditions. For example, the debate centering on the designation of cartilages as cranial versus mandibular can be analyzed in the context of those palatoquadrate modifications identified in the autodiastylitic to hyostylic or holostylic transition. This is so because the Bear Gulch fossil evidence contributes considerable information regarding the nature of the cartilaginous elements which have been tied or attributed to the lateral orbital wall and orbital floor cartilages of Holocephali. My morphoclinical analysis and paraselachian data offer the greatest support to DeBeer's theories rather than Holmgren's in the comparative nature of chondrichthyan features (Figure 14).

(a.) The Question of an Otic Process versus Subotic Shelf

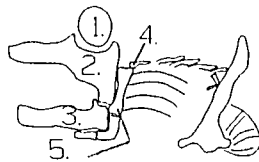
Certain Bear Gulch paraselachians (H. elegantulus, Superfish 1) possess a postorbital process and a complimentary process which extends dorsally from the palatoquadrate. It is this latter process which can be identified, *sensu stricto*, as an otic process and, by no means whatsoever, should carry the connotation of being a

Figure 13 : Transition Series of Bear Gulch Suspensoria

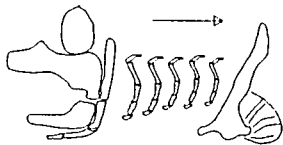


Stage 1: Orodus

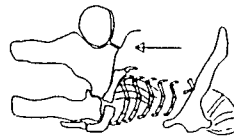
Stage 2: Heteropetalus elegantulus



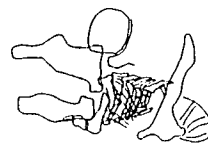
Stage 3A



Stage 3B: Superfish 1



Stage 4: Het 2



Stage 5: Erismacanthus



Numbered elements are: 1. orbit, 2. upper jaw, 3. lower jaw, 4. pharyngohyal, 5. epityal thymomandibula (in 3A)
Although these are given for one figure, they apply to all forms drawn.

selachian-type palatoquadrate otic process attaching to a more posterior otic capsule. Thus, it is possible and clearly demonstrated in the lower Carboniferous Harpagofututor that an otic process may be found in a holocephalic form. As to how this may have come to pass in a form which does not possess a suspensorial hyomandibula, I agree with DeBeer and Moy-Thomas (1935) that the otic connection "must be inherited from the nonfused autostylic or autodiastylic ancestor shared by Holocephali and Selachii." This process develops with the basal connection to provide a stable association between jaw and neurocranium as the suspensorium is developed.

The paraselachian data indicate that, during the autodiastylic to holostylic transition, there are gradual but significant changes in the autodiastylic state which are seen to accompany a trend in cranial remodeling. From H. elegantulus to Erismacanthus the cranial reshaping initiates in the otico-occipital region and progresses forward. The palatoquadrate is displaced forward such that the rostroethmoidal region appears to develop at the expense of an increasingly reduced otico-occipital region. In this transition there is such a dramatic shifting of cartilages that the ventral extension of the postorbital and posterior extension of the otic processes come into close proximity to one another at the hind margin of the orbit and, thereby, come to be more intimately situated with the subocular or

basis cranii cartilage. Consequently, the posterior remodeling appears to force both the postorbital process and otic process into positions which can be interpreted as the "lateral wall and floor" of the orbit. One need only consider the similar repositioning of the quadratic articulation, now found at a level which is parallel to either the anterior or mid-level of the orbit, to substantiate the fate of the postorbital and otic process cartilages. (The position of the quadratic articular process can be used to indicate the extent to which development or enhancement of the posterodorsal process occurs.) In one of the more extreme cases of otic process development affecting the appearance of subsequent holocephaly, a strong, laterally flaring suborbital shelf may be formed, as in Harpagofututor. The other extreme concerns the most extensively displaced palatoquadrate cartilage. As exemplified by Het2, the postorbital cartilage in this state is distorted to the extent that it is a strong cartilage angled around the posterior margin of the orbit. It thereafter continues forward to meet the extensively calcified posterodorsal palatoquadrate articulation at a level parallel to the mid- to anterior orbital margin. Occasionally the extensive nature of this cartilage can be truly appreciated when preservation is such that the head is obliquely crushed and the postorbital process can be seen as a plate, distinct and flaring laterally away from the

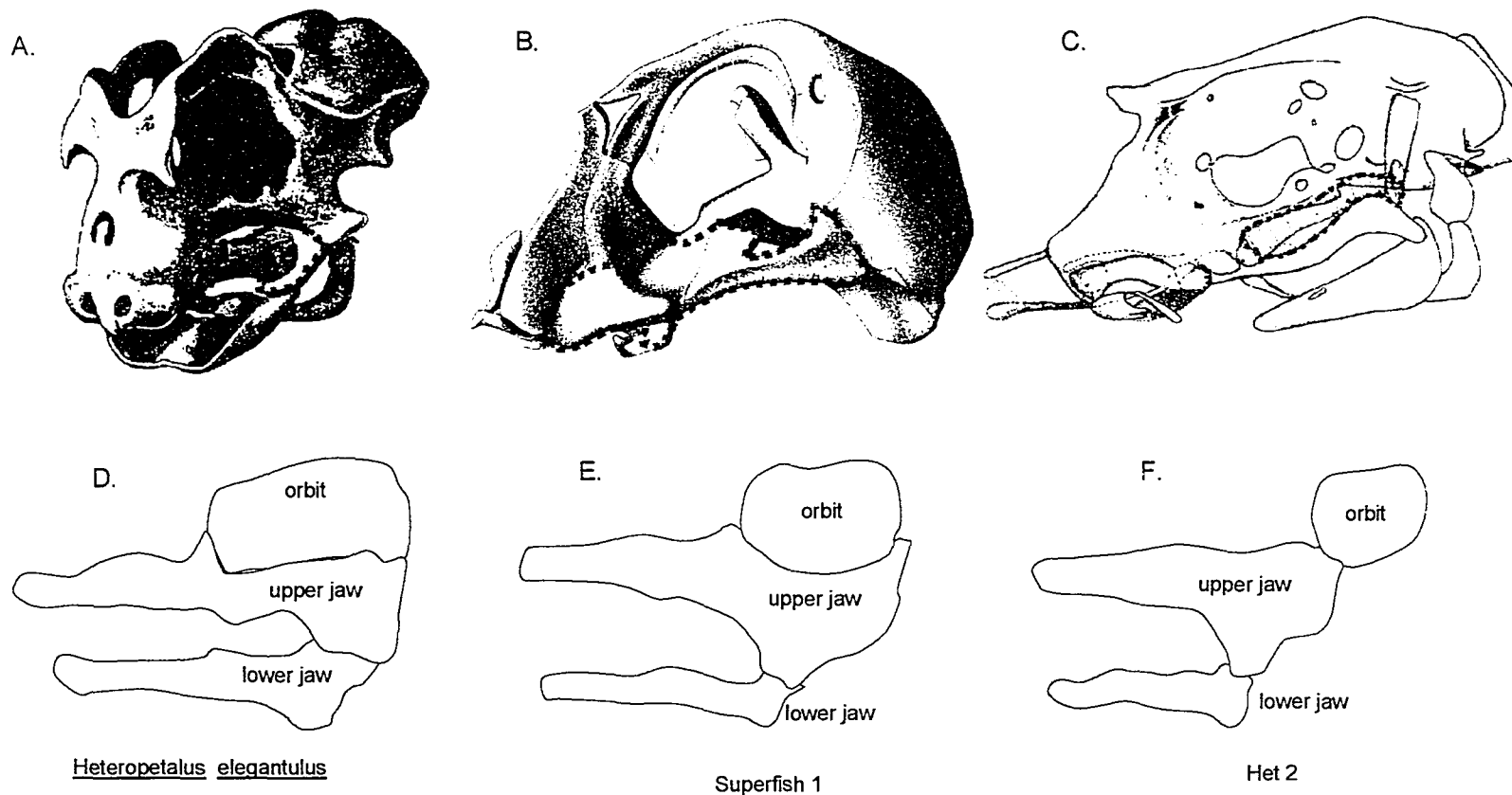
cranial floor

Is there evidence from the earlier studies to support the interpretations offered here? Dean's Chimaera provides the best evidence to support my contention that the palatoquadrate and postorbital process undergo a "subduction" around and under the orbit in an overall anterior direction. What Holmgren has labeled as the postorbital process is a feature often observed in those paraselachians with the branchial basket situated in a forward position (Harpacanthus, Het2, Heteropetalus) such that either the anterior arches or the complete series of arches are subcranial. This feature is the anterior limit of a concavity in the cranial cartilage of the otic region which accommodates the dorsal portion of the branchial arches. The segment identified as the basitrabecular process (DeBeer's otic process) actually corresponds to that portion of the the ventrolaterally and anteriorly displaced postorbital process of autodiastylic paraselachians which meets the posteriormost end of the palatoquadrate. If this latter region of the autodiastylic palatoquadrate is defined as the otic process (in agreement with DeBeer's analyses) then this condition sets the stage to explain how the holocephalan jugular (postorbital) vein passes through a short cranial canal as it travels backwards to the anterior cardinal vein. The selachian vessel, on the other hand, most often travels in a depression alongside the otic region when

traveling caudad. The holocephalan condition can be attained through the progression series highlighted in the sequence of stages 2, 3B, and 5 of Figure 13. This can be described as the trend in which the postorbital process envelops and carries the vessels and nerves of the region into more of an anteroventral position as it is shifted to a point of fusion with the subocular cartilage and the otic process. As for the extent of the palatoquadrate element in extant forms relative to what is observed in the autodiastylic to holostylic trend of paraselachians, the data agree with the anterior and posterior limits demarcated in Dean's illustrations. As it relates to the 60mm Callorhynchus diagram, Holmgren's suborbital shelf is the mid to posterior region of the autodiastylic palatoquadrate. Thus Figure 14 has been constructed to show the similarities between the palatoquadrate dimensions of the extant chimaerid embryos, Holmgren's scyliorhinid embryo, and that of the autodiastylic paraselachians.

With regard to modification of palatoquadrate dimensions, Dean confirms there is ontogenetic evidence for a reduction and shifting of the palatoquadrate to a more anterior position in extant forms. This may be taken as a recapitulative event, reflecting those observations made in the paraselachian morphocline which demonstrate the possible derivation of either holocephalan or selachian conditions from the autodiastylic state. It is in context with the

Figure 14. : A Comparative Morphology of Chimaerid, Embryonic Scyliorhinus, and Paraselachian Jaws



Dotted lines approximate the dimensions of the holocephalan palatoquadrate. The selachian embryonic connecting membrane is indicated in C. A. Dean's Chimaera; B. Schauinsland's Callorhynchus; C. Holmgren's Scyliorhinus with embryonic membrane. D., E., and F.: Paraselachian Upper and Lower jaws

observation on the ontogenetic shifting of the palatoquadrate and in comparing his Chimaera to the Callorhynchus embryos that Dean mentions that the palatoquadrate is not nearly as distinct an element as Schauinsland has figured it to be. Therefore, the outline of this element which gave rise to Holmgren's identification of a subocular shelf was, a priori, misleading and does not depict the true limits of the palatoquadrate cartilage.

**(b.) The Nomenclature of Connections Between the Jaw and
Cranium**

An extensive controversy surrounds the identification of the palatoquadrate processes of articulation. The dilemma affects both fossil and extant material and appears to be centered around that process identified as the basal connection. My observations on the changes in palatoquadrate position and the nature of the postorbital process provide notable information on the status of a basal connection in its earliest known form. If the basal connection is to be the initial contact between mandibular arch and neurocranium then, what is observed in the paraselachian orbital remodeling is a shifting forward of this. The Bear Gulch data demonstrates the plesiomorphous contact between cranium and upper jaw occurs at the mid to posterior level of the orbit. As shown in the morphocline stage 3A and 3B respectively, any changes in the palatoquadrate dimensions

following the pleisiomorphous contact between upper jaw and cranium are either shifted forward or posteriorly of the original orbital (basal) connection. Thus, if the earliest and simplest autodiastyllic condition is described with otic and basal articulations then the articulations observed in Superfish 1 are otic and basal. In Het 2 however, some authors may describe the articulations as ethmoidal and orbital (see appendix note #4 for a discussion of this relative to the discrepancies in defining the articulations in both fossil and extant forms). Yet, as both the fossil and ontogenetic data reveal, the latter Het 2 connection is secondarily displaced forward and therefore a derived position for the basal connection. The ethmoid articulation (being distinct from any orbital articulation) is defined as secondary and evident as the contact between the palatine portion of the pterygoquadrate and ethmoid region of the neurocranium. This interpretation is supported by DeBeer and Moy-Thomas (1935, p.289). Furthermore, these trends of the morphocline are consistent with the comparative selachian information Holmgren collected on the two patterns of trabecular growth and cranioquadrate passage positioning. In these analyses Holmgren interprets the cranioquadrate passage as that point of the selachian basis cranii which demarcates where the palatoquadrate will articulate with the orbital region. (This is taken to be fact, a priori, since it is the fusion of the palatoquadrate onto the lateral edge

of the trabecular plate which forms the cranioquadrate passage.) In squaloid embryos he describes the cranioquadrate passage to be found midlevel to the trabecular cartilages. That is, the trabeculae can be seen to extend in front of and behind the position of the somewhat lateral process. Subsequent growth of the trabeculae occurs principally in a frontal direction, resulting in the more posterior positioning of the jaw/trabeculae connection in what would be called by most as the basal region. In galeoids, on the other hand, the trabeculae are first seen as short rudiments with the cranioquadrate passage situated at the level of their anterior ends. At later stages of development the trabecular cartilages are not observed to extend much beyond the cranioquadrate passage. As such, the apparent position of the jaw/cranial articulation would be interpreted by most, based on its anterior orbital position, as ethmoidal rather than orbital.

This evidence suggests that, irrespective of where the articulation is situated within the orbit, i.e. from the anteriormost margin of the orbit to the posteriormost margin where the foramina for cranial nerves V and VII are found, these should all be considered the orbital, and therefore, the basal connection. There are other concerns regarding the development of a cranioquadrate passage and its values as a landmark in comparing selachian and holocephalan

crania. Therefore, the nature of this feature is more closely evaluated here.

(c.) The Value of the Cranioquadrate Passage

In the adult holocephalan there are three orbital foramina which are associated with the cartilage spanning the region between the basal and otic fusions. These foramina permit passage of the (1) efferent pseudobranchial artery, (2) palatine nerve and orbital artery, and (3) the hyomandibular nerve and vena capitus lateralis in an anterior to posterior arrangement respectively. In a phylogenetic shift from a free to a fused upper jaw these foramina are postulated to represent the vestiges of the cranioquadrate passage; the space enclosed by the palatoquadrate, chondrocranium, basal processes and otic process (Goodrich, 1930). Therefore, as a direct consequence of differing interpretations on the development of holocephalan palatoquadrate and cranial cartilages, Holmgren and DeBeer and Moy-Thomas also disagree on the identification of these foramina in the holocephalan embryo. Since the controversy regarding the cranioquadrate passage is intimately tied to the same argument on the basal connection, this debate is also settled by the the paraselachian morphocline evidence.

Callorhynchus, as the least derived of the extant chimaerids, is most important to understanding the mode of holocephalan cranioquadrate passage development. The embryo

shows two foramina in the region of the basal process. The anterior foramen (transmitting the palatine nerve & orbital artery) is separated from the second (carrying the hyomandibular nerve and vena capitis lateralis) by a short region of fusion between the pterygo-quadrate and neurocranium. Therefore the passage has the appearance of being divided in two. Holmgren argues the partition is a post palatine commissure related to the merging of foramina identified in connection with internal and external otic processes between the basal and otic fusions. DeBeer avoids the problem as he more cautiously debates, "As to the relative participation of basal process and basitrabecular process in establishing the basal connection little can be said. Judging from the condition in *Selachii*, where the basitrabecular process is only feebly developed and represented by the major part of the subocular shelf, it is probable that the major part of the basal connexion in *Callorhynchus* is formed by the basal process."

The debate is simply answered by the paraselachian morphocline. The orbital pigmentation patterns of those forms with the more plesiomorphous autodiastylitic suspensorium suggest the vascular foramina were located at four particular levels of the orbit. In a counterclockwise direction these were positioned at the anterodorsal, anteroventral, posteroventral and midposterior margins of the orbit. The latter connected with a jugular canal formed

by the ventroanterior extension of the postorbital process extending toward the palatoquadrate. The first two foramina are believed to carry the superficial ophthalmic nerve and orbitonasal veins respectively. Finally, that foramen at the ventroposterior orbital margin is that which is posterior to the "basal" connection and is believed to have carried the palatine nerve and orbital artery.

Once there is an anteroventral shifting of the postorbital process and anterior movement of the palatoquadrate these foramina and their associated structures are displaced and reoriented with respect to the cranial plan. The shifting mechanism forces the foramina of the jugular vein and hyomandibular nerve to merge with that of the orbital artery and palatine nerve. In doing so a cranioquadrate passage is formed which agrees with the appearance of that in Callorhynchus. Thus, as in many of the paraselachians, there appears to be one large foramen at the ventroposterior angle of the orbit, in addition to the two foramina at the anterior orbital margin. The large foramen has come to be identified as the cranioquadrate passage because it is the major jaw/neurocranial space located between the basal and otic articulations (Table 2).

Non-cranial Features Which are Involved in the Jawed Transition

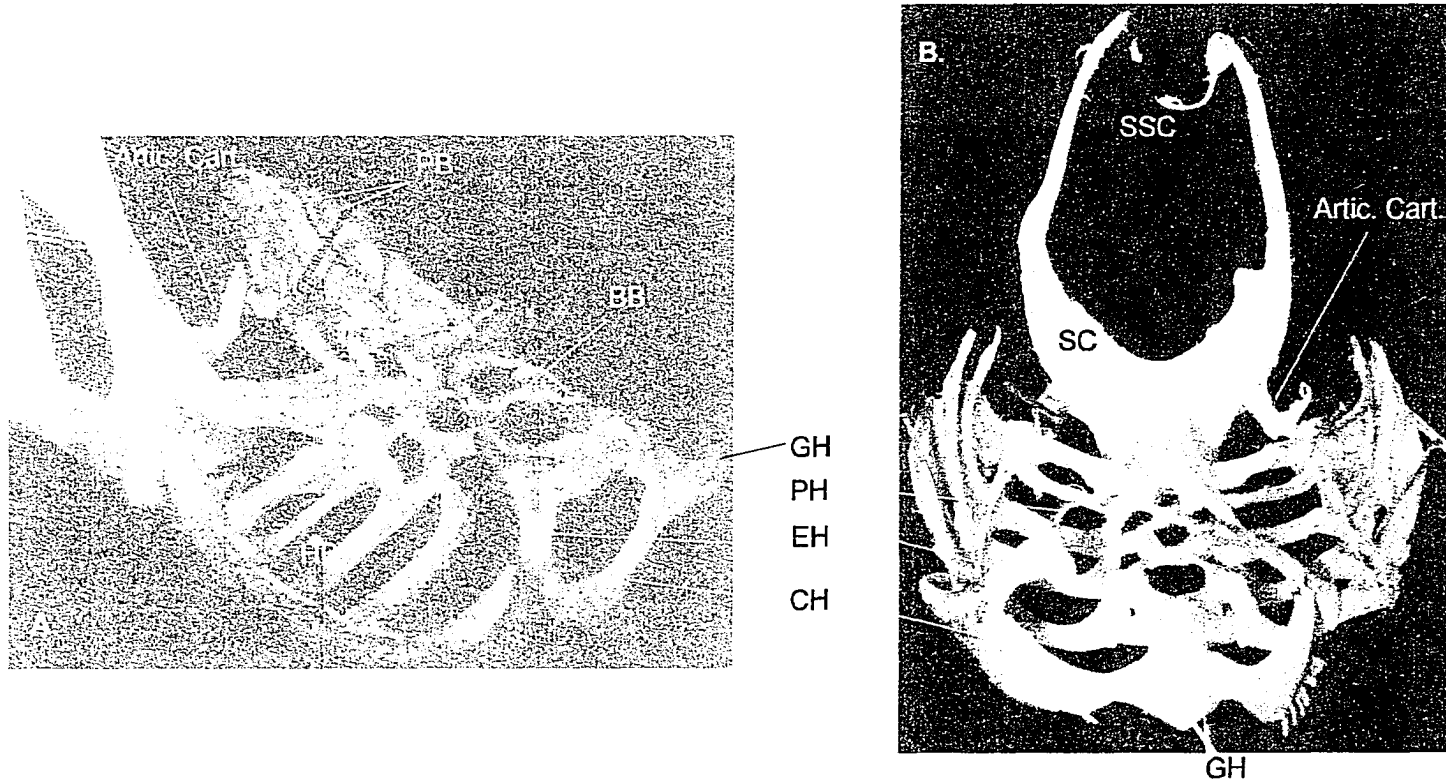
There are a number of physical changes noted in the morpho-clinal transition which are apparently driven by

Table 2 : Identifications of the Foramina in Fossil and Extant Fish Exhibiting Holocephaly

Specimen	Author	anterior	posterior
<u>Helodus</u>	Patterson	none	two for the pseudobranchial artery
<u>Squalo- raja</u> *	DeBeer & Moy-Thomas Patterson	orbitonasal vein ef. pseud.	cranioquadrate passage (jugular)
<u>Callo- rhynchus</u> (embryo)	Holmgren DeBeer & Moy-Thomas	orbitonasal vein orbitonasal vein	cranioquadrate passage cranioquadrate passage
<u>Callo- rhynchus</u> <u>Chimaera</u> <u>Rhino- chimaera</u>	Stahl	orbitonasal vein	efferent pseudobranchial artery and posterior palatine vein

ecomorphological pressures relating to feeding and predatory swimming dynamics. This phenomenon has apparently lead to the convergent or parallel development of features which, in this assemblage of closely related fishes, results in a seemingly haphazard combination of character states in paraselachians. Yet, the morphocline suggests that the radical divergence of the extant sistergroups involve characters which are linked and reflect an integration of various systems. To assess this interconnectivity, dissections were performed on recent chondrichthyans. Reflecting upon those observations made from both fossil and extant material it has been determined that the chimaerid features of synarcual development, branchial basket positioning, and pectoral girdle structure and location are characters which should be considered as a collective unit when attempting to clarify the interrelationships of selachians, holocephalans and paraselachians. As a unit the characters of this complex affect features of the respiratory and circulatory systems which, themselves, concentrate those characters representing the obvious divergences between holocephalan and selachian conditions. The close relationship between the holocephalan branchial skeleton and shoulder girdle (Figure 15), and "stabilization" of the latter against the posterior cranial margins and synarcuum suggest divergence not only in the respiratory mechanism but also the cardiac pumping mechanism

Figure 15: Holocephalan Branchial Basket Architecture as Demonstrated by *Chimaera* sp.



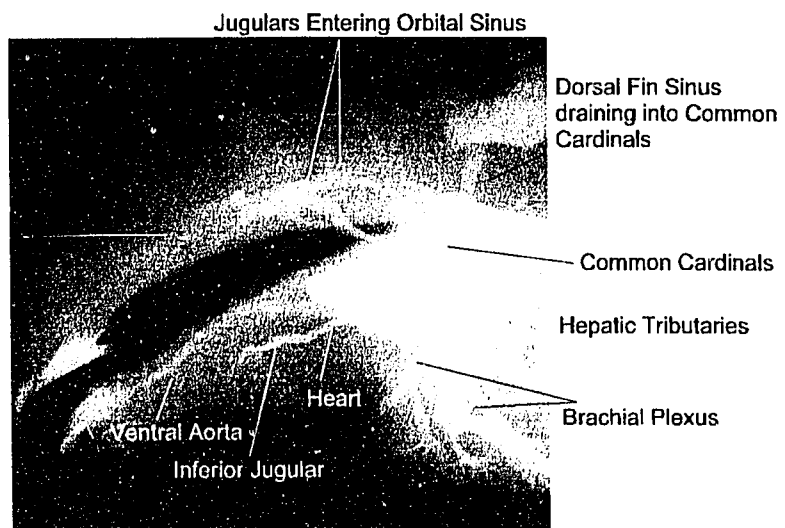
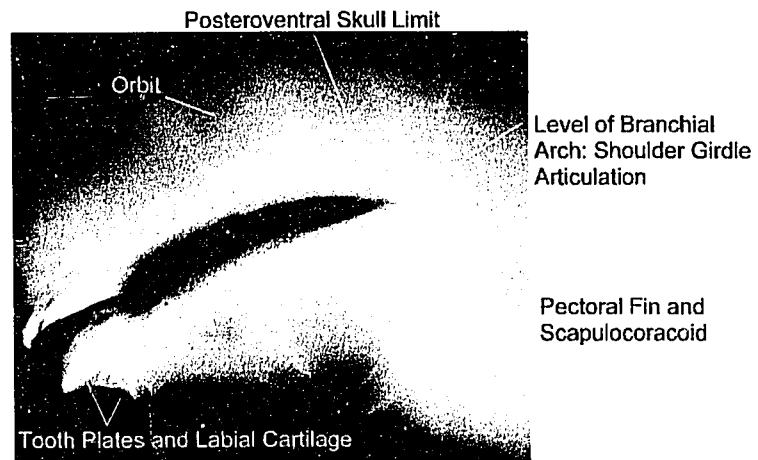
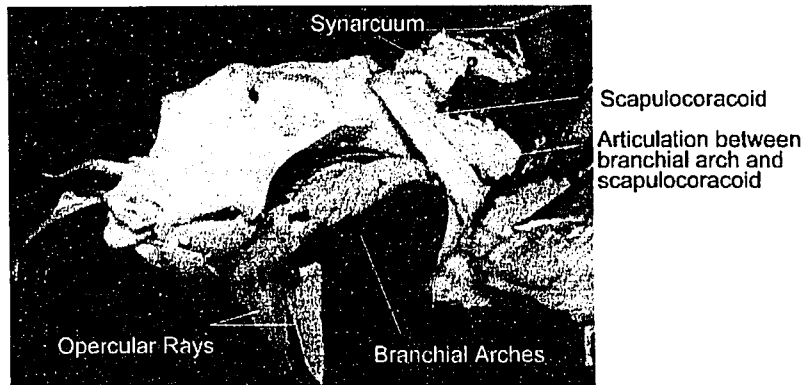
A: Lateral View. B: Anteroposterior View. Artic. Cart.: articular cartilage between the shoulder girdle and branchial basket, BB: basibranchials, CH: ceratohyal, EH: epihyal, GH: glossohyal, HB: hypobranchial, PB: pharyngobranchial, PH: pharyngohyal, SC: scapulocoracoid, SSC: suprascapular cartilage

between Selachii and Holocephali. Yet, as the fossil material has indicated, the steps required for transition from one state to the next are minimal and can be attributed to those ecomorphologically driven modifications correlated with feeding guild specializations. To appreciate the simplicity of this shift, one would need to understand the interconnectivity of characters in this complex.

The unusual orientation of the chimaerid branchial basket is a central feature of the character unit or functional complex (Figure 16). Those conditions which suggest the branchial basket as a whole is modified include (i) the sequential "nesting" of each arch in the successive one, (ii) the relatively strong development of the pharyngobranchials and (iii) the modification of the ceratobranchial element of arch V for articulation with the pectoral girdle.

It appears the articulation between the last branchial arch and the pectoral girdle may be one of several links noted between the feeding, respiratory, and circulatory systems of these animals. This connection may act to ensure the support of the shoulder girdle in generating a respiratory and circulatory pump. The link between the lower jaw and hyoid arch is through the glossohyal, thus lower jaw movements possibly carry over to opercular motions. Extending posteriorly from this area the musculature inserting on Meckle's cartilage from its origin at the

Figure 16:
Branchial Basket, Shoulder Girdle, and Vascular Relations of Callorhynchus



coracoid bar and attaches onto the ventral aspect of the branchial arches. Thus contraction or extension of these hypobranchial muscles influences the lower jaw and branchial arch motions but additionally appears to affect the volume and pressure of the cardiac cavity since the posterior branchial arches and shoulder girdle border the heart to such a degree that they provide a structural encasement for the heart. The basal elements (probably a combination of hypobranchials and basibranchials) of the last two branchial arches are found to fuse into a plate which serves as the roof to the cardiac cavity. Posteriorly, the heart is seated in the ventral crux of the coracoid bar and in that region generated by the nesting and increasingly dorsal positioning of posterior arches through arch reduction (Figure 15). Laterally the direct articulation of scapular and ceratobranchial cartilages provides the basis of a lateral enclosure. (The precise attachment of this interconnection occurs on the mesial side of the scapula at that point where the lateral extent of the shoulder girdle arches anteriorly). Thus the outward appearance of the cardiac and branchial regions suggest the heart depends upon the actions of the surrounding skeletal elements to assist in maintaining the appropriate pressure flux for blood circulation.

Another character in the complex is the synarcuum, found to provide the structural support for a significantly

enlarged and movable first dorsal fin spine and the insertion point for muscles lying just below the suprascapular and scapular cartilages. The motion of the dorsal fin spine acts to drive the pumping mechanism which drains the large first dorsal fin sinus into the anterior cardinal system, located at a level between the branchial arches and shoulder girdle.

Thus the pumping actions associated with lower jaw, first dorsal fin spine, and pectoral girdle movement all serve to facilitate the overall circulatory pump. These observations and those additional supporting notes listed in Table 3 were taken from dissections of Hydrolagus, Rhinochimaera, Callorhynchus and Chimaera.

That some paraselachians also possessed a link between the branchial basket and pectoral girdle is demonstrated by both Erismacanthus and Heteropetalus elegantulus. In consideration of the distribution of (1) a synarcuum, (2) dorsal fin sinus and enlarged first dorsal fin with a mobile fin spine, (3) position of the gill arches relative to the lower jaw and neurocranium, and (4) the position of the shoulder girdle, those paraselachians more closely aligned to the holocephalan condition are Het 2, Erismacanthus, and the cochliodonts. Of these, the cochliodont condition is virtually, if not exactly, identical to the conditions of extant holocephalans even to the extent of denticulation patterns. The features of these

fish contrast with those of Superfish 1 which are more reflective of the selachian state.

Table 3: Comparative Features of the Selachian versus Holocephalan Character Complex

Feature	Selachian	Holocephalan
hyoid sinus	present	absent
jaw mobility	appreciable	restricted
pharyngeal dimensions	simple anterioposterior directed "tube"	convoluted, apparently reduced in the dorsoventral plane and shifting dorsad in between the oral cavity and the end of the branchial region
branchial arch position	generally posterior to the cranium	subcephalic
Pectoral girdle	fused or ligamentously tied halves	fused halves; high dorsal extension of scapula and suprascapula
range of pectoral fin mobility	limited in dorso-ventral plane	moderately flexible in an oblique dorsoventral and anteroposterior plane
nature of pericardial enclosure	tough, fibrous pericardial sheath	thin sheath; cardiac region encased by branchial and scapulocoracoid elements
scapular: ceratohyal (V) articulation	absent	present
synarcuum	absent	present

THE ETHMOID CANAL CONTROVERSY

The Holocephali are said to hold a sistergroup status to the Selachii principally due to the common character trait of a prismatically calcified cartilaginous endoskeleton. Yet, given examination of the selachian and chimaeroid chondrocrania, the closeness of this relationship is not intuitively obvious and is even less fathomable considering the appearance of the ethmoid region (Figures 17-20). In the extant holocephalans this region is primarily occupied by the ethmoid canal, a structure described as the cavity which lies dorsal to the level of the nasal capsule and dorsal to the neurocranial cavity. This canal carries the superficial ophthalmic and profundus nerves forward from the orbit to an anterior opening where they exit onto the snout. It also carries a tributary forward from each side of the orbital sinus, the ethmoid vein, which is responsible for drainage of the rostral area. In contrast, the corresponding region of the selachian cranium is found to be unchondrified; occupied by a precerebral fontanelle which is covered over by a thickening of the dura mater. The positions for the superficial ophthalmic and profundus nerves are similar to the holocephalan condition but these structures typically run forward on the surface of the nasal capsule rather than

Figure 17 : The Major Nerves and Veins Associated with the Holocephalan Orbit and Ethmoidal Region

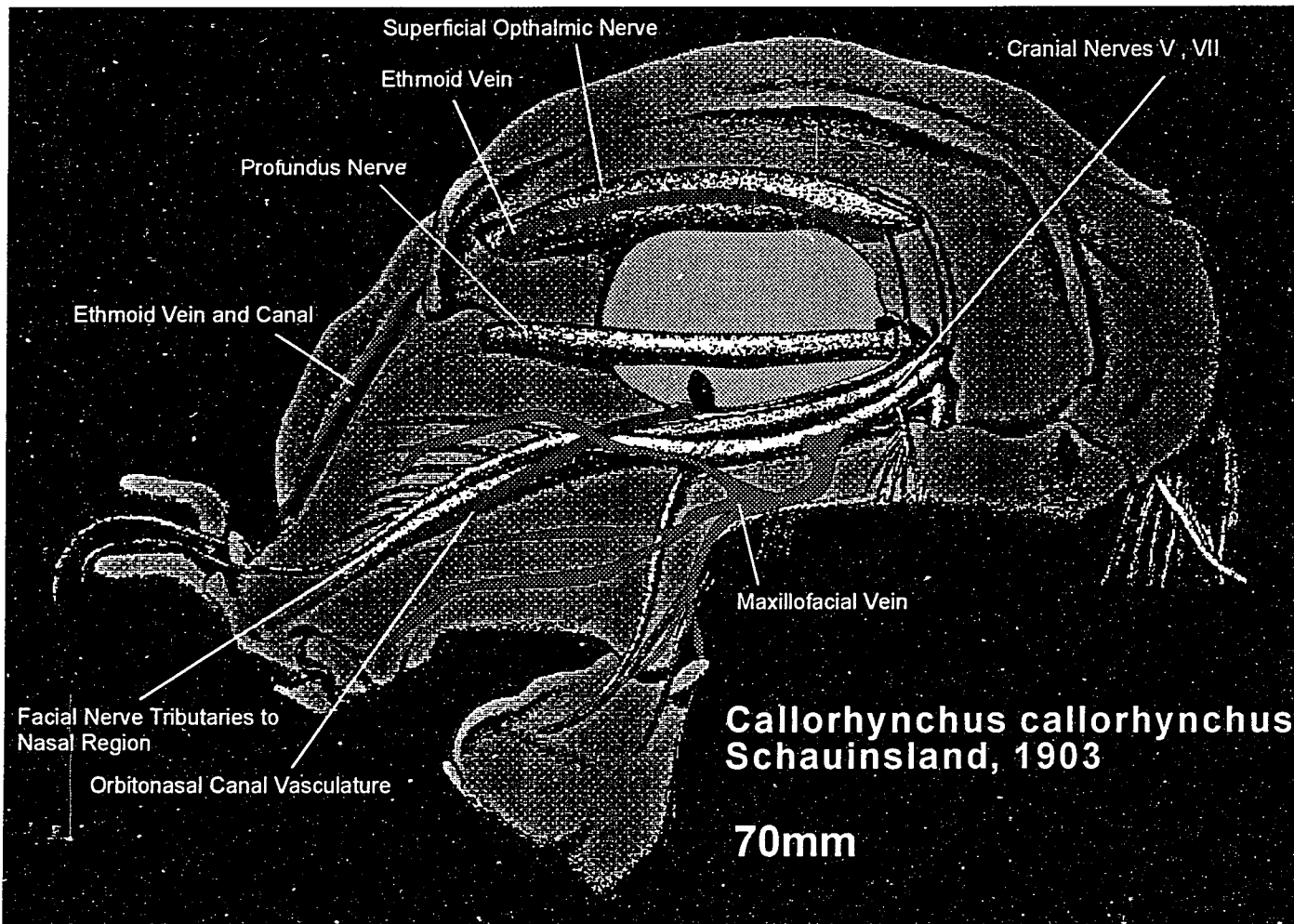


Figure 19: The Major Nerves and Veins of the Shark Orbit and Ethmoidal Region

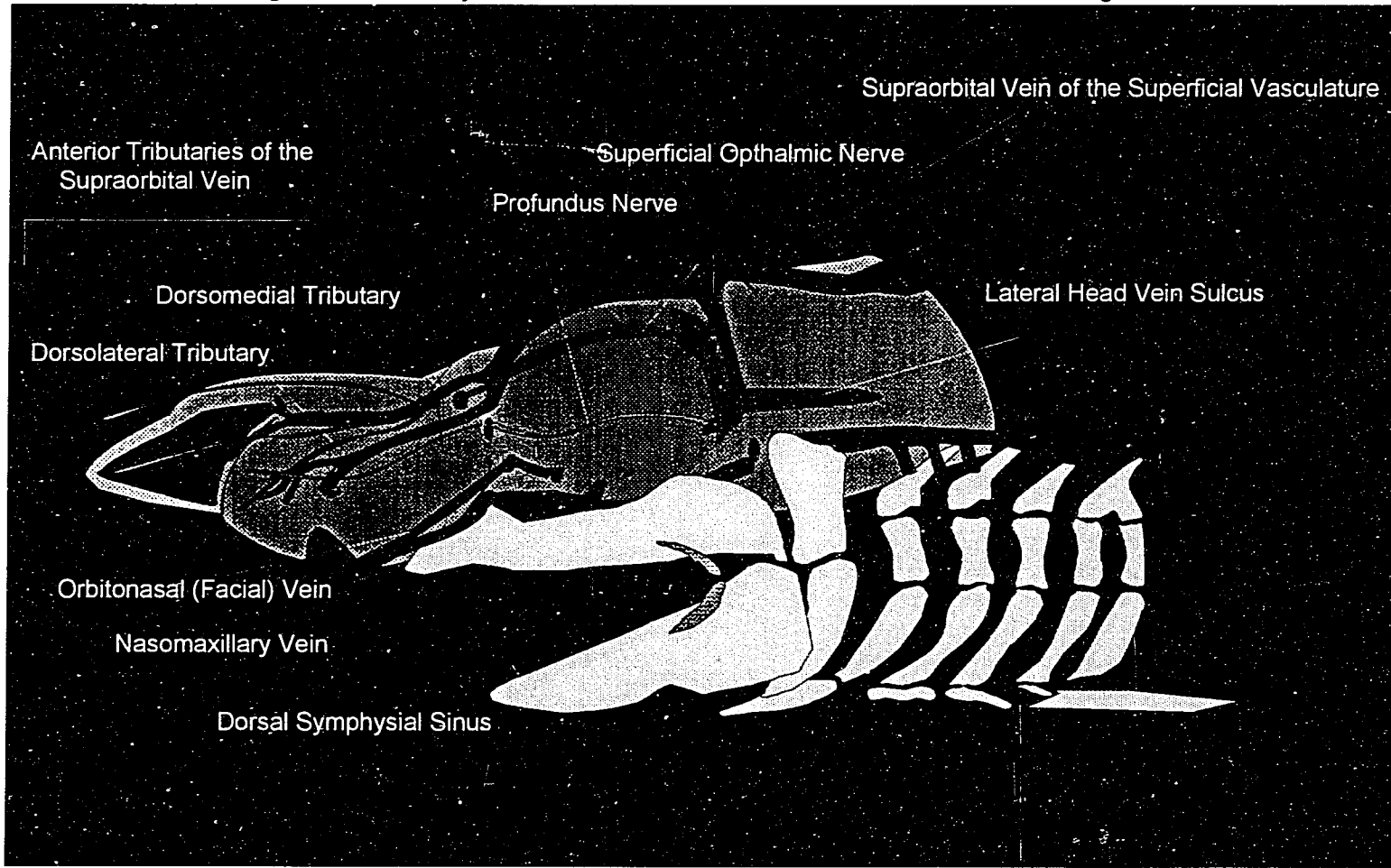


Figure 18 : Contrast Radiograph of Callorhynchus capensis

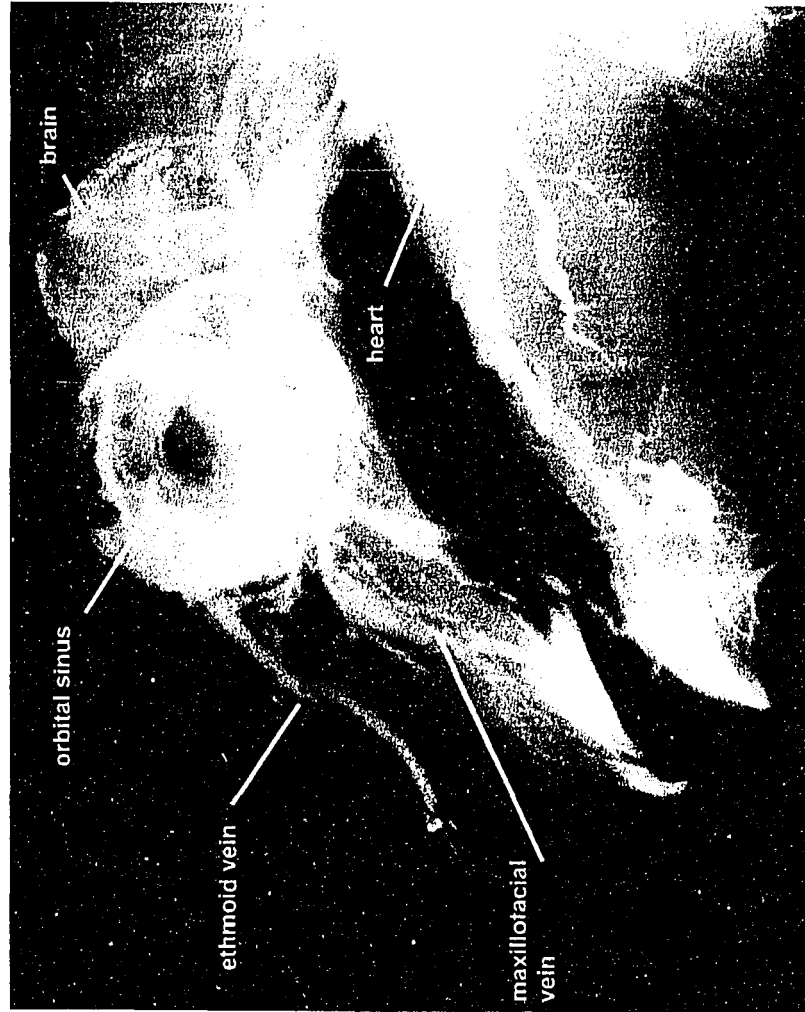
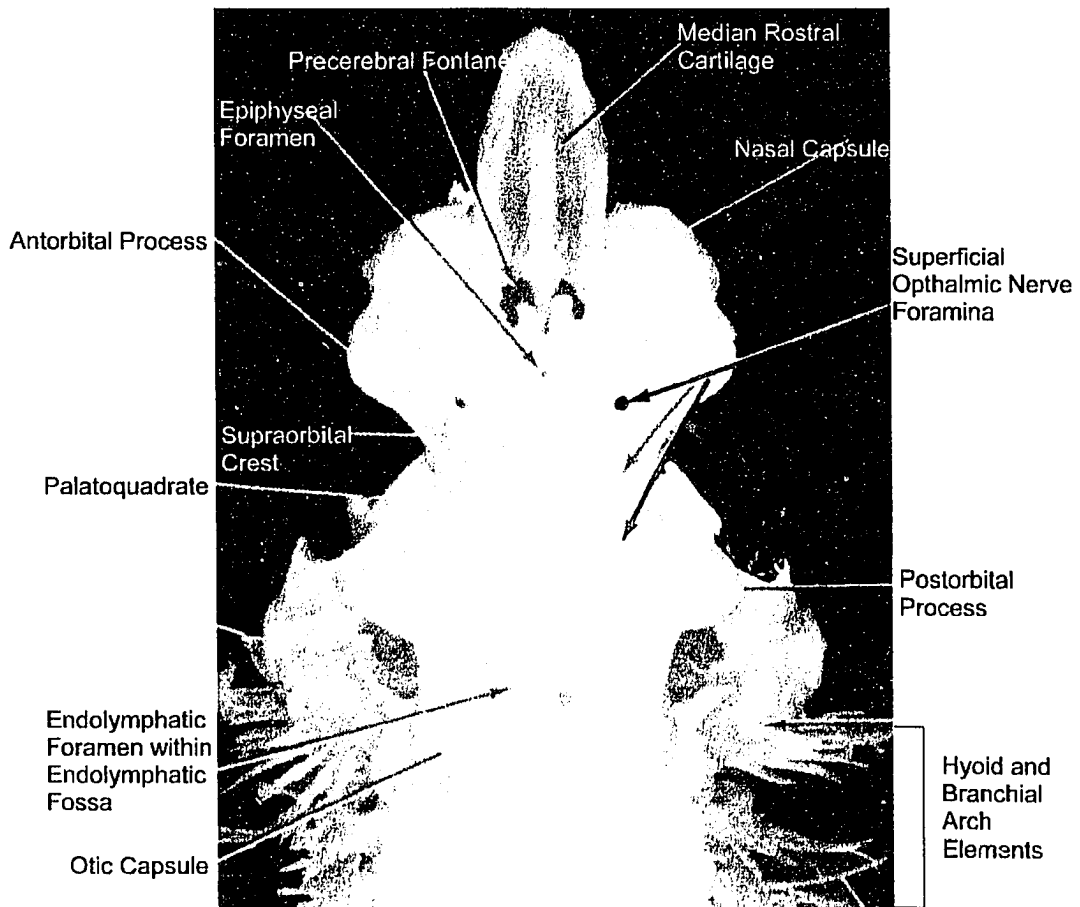
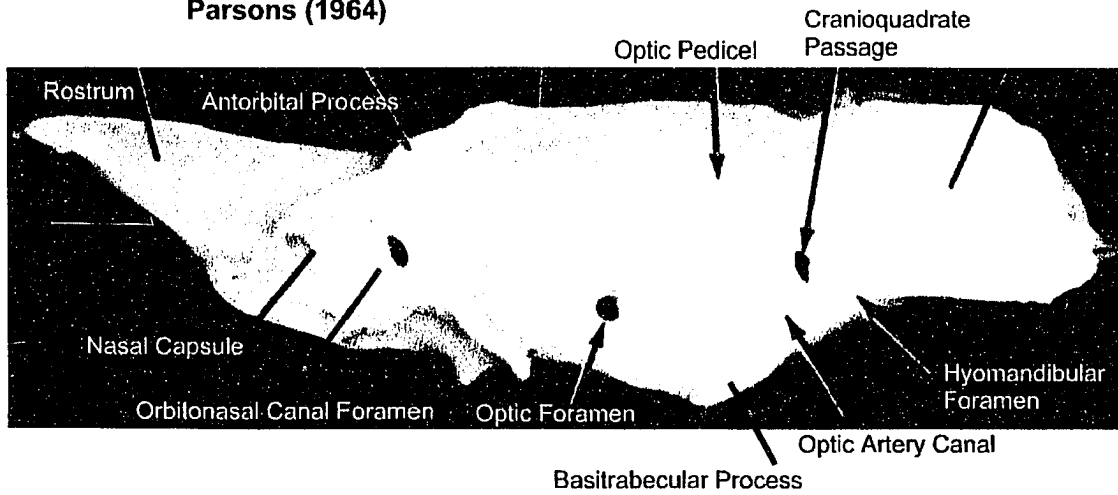


Figure 20: Cranial Anatomy of *Squalus acanthius* Modified from Gans and Parsons (1964)



within a canal or canals. Yet, infrequently, a condition closer to the chimaeroid state is described wherein the selachian superficial ophthalmic nerves are found to run forward in a short preorbital canal from each orbit as in Heterodontus (Holmgren, 1942) but these canals are far removed from the condition of an ethmoid structure. The rostral region is vascularized, not by ethmoidal veins arising from the orbital sinus but, by a component of the superficial vascular system, the lateral and medial rostral branches of the supraorbital vein. The main branch of the supraorbital vein is indirectly in contact with the selachian orbital sinus as it sends off a branch through the supraorbital cartilage before continuing forward to the snout.

This discussion proposes that if the sistergroup status is to be justified then the ethmoid canal, as one of the four major divergences between the selachian and holocephalan conditions addressed in this research and as a unique holocephalan character, must be explained either in relation to the selachian state or to a common ancestral state. There is a general consensus among these researchers who have compared selachian and chimaerid crania that those cranial features directly correlated with the presence of a holocephalan ethmoid canal include the position of the orbit and orientation of the eyes to each other, the development of an interorbital septum, and general cranial dimensions

which include a short oticooccipital region and narrow interorbital space. The interpretation of the causative versus indirect, and yet, confounding nature of each of these characters will be shown to vary according to the theories of ethmoid canal development. The two principal arguments regarding the origin of the ethmoid canal are both based on the premise of a holocephalan/selachian relationship and rely heavily on data collected in those embryonic studies referred to earlier on the interrelationships of chondrichthyan suspensoria.

The first theory, the product of analyses carried out by Allis, Kappers, and Holmgren, is one which professes the canal to be a derivative of the cranial cavity. Allis (1926) initially theorized the canal to be the consequence of a downward displaced telencephalon. He professed the appearance of an embryonic vessel between the chimaerid mid- and forebrain which would cause a downwardly displacement of the telencephalon from the traditional selachian orientation. In doing so, a lateral displacement of cranial trabeculae is said to be induced. With continued upward and medial movement of these cartilages, Allis envisioned they would eventually cut the cranial cavity in two such that the trabeculae would now constitute the floor of an ethmoid canal and roof of the telencephalic enclosure. As for the floor of this enclosure, Allis could only theorize this would have to arise from the development of intratrabecular

tissue, and possibly benefitting from some additional contribution from the fused palatoquadrate.

Kappers (1912, as cited by Stahl, 1967) has offered the only evidence in support of Allis' theory. He noted the depression of the holocephalan telencephalic cavity during embryogenesis, but he argued the more logically acceptable interpretation that this was the result of a dorsal-medial expansion of the eyes. Thus, the ethmoid canal would be originally cranial in nature, as argued by Allis, but is formed as the result of a change in orbital placement and dimension, not some embryonic vesicle which has yet to be verified.

Kapper's description is the favored mechanism of induction, for the shift in orbital positioning can be used to explain the formation of another holocephalan character, the interorbital septum. In the transition toward the holocephalan state, Kapper's suggestion forms the basis of a model in which the interorbital septum is generated as the orbits converge and increasingly encroach upon the interorbital space. The comparative conditions of the septum in extant forms has been cited to support this interpretation. There is a greater expanse of the Chimaera septum compared to that of the more primitive Callorhynchus and this has been attributed to a greater medial expansion of the eyes in Chimaera (Hubrecht 1877). Therefore, these data are considered to uphold the model of progression

outlined here (Stahl p.196). Additionally, information derived from comparative transverse sectioning of the Chimaera and Rhinochimaera orbital region is also considered to substantiate Kapper's interpretation of shifting orbital positions (Holmgren, 1942). In this latter work a continuous channel is said to extend from the main cranial space (at the rear of the skull) forward over the interorbital septum to a point where it opens into the ethmoid canal. To Holmgren, who believed Rhinochimaera to be more primitive than Chimaera, the wider expanse of the channel in the former confirms the notion that the ethmoid canal is a vestige of the original cranial cavity.

As an expanded argument in favor of the cranial derivation of the ethmoid canal, Holmgren has postulated that the condition ancestral to chimaerids must involve a shark-like condition in which two separate (preorbital) canals carry the superficial ophthalmic nerves forward from the orbits. In the transition from the ancestral to a chimaeroid state, compression of the interorbital space would result in a concomitant loss of the medial wall cartilages as the two ancestral preorbital canals are forced to fuse into one. Consequently, the nature of the ethmoidal cartilages as described by this scenario are explained as follows; the side wall of the canal is composed of preorbital cartilage which forms outside the ophthalmic nerve at the anterodorsal margin of the orbit. Subsequently, this

supraorbital crest derivative continues to grow frontally and dorsad until the superficial ophthalmic nerves are completely enclosed. The canal floor is either a neomorph, as suggested by its late chondrification relative to the remaining cranial cartilages (Schauinsland, 1903) or, as Allis proposed, it is formed by the united upper borders of the laminae orbitonasalis but, as Holmgren stipulates, the laminae orbitonasalis do not reach further dorsad than the ventral border of the preorbital cartilage.

Holmgren further supplemented his theory with the prevailing paleontological evidence of his time to define those features one would hope to find in the ancestral condition from which both Holocephali and Selachii may develop. The popular theories on the phylogenetic status of chimaerids and selachii were (a) of a sistergroup relationship with the origin of both groups in the Bradyodonts and (b) that these were not closely related groups, there being a separate evolution of the Selachii from petalichthyids and Holocephali from arthrodirans (Ctenurella and Pycnodus-like forms). Holmgren sided with the former theory and favored a cochliodont rather than placoderm ancestry for Holocephali. Thus, in his analyses he argued the holocephalan ancestral form would have had to be a dorsally flattened, broad-headed form with dorsally placed eyes in order to force the brain downward upon medial expansion. He, therefore proposed Helodus to be a likely

ancestor since this fossil was believed to be a cochliodont and the only bradyodont representative to have persisted into the early Carboniferous, a period in which forms related to the extant chondrichthyans could be found. [This species is now known not to be a cochliodont but a different form requiring separate classification. It is currently placed in the Helodontiformes as part of a holocephalan assemblage (Patterson 1965, Lund 1977).]

The alternative view for the origin of the ethmoid canal also centers around the interorbital septum but focuses on the overall shifts in cranial dimensions. DeBeer and Moy-Thomas (1935) consider the canal to be an extracranial entity whose formation is the direct mechanical consequence of cranial changes precipitated by a change in orbital positioning. Since the transition sequence stipulates derivation from a selachian-type form, it was imperative to the paradigm of DeBeer and Moy-Thomas that they rely on the classical descriptives regarding the nature of selachian chondrocranial cartilages and foramina. The major concerns of the transition sequence involve the the cartilages involved in formation of the foramina for the superficial ophthalmic and profundus nerves, the cartilages determining the formation of a foramen for the orbitonasal canal, and the nature of the precerebral fontanelle. In the ethmoidal region, the selachian precerebral fontanelle is regarded by DeBeer as the anterior portion of the cranial

roof which is separated from the extracranial space by a thickening of the dura mater.

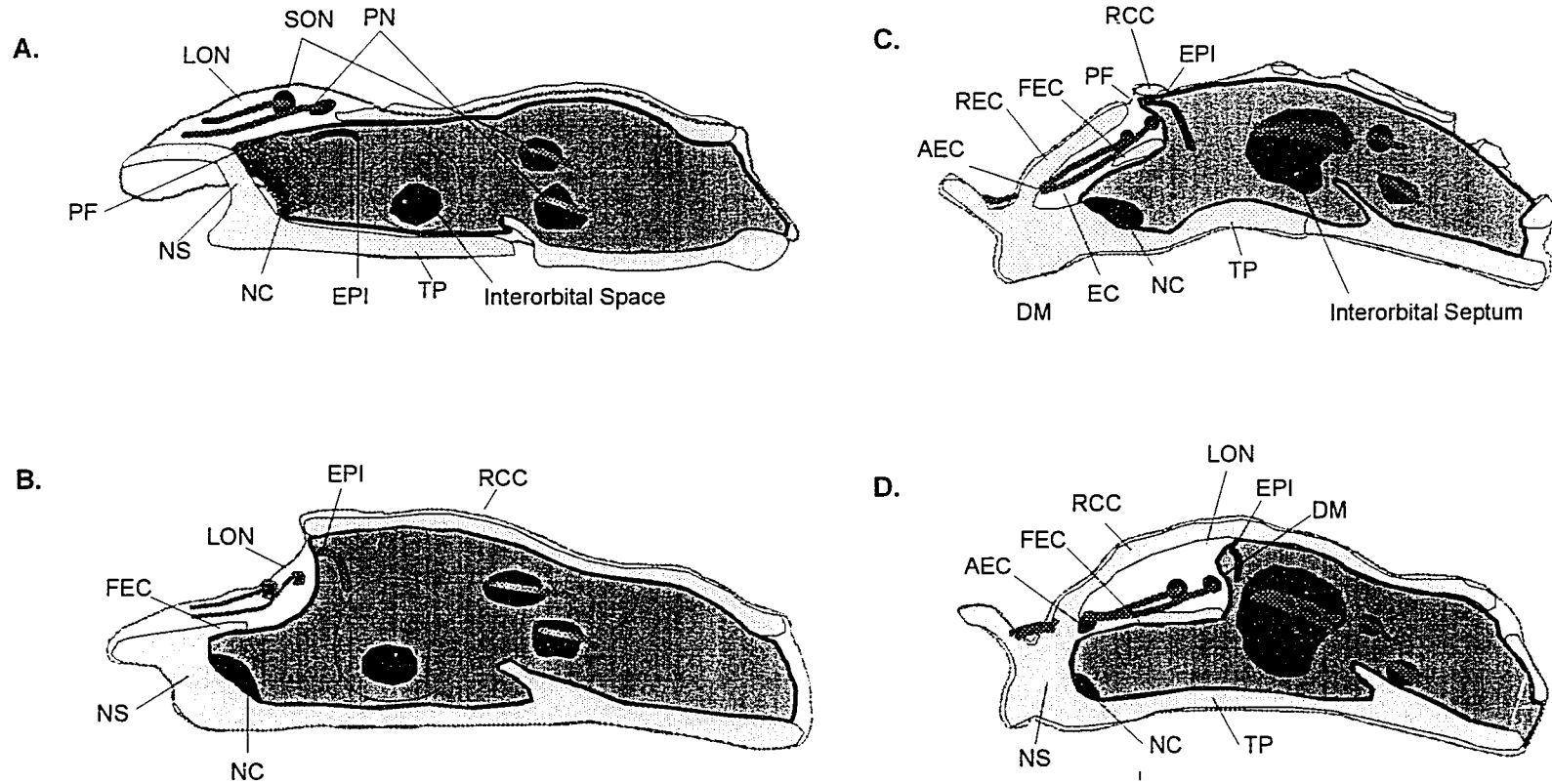
As the basis for the transition of cranial morphotypes DeBeer qualified that the anterior wall of the orbit is delimited by the junction line between the lamina orbitonasalis and the preoptic root of the orbital cartilage; a condition represented in ontogeny by the orbitonasal fissure and, most dorsally, by the profundus' orbitonasal foramen in the mature form. Dorsal to this, the supraorbital crest cartilage meets the lamina orbitonasalis to form the efferent foramen of the superficial ophthalmic nerve and thus permits this nerve to come to lie on the roof of the nasal capsule cartilage after having traversed the orbital foramen. The ventroanterior limit of the orbit is indicated by the foramen for the orbitonasal canal (the orbitonasal canal is not associated with the orbitonasal foramen which was noted previously). This foramen is established by the ventralmost line of attachment between the cartilages of the lamina orbitonasalis and the true side wall of the cranium. Dean's description of the selachian ethmoid region and the ectoethmoid chamber agrees with DeBeer's configuration of the cranial cartilages. Thus, the selachian ectoethmoid chamber is described as posteriorly continuous with the orbitonasal canal; a canal which extends between the external surface of the preoptic root of the orbital cartilage and the medial surface of the lamina

orbitonasalis.

Having distinguished the origin of both the relevant cranial cartilages and foramina, DeBeer and Moy-Thomas propose a model for ethmoid canal formation which also features a shifting of the orbital position. They argue, a medial migration of the eyes and reduced interorbital space would alter the ancestral cranial dimensions such that there is an uplifting of the cranial roof. As the cranial roof is lifted, the lamina orbitonasalis of the rostroethmoidal region (defined by the orbitonasal fissure) is distorted dorsally, and somewhat obliquely to generate a wall equivalent to the ethmoid canal. Since this architecture is mechanically unstable, leaving the anterior cranial cavity exposed to severe stresses, DeBeer further postulated that portion of the lamina orbitonasalis which forms the roof of the nasal capsule would extend posteriorly to cover the selachian-type precerebral fontanelle. In doing so this cartilage would thus form the floor of an ethmoid canal and roof to the telencephalic cavity. The roof of the ethmoid canal would be a secondary acquisition, which when developed, covers the equivalent of the pineal foramen.

DeBeer and Moy-Thomas have presented a theoretical transition of cranial dimension and structure to support their interpretation of canal formation. This morphocline depicting the shift from a selachian to holocephalan state is shown in Figure 21, with a theoretical form and the

Figure 21: Median Saggital View of Crania in the DeBeer and Moy-Thomas Ethmoid Canal Transition Series



A: Selachian Condition B: Hypothetical Intermediate C: Embryonic *Callorhynchus* D: Adult Holocephalan
AEC: anterior ethmoid canal opening; DM: dura mater; EC: ethmoid canal; EPI: epiphysis; FEC: floor of the ethmoid canal; LON: lamina orbitonasalis; NC: nasal capsule cavity; NS: nasal septum; PF: precerebral fontanelle; PN: profundus nerve; REC: ethmoid canal roof; RCC: cranial cavity roof; SON: superficial olfactory nerve; TP: trabecular process.

embryonic Callorhynchus representing intermediate transitions. Schauinsland's Callorhynchus is important in this transition for it is said to possess a pineal foramen up to a certain stage of development and that this structure is found in the selachians in close proximity to the precerebral fontanelle. Additionally, Schauinsland depicts a triangular gap through which the superficial ophthalmic and profundus nerves are permitted to exit the orbit. This configuration of cartilages, according to DeBeer's interpretation, is generated by contributions of the lamina orbitonasalis, supraorbital, and preoptic root cartilages and shows how the lamina orbitonasalis comes to flank the ethmoid canal. Thus, this is taken to represent the stage, reminiscent of the selachian arrangement of nerves, where these structures have not yet been enclosed in the ethmoid and orbitonasal canals. In seeking further support for their sequence of transition, DeBeer and Moy-Thomas cited the "laterally flaring" laminae of the Upper Carboniferous Helodus as evidence for the plausibility of lamina orbitonasalis displacement.

**Contribution of the Bear Gulch Evidence to the Question of
Ethmoid Canal Formation**

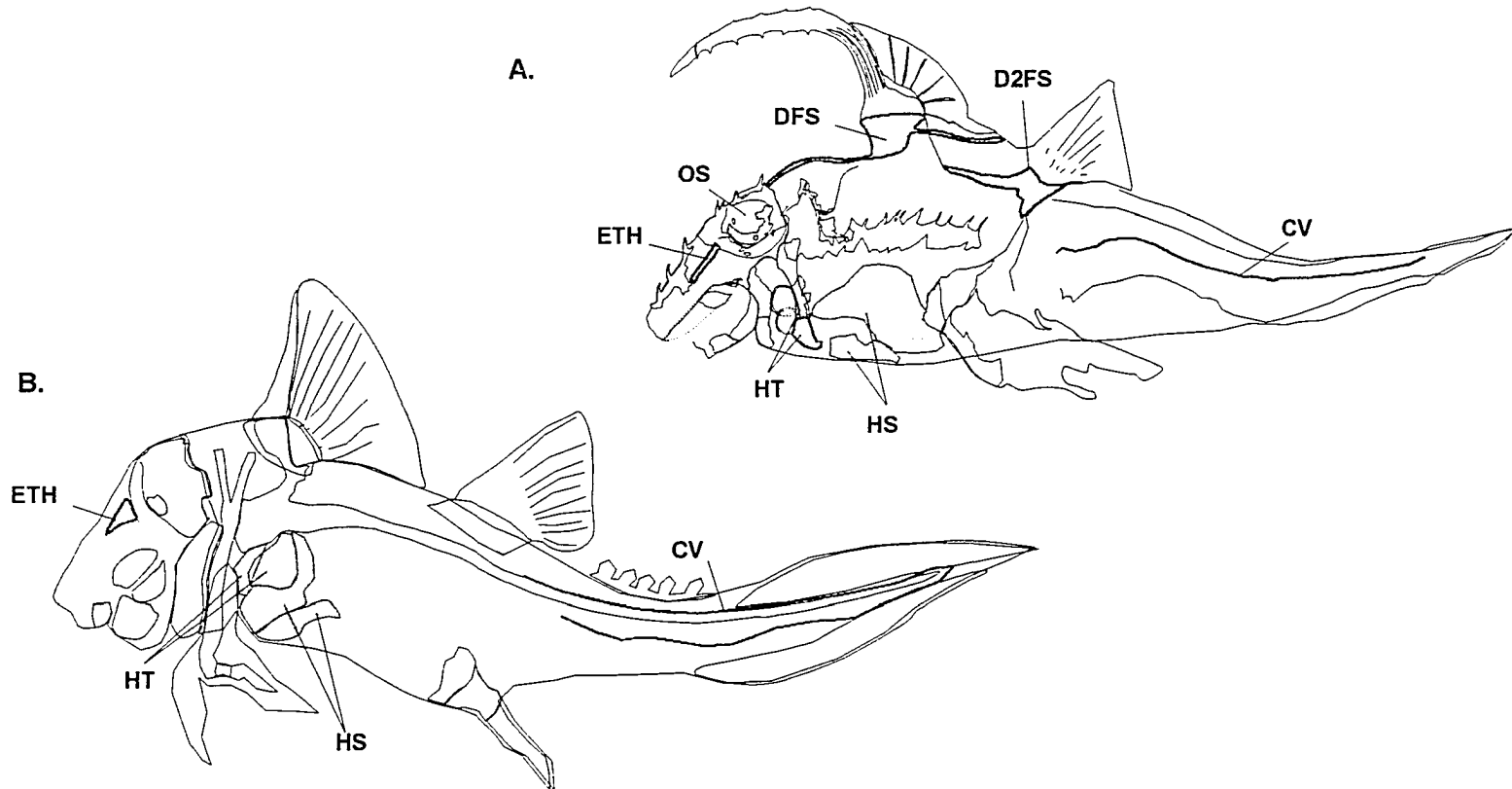
The value of the paraselachians to the question of the ethmoid canal origin is essential, a point which emphasizes the integral contribution the paraselachians make to the unresolved basal complex. This point is further emphasized

by the variation observed in the autodiastolic condition and the degree to which this variation is correlated with changes in the rostro-ethmoidal architecture. Thus, Bear Gulch paraselachians, selachians, and holocephalans were also analyzed in the context of ethmoid canal formation. The fine preservation of endocranial elements, vascular pigments and orbital features in the Bear Gulch assemblage provide the data upon which confident interpretations and conclusions can be made with regard to the development of an ethmoid canal and inferences can be made with regard to the inductive pressures leading to canal formation.

A true ethmoid canal is indicated in both Erismacanthus and the type 1 Bear Gulch cochliodont, herein referred to as Coch1 (Figure 22) and suggested in Echinochimaera. Descriptions of those paraselachian fish most relevant to my studies (Superfish 1 and Het 2) are presented here with an emphasis on those features critical to determining the transition stages from a selachian to holocephalan ethmoid arrangement.

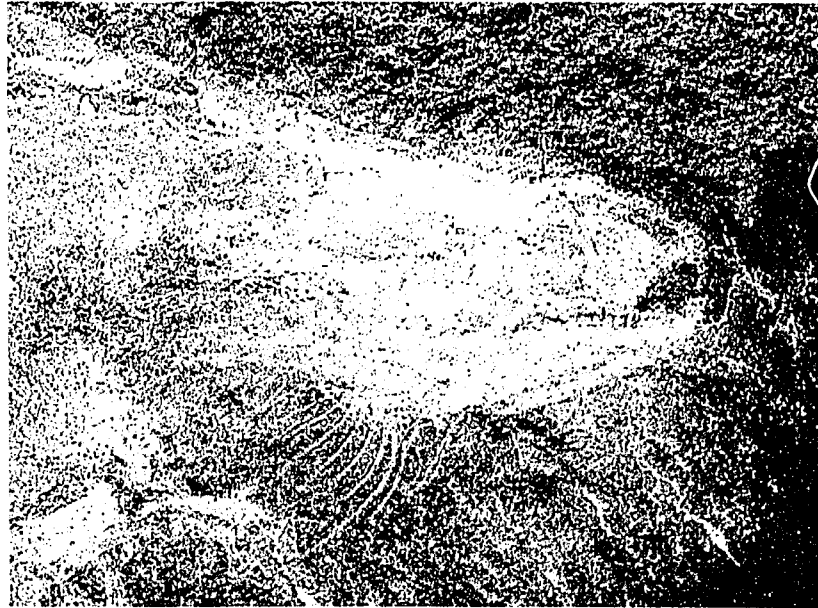
For the purpose of these analyses Superfish 1 is considered to be closest to the selachian condition in a selachian/paraselachian/holocephalan morphocline (Figures 23-26). The features upon which this determination is made include the overall body shape, soft anatomical data, and immovable dorsal fin spines. It differs from the typical selachian plan in the forward positioning of the shoulder

Figure 22: A Sketch of the Gross Anatomy and Circulatory Pigmentation Patterns in true Holocephalans



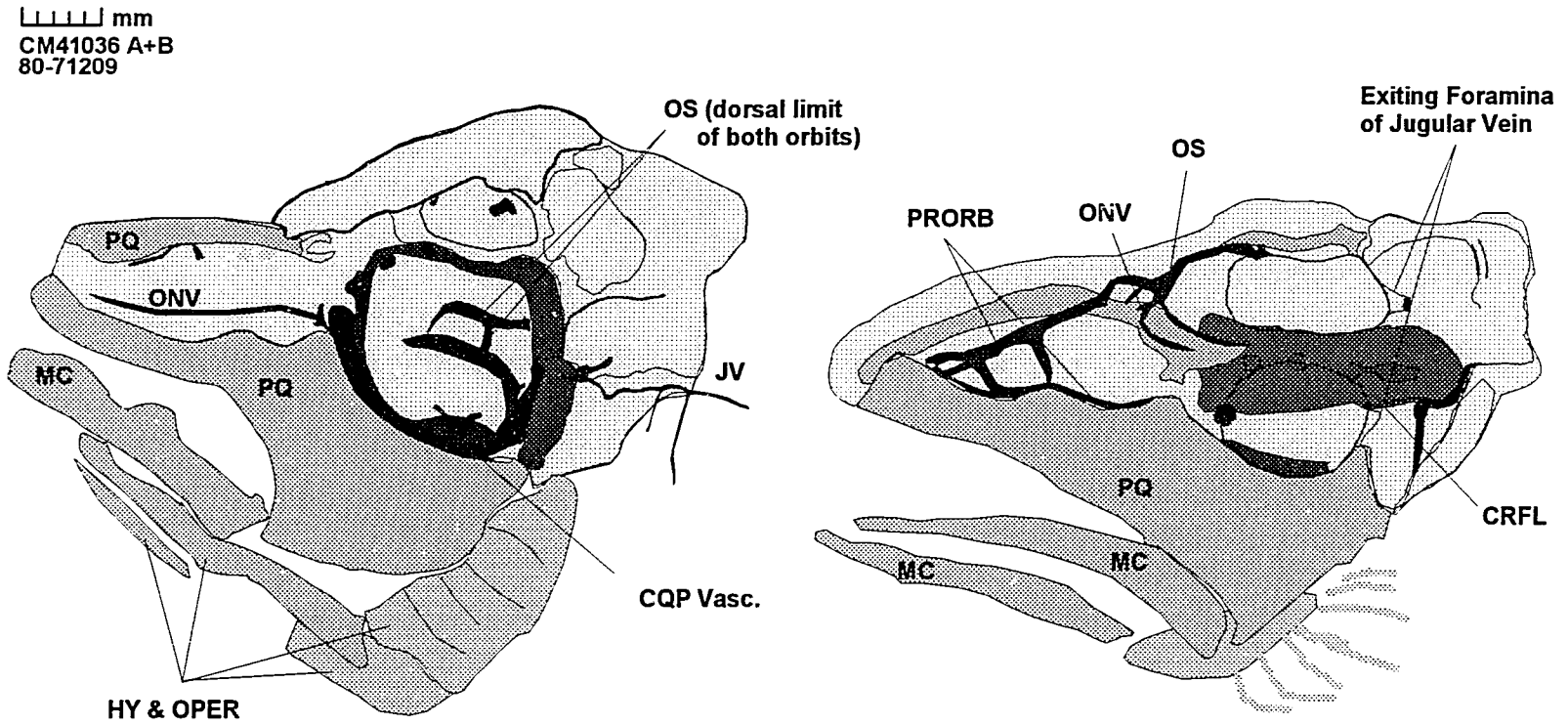
These rough sketches are of those Bear Gulch autostylic fish (A. *Erismacanthus*, B. *Cochliodont* species #1) which most closely reflect those characters attributed to extant forms. Abbreviations for identified pigmentations are as follows; CV: caudal vein; DFS: first dorsal fin sinus (major); D2FS: second dorsal fin sinus (minor); ETH: ethmoid veins within the ethmoid canal; HS: hepatic sinus and liver tissue; HT: heart and portions of the common cardinal sinus; OS: orbital sinus.

Figure 23 : The General Cranial Morphology of Superfish 1



The outlines are given for the palatoquadrate (PQ), Meckel's cartilage (MC), opercular covering (OC), orbit (ORB), preorbital canal (POC), and partial pathway of the jugular vein (JV).

Figure 24 : Partial Reconstruction of Sup1's Chondrocranium



CRFL: floor of neurocranium; HY & OPER: elements of hyoid arch and opercular covering; JV: jugular vein; MC: Meckel's cartilage; ONV: orbitonasal vein; OS: orbital sinus; PRORB: preorbital canal veins; PQ: palatoquadrate. A and B are labels for the part and counterpart faces.

Figure 25 : Line Drawing of CM41036A and B Featured in Figures 23 and 24

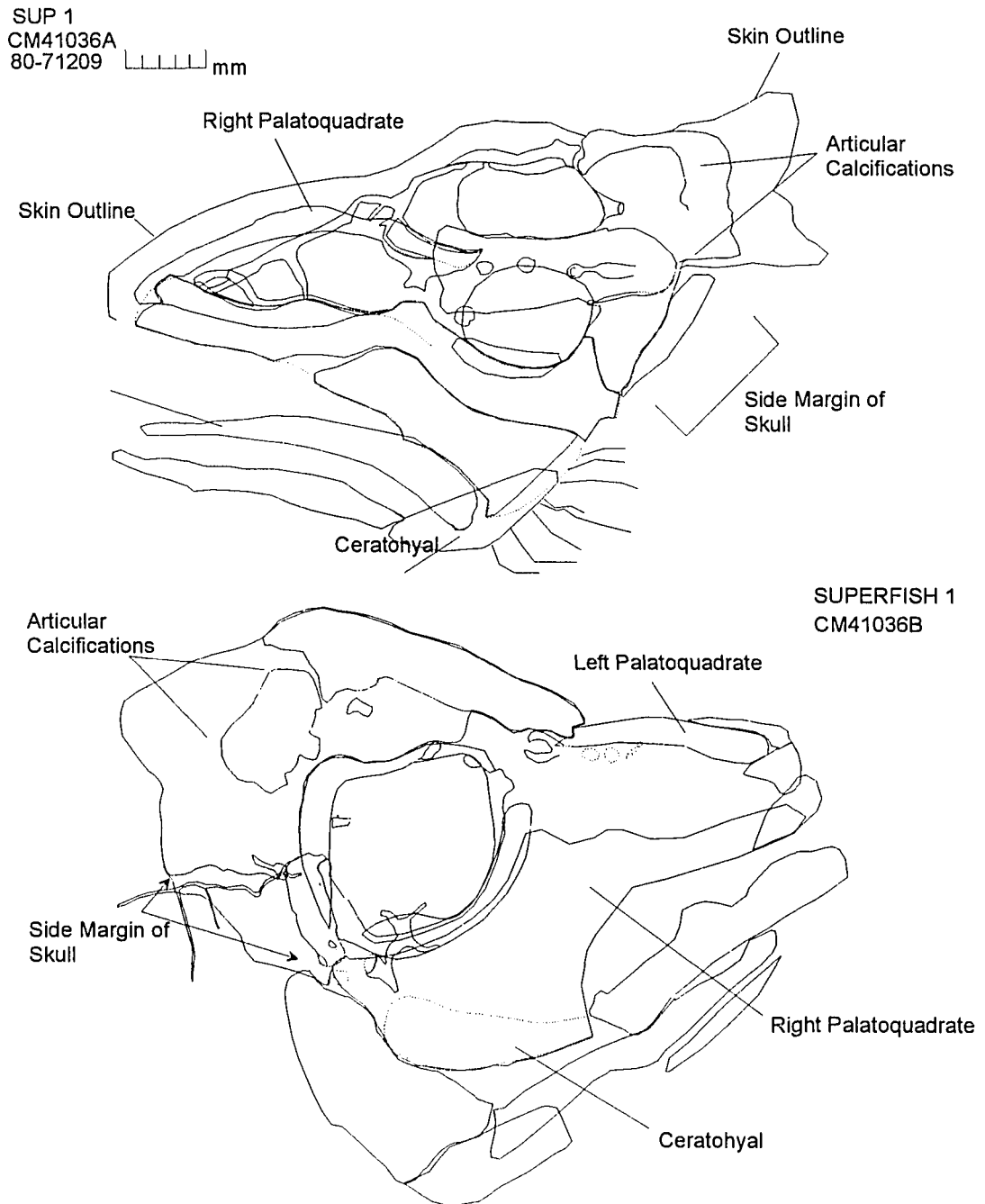
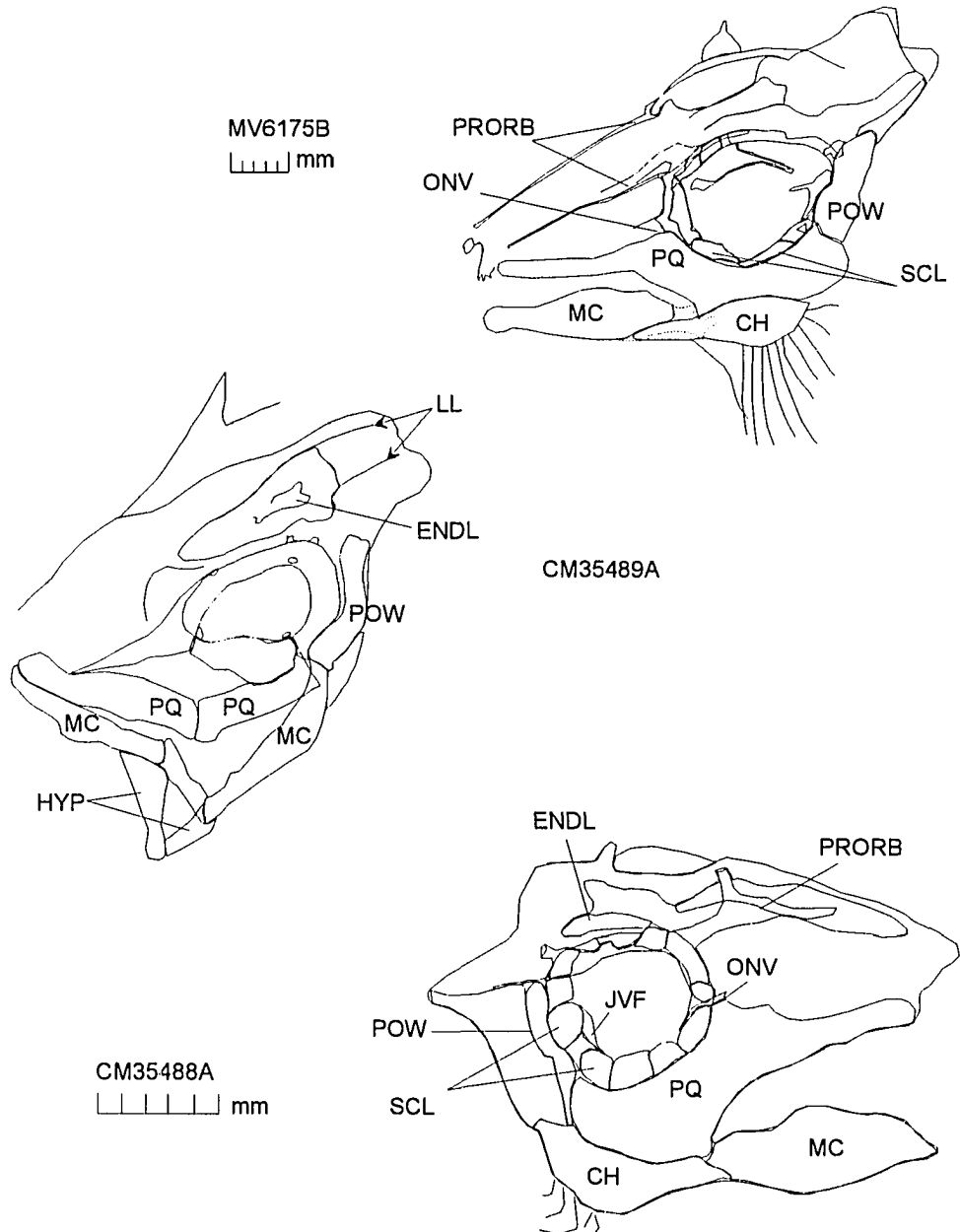


Figure 26 : Line Drawing of Juvenile Sup1 Specimens



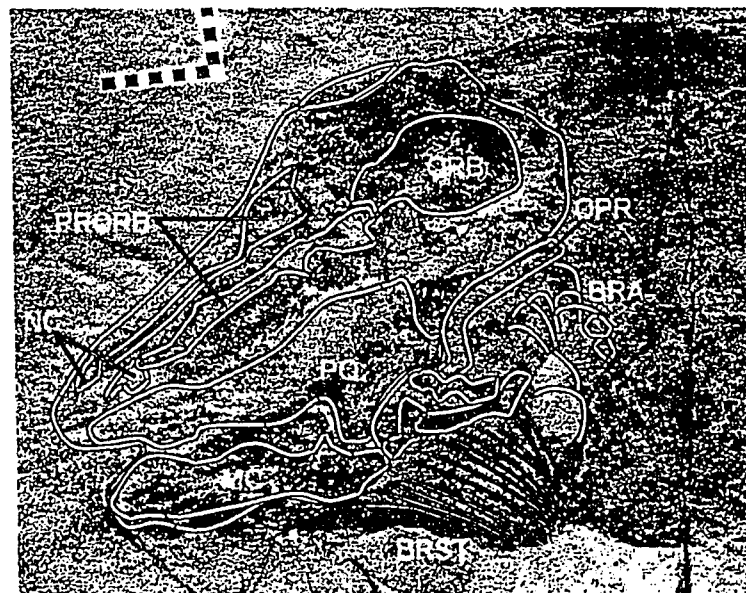
CH: ceratohyal; ENDL: endolymphatic fossa; HYP: hypobranchial elements; JVF: foramen for jugular vein; LL: lateral line; MC: Meckel's cartilage; ONV: orbitonasal vein; POW: postorbital wall cartilage; PRORB: preorbital canal and vasculature; PQ: palatoquadrate; SCL: unfused sclerotics

girdle and branchial basket. The cranial features include a mixture of selachian and holocephalan-type characters. The shoulder girdle with its dorsally developed scapular process is in close proximity to the dramatically foreshortened occipital region. A selachian-type lateral head vein is found to pass posteriorly from the orbit where pigmentation indicates the presence of a well developed orbital sinus. This vessel appears to enter the orbit slightly posterodorsal to the level of the cranioquadrate passage and thus is separated from it by a short distance. The moderately narrowed interorbital region appears, in certain specimens, to be traversed by a selachian-type supraorbital vein which subsequently pierces the orbital cartilage to join the orbital sinus (CM41036B, CM35488A, MV6175B). The orbital sinus appears to have two tributaries exiting forward from the anterior margin of each orbit. The bilateral ventroanterior extension follows the pathway of the orbitonasal canal while the dorsoanterior extension proceeds forward along the length of the rostromoid region, a route best described within a preorbital canal. There is a continuity between the vascular pigments of the preorbital and orbitonasal vasculature along the anterior orbital margin. The suspensorium is autodiastylitic with postorbital (*sensu stricto* otic) and orbital (anterior-ventral orbital) processes. This suspensorium differs from the early autodiastylitic form in the development of the

palatine segment of the palatoquadrate, a phenomenon which accompanies the development of the rostroethmoidal cranial region at the expense of the otico-occipital region.

Het2 is the species closest to the holocephalan-like morphotype in a selachian/paraselachian/holocephalan clinal analysis (Figures 27-32). The overall body proportions, extreme forward positioning of the branchial basket and shoulder girdle, eye positioning, and enlarged first dorsal fin with a movable fin spine are those overt features correlated with a holocephalan anatomical plan. As in holocephalans, the shoulder girdle is found immediately behind the short posterior margin of the cranium, contact being indicated by the presence of well formed condyles or articular processes at the dorsal and ventral lateral margins of the occipital region. The branchial basket is typically chimaeroid; completely subcranial with nesting of the successive arches and having contact established between the last arch and the scapulocoracoid element. With regard to cranial dimensions, although the rostroethmoidal region is also developed at the expense of the reduced otico-occipital region the side walls of the Het2 head are obliquely oriented in such a fashion that the cranium appears more triangular in cross section. Similarly the interorbital region is considerably narrower than in Superfish 1 and the orbits are obliquely oriented to each other. This form of autodiastyly is considered to be

Figure 27 : The Cranial Morphology of Het2

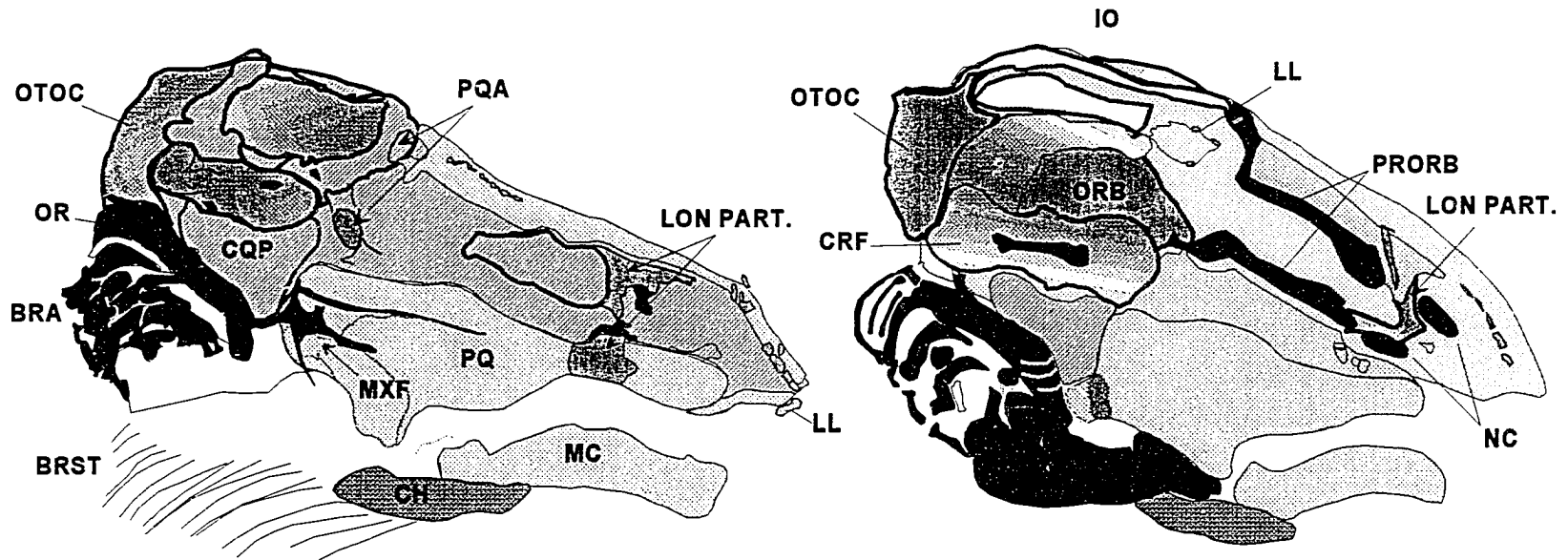


The features outlined in the lower image of Het 2 include the palatoquadrate (PQ); Meckle's cartilage (MK); orbit (ORB); branchiostegal rays (BRST); opercular rim (OPR); preorbital vascularization (PRORB); branchial arch elements (BRA); nasal capsule (NC)

Figure 28 : Partial Reconstruction of Het2's Chondrocranium

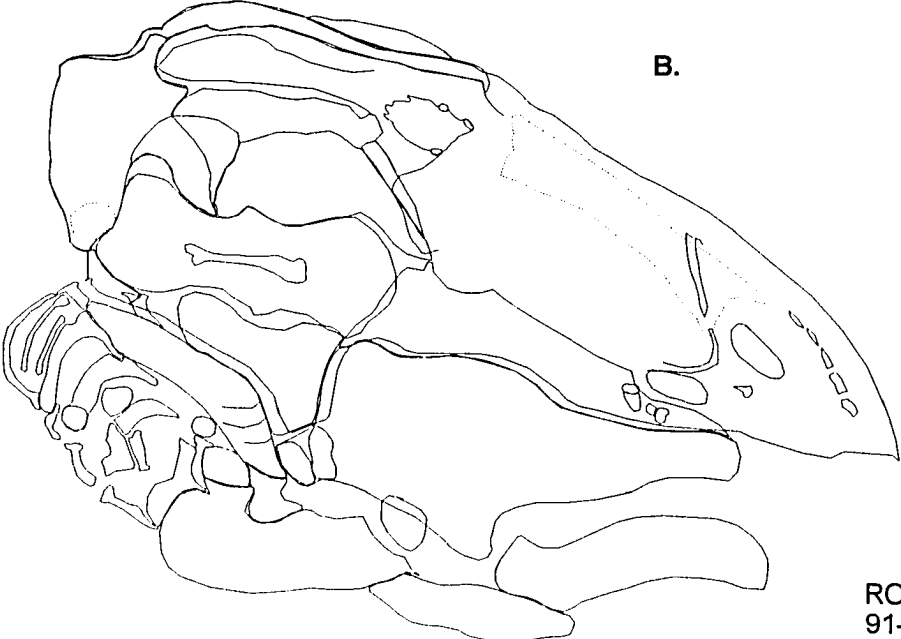
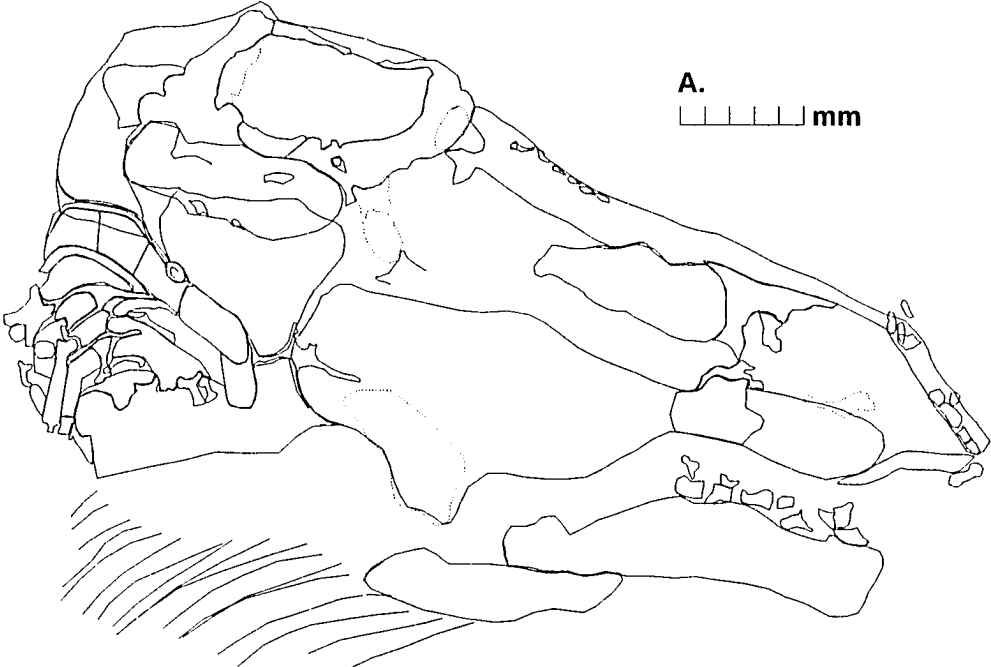
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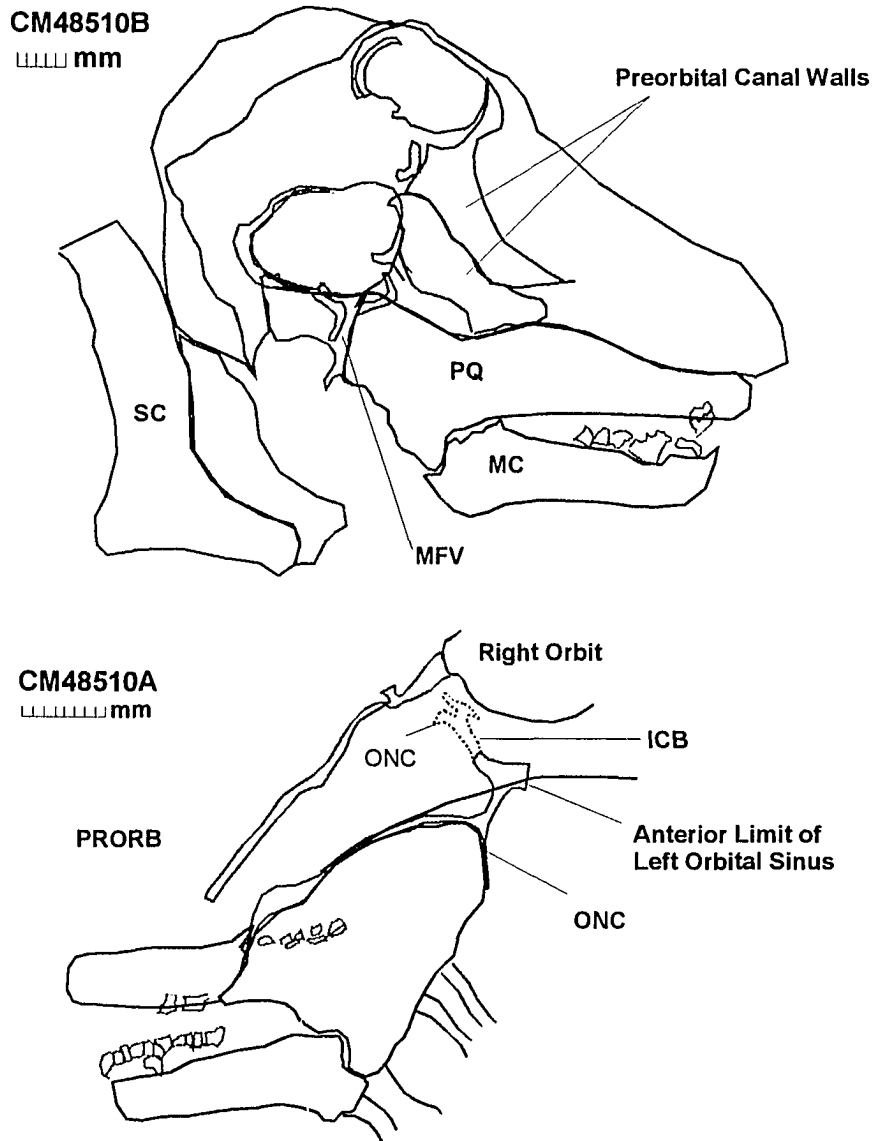
BRA: branchial arches; BRST: branchiostegal-like rays; CH: ceratohyal; CRF: neurocranial floor; CQP: cranioquadrate passage; IO: narrow interorbital region; LL: lateral line; LON PART.: wall partition found between the nasal capsule and anterior limit of the preorbital canals, believed to be derived from the lamina orbitonasalis; MC: Meckel's cartilage; MXF: maxillofacial vein; NC: nasal capsule; OR: opercular rim; ORB: orbit; OTOC: shortened otoic-occipital region; PRORB: preorbital canals and pigmentation; PQ: palatoquadrate; PQA: calcified articular facets for the palatoquadrate.

Figure 29 : Line Drawing of ROM 43174 As Featured in Figures 27 and 28



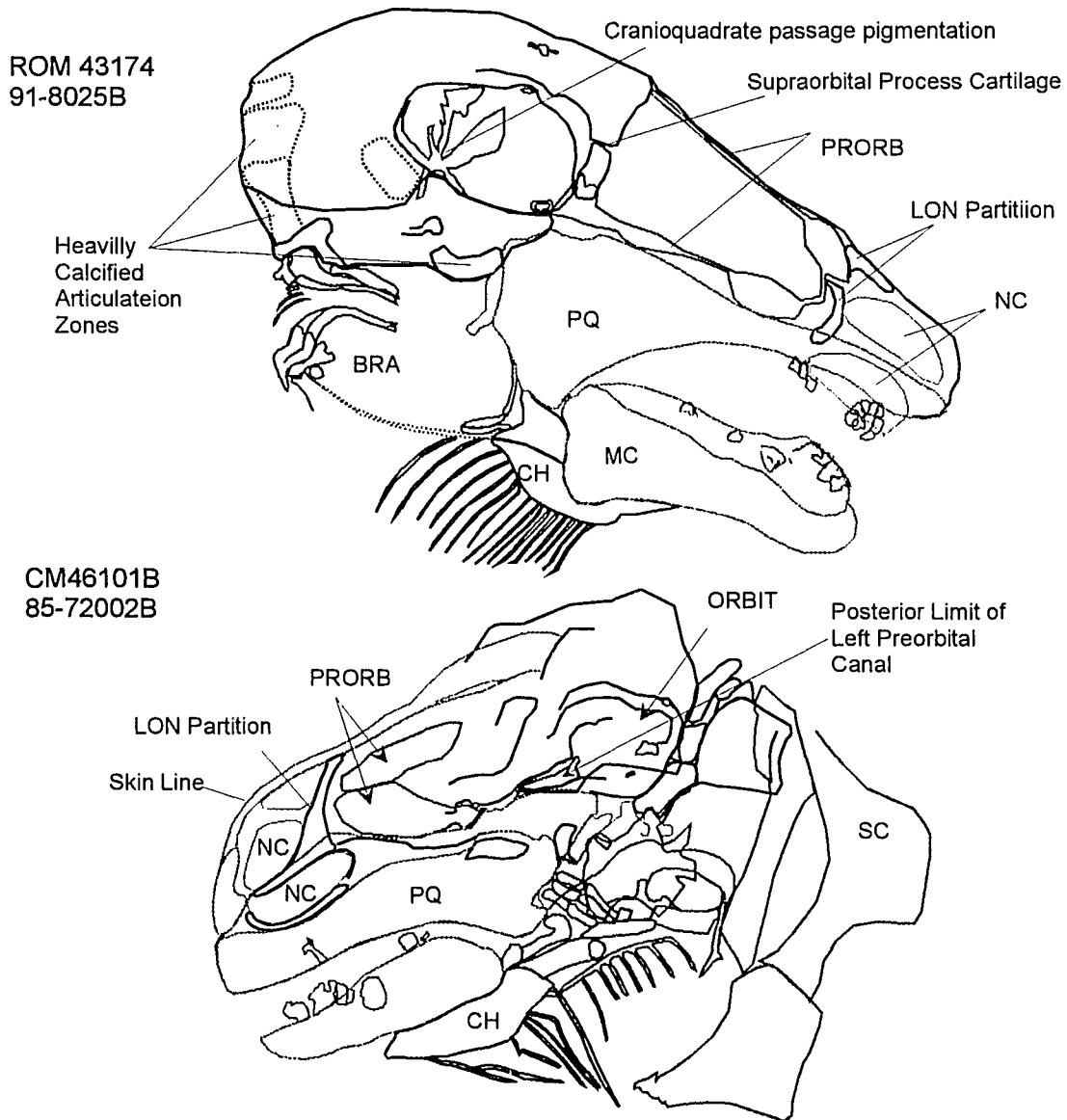
ROM 43173
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Figure 30 : Preorbital Canal walls and Orbital Vasculature From CM48510



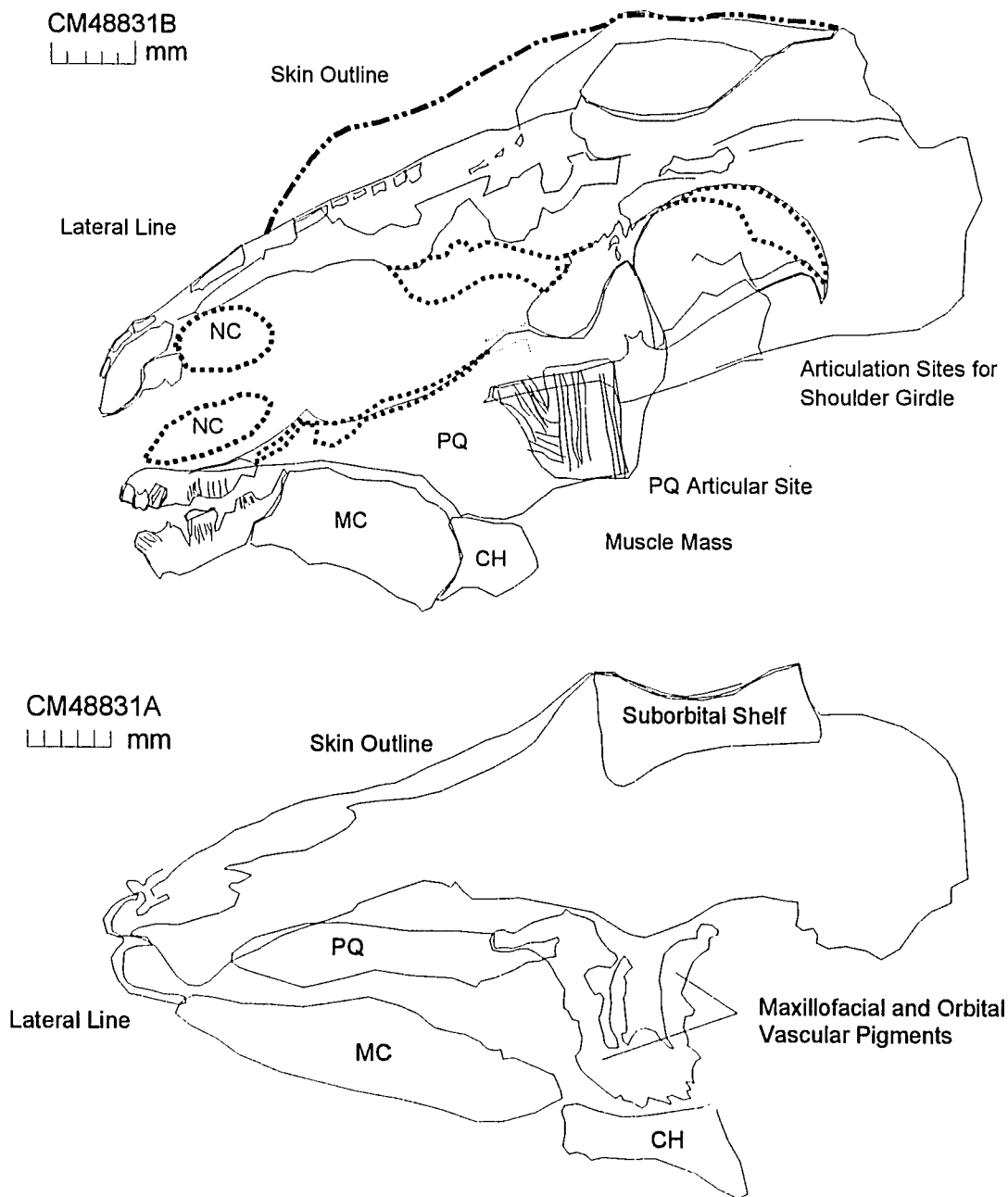
The preorbital canal walls indicated in the "A" counterpart are considered to be the equivalent of the flaring cartilages in *Helodus*. The "B" counterpart reveals an interconnecting bridge between the sinuses of each orbit. ICB: interconnecting bridge; MC: Meckel's cartilage; MFV: maxillofacial vein; PRORB: preorbital canal vasculature; PQ: palatoquadrate; ONV: orbitonasal vein; SC: scapulocoracoid .

Figure 31 :
Line Drawings of Het2 Specimens With Extensive Pigmentation and Cranial Detail



Note, in both specimens, the position of the lamina orbitonasalis partition with respect to the anterior limits of the preorbital canals and anterior expansion of the preorbital pigmentation. The dimensions of the preorbital canals are best understood from CM46101B. Articular calcifications between the occipital and shoulder girdle cartilages are shown in the top sketch while the lower sketch shows the close relationship between these two entities. The abbreviations used in both diagrams follow those of Figures 29 and 30.

Figure 32 : Line Drawings of Het2 Specimen CM48831A



extremely derived with respect to other Bear Gulch paraselachians. The jaws are placed far forward. The palatoquadrate articulations occur at a level parallel to the anterior orbital margin (basal connection sensu stricto) and between the palatine and ethmoidal cartilages (ethmoidal connection). At the hind limit of the palatoquadrate, an extensive maxillofacial-type vascularization occurs between the orbit, anterior branchial arches and opercular cartilage85D rim and portions of the mandibular arch (ROM43173, CM48510, CM62751). In keeping with the maxillofacial designation there is no apparent orbital foramen for the main branch of this vascular network. There are, however, four clearly distinguishable orbital foramina, labeled as cranioquadrate, orbitonasal, ethmoidal, and supraorbital crest foramen in these analyses. Extensive pigmentation may be found in the rostroethmoidal region, having originated from the orbital sinus and ethmoidal and orbitonasal foramina. The ethmoidal foramen, located at the anteromesial margin of the orbit, appears to have conveyed an ethmoid-type vein which remains independent up to the level of the ethmoidal articulation. At this point this vessel appears to unite with the corresponding vessel of the other side or is at least adjacent to it between this point and the more anterior nasal capsules. The nasal capsules are clearly demarcated from the anterior limit of the preorbital canals and their vascular pigmentation by a wall of cartilage identified as

the lamina orbitonasalis. The vascularization arising from the orbital sinus via the orbitonasal foramen is often partially occluded by the preserved palatoquadrate but in some specimens (CM46101, ROM43173) the continuity with the orbital sinus and anterior ethmoidal extension is clearly demonstrated.

In collating these observations with those made on other Bear Gulch chondrichthyans, specific conclusions can be made about those conditions believed to precede and/or promote ethmoid canal formation. First, certain paraselachians exhibit those features typifying the holocephalan orbit and orbital vascularization. These features include the foramina of the cranioquadrate process and palatine and superficial ophthalmic nerves, a maxillofacial vein, and orbitonasal canals with orbitonasal vascularization. These paraselachians also exhibit preorbital or rostro-ethmoidal canals. In particular, *Sup1* and *Het2* both possess the precursor bilateral canals but the latter species shows a partial merging or union of the two anteriorly. It is the ethmoid articulation of *Het2* which is derived and as such is considered fundamental to inducing the anterior union of the otherwise bilateral canals. Those cranial features which have been found in association with the canals include

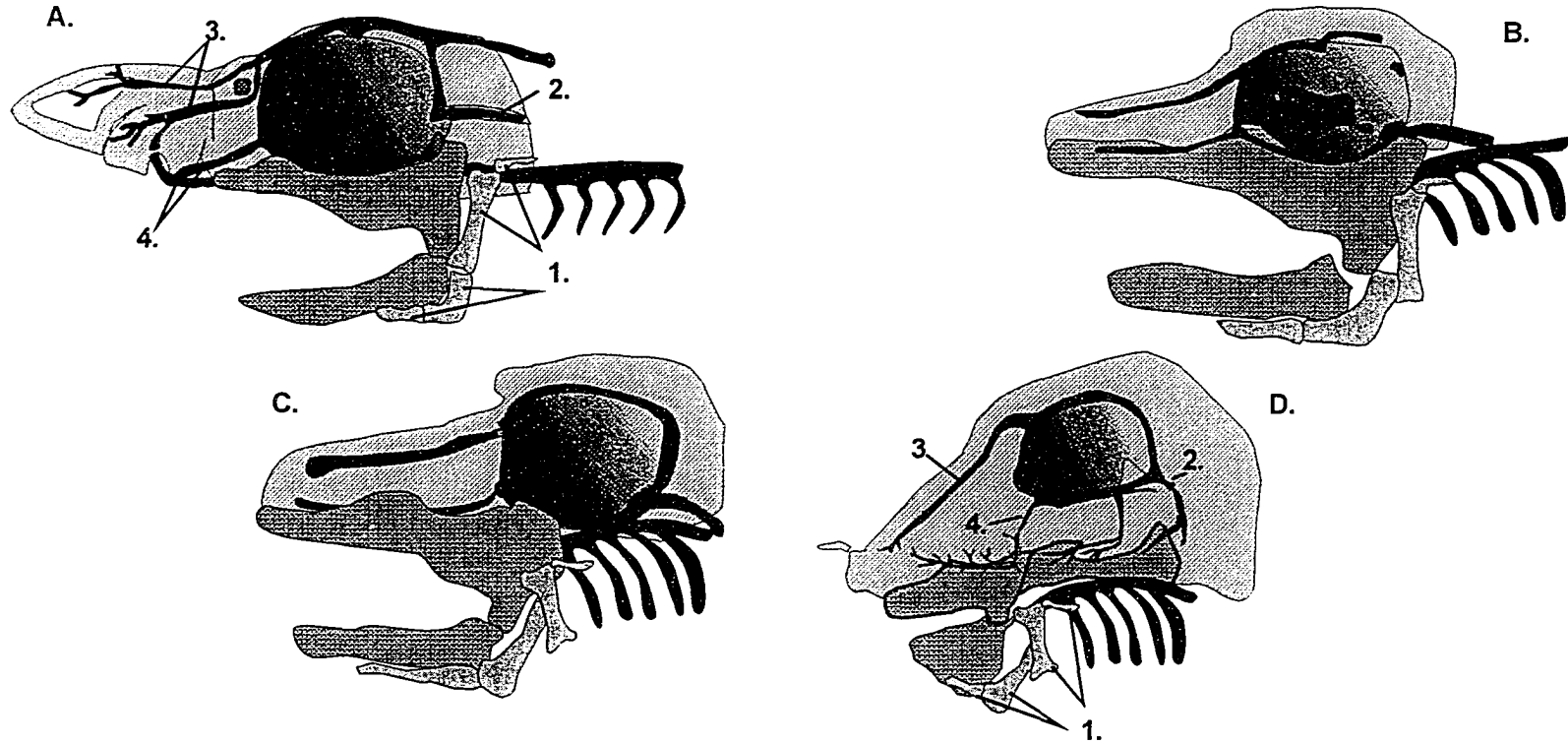
- (i) a narrow supraorbital ridge,
- (ii) oblique lateral cranial walls in the ethmoid region,

- (iii) autodiastyly or holostyly,
- (iv) a forwardly placed shoulder girdle, and
- (v) a forwardly placed branchial basket (entirely subcranial or anteriorly subcranial).

These and other observations on distinct paraselachian conditions have been included in the morphoclinal analysis based on cranial and suspensorial features. Consequently, those conditions highlighted in the clinal transition from autodiastyly to holostyly can also be used to explain the vascular pigmentation patterns observed in the shift from Orodus to Sup1 to Het2 and these patterns in relation to theory of ethmoid canal development.

The trend in cranial remodeling which leads to ethmoid canal formation involves the fusion of initially bilateral preorbital canals, but what actually induces this phenomenon is a series of interconnected events initiating with the early autodiastylic state. As depicted in Figure 33 this transition originates with an autodiastylic form characterized by a pterygoquadrate which shows some development of the palatine segment. Based on the preserved pigment patterns in Bear Gulch chondrichthyans, this form probably is best represented by a vascularization plan similar to the shark. This plan features a dorsal symphysial sinus, lateral head vein, and supraorbital vein. The only exception regards the hyoid sinus, due to the operculated condition. The first stage of transition

Figure 33 : The Transition Series as Influenced by Bear Gulch Paraselachians



This transition series progresses from an autodiastylic selachian endoskeletal and vascular plan (represented by A) to the holostylic chimaeroid endoskeletal and vascular plan (indicated by the embryonic *Callorhynchus* figured as D). The intermediate transitional forms are those of Superfish1 (B) and Hel2 (C). The changes in vascularization, indicated by cranial remodeling, are described in the text. The selachian elements numbered 1 through 4 are the hyoid arch, lateral head vein, dorsolateral and dorsomedial tributaries of the supraorbital vein, and the orbitonasal and nasmoaxillary veins respectively. The corresponding holocephalan elements are the hyoid arch, postorbital (lateral head) vein, the ethmoid vein and orbitonasal vein.

involves a forward shifting of the shoulder girdle and branchial basket. Although this change is not dramatic it is sufficient to warrant a reduction of the oticooccipital region as the anterior branchial arches occupy a position beneath the hind margin of the cranium. A reduction in the posterior dimensions of the cranium appears to be compensated by the anterior development of the rostromethmoidal region. In concert with these changes in overall cranial dimensions, the upper jaw also undergoes extreme modification. The otic process is developed to establish a strong connection to the postorbital skull wall while the dimensions of the palatine section are further enhanced to parallel the expanded ethmo-rostral zone of the cranium. This line of attachment between the upper jaw and cranium is demarcated by formation of a canal extending from the ventroanterior margin of the orbit to the nasal capsule, identified here as an orbitonasal canal. Reduction of the posterior cranial dimensions, the increased mass of the upper jaw and the closer association of cranial and mandibular elements have collectively contributed to a medial compression of the interorbital space. This, in turn, draws the selachian-type supraorbital vein into an interorbital space which is sufficiently reduced to impede the forward continuation of this vessel. Originally, this vessel would give off median and dorsolateral tributaries to the snout before piercing the supraorbital

cartilage to empty into the orbital sinus. Now, due to the interorbital compression, the anterior tributaries are selected against and the supraorbital vein drains directly into the orbital sinus. Instead, the newly enhanced rostroethmoidal region is bilaterally vascularized by a direct tributary of the orbital sinus which, in the company of the superficial ophthalmic nerve, exits the orbit via an elongate preorbital canal. This canal would form as cartilages of the lamina orbitonasalis and, to a lesser degree, the supraorbital crest are modified (1) as the palatoquadrate establishes a greater degree of contact with the rostro-orbital segment of the cranium and (2) the reduced interorbital space forces a forward displacement of the supraorbital cartilage.

Consequently, the positions of nerves, vasculature, and orbital foramina now reflect a holocephalan plan of orientation (Figure 33b). The orbital sinus tributary which traverses the preorbital canal is now found to travel with the superficial ophthalmic nerve. The profundus' orbitonasal foramen maintains its original position but, due to inter- and supraorbital modifications appears to be in closer proximity to the superficial ophthalmic nerve foramen. It is now enclosed in the preorbital canal due to the posterior-dorsal extension of the lamina orbitonasalis.

Between this and the next stage of the transition, there is an intensification of the general trends of

remodeling. With progressive shifting of the mandibular arch forward a significant articulation develops between the upper jaw and ethmoid segment of the cranium.

Concomitantly, the side wall of the skull in the rostromethmoidal region (the orbitonasalis) becomes more obliquely oriented. Thus the development of a significant ethmoid articulation forces the medial displacement of the two separate canals. This condition is obvious in *Het2* for it is at the level of the ethmoid articulation that the bilateral preorbital canals appear to merge or at least change the angle of their passage towards the rostrum. All cranial transformations noted in this transition sequence are interpreted as those modifications required to relieve the mechanical stresses induced by the morphological shifts from one form of autodiastyly to another.

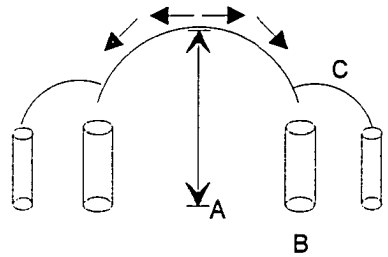
Therefore, the paraselachian assemblage provides the data necessary to explain formation of an ethmoid canal in conjunction with the shift to holostyly. Within the morphocline, the development of an ethmoid canal is preceded by a series of autodiastlyic states. In the more advanced states bilateral preorbital canals are found. These bilateral canals are formed as (a) a side wall is generated from the combination of preoptic root cartilage and a posteriorly extending lamina orbitonasalis cartilage, (b) the floor is represented by the telencephalic roof, and (c) both the roof and medial wall form from lamina

orbitonasalis and the forwardly displaced supraorbital cartilage. A single ethmoid canal is formed as the preorbital canals are forced into a more medial position with the encroachment of space by a more obliquely directed lateral cranial wall and ethmoidal palatoquadrate articulation.

The immediate question I am faced with, given the identification of ethmoid canal cartilages, is a causal one. What would induce the lamina orbitonasalis to develop so extensively in the posterior and posterodorsal directions. If lamina orbitonasalis displacement is due to the degree of palatoquadrate development in the transition of autodiastyllic palatoquadrates then the answer to this quandary is a mechanical one. The question is then redefined. Does the posterior development of the lamina orbitonasalis provide strength to the lateral cranial wall as (1) the rostro-orbital region elongates, (2) the jaw transfers increasingly more stresses along this region, and (3) the preorbital cranial wall becomes more obliquely oriented? If so, how is this related to ethmoid canal formation once the suspensorial nature and transitional stresses are lost as holostyly develops?

To answer these questions, I have relied on the engineering logic behind building construction (Figure 34). The development of a wall of lamina orbitonasalis cartilage would have the effect of buttressing or "shoring-up" the

Figure 34 : Mechanical Stress Analysis

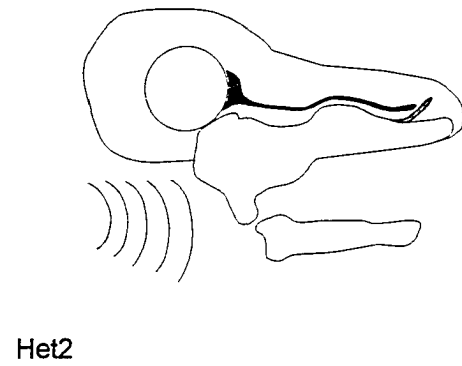
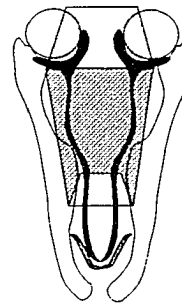
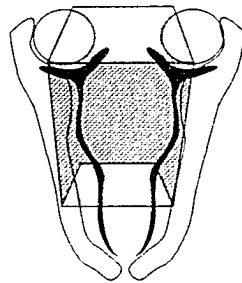
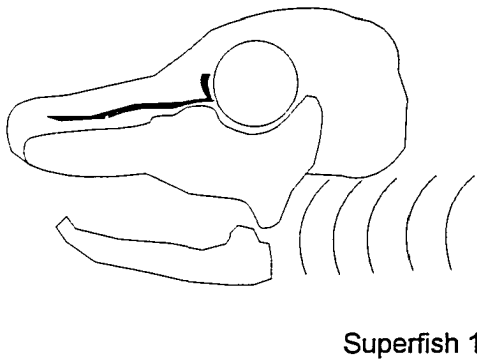


ARCHITECTURAL VARIABLES

- A: VAULT HEIGHT = CRANIUM HEIGHT \longleftrightarrow
- B: COLUMN WIDTH = THICKNESS OF CRANIAL WALLS
- C: FLYING BUTTRESS = ARTICULATING OR FUSED REGIONS OF PALATOQUADRATE CARTILAGE

RESULT:

- (I) DISPERSAL OF INTERNAL STRESSES \longrightarrow
- (II) RESISTANCE TO EXTERNAL FORCES
- (III) STRUCTURAL INTEGRITY PERMITS DEVELOPMENT OF LARGE FORAMINA OR DISCONTINUITIES IN THE SKULL FLOOR, ROOF, OR SIDE WALLS



cranial wall cartilage in the rostro-orbital region. This is necessary not only to facilitate the dissipation of mandibular and biting stresses but also to do the same for those stresses generated from ligamentous and muscular attachments developing in this region. This construction has the additional benefit of accommodating any subsequent remodeling or addition of structures forward of the orbit (eg rostral feelers, sexually dimorphic rostral rods or claspers, etc). In the latter condition, the buttressing would also provide protection for the vascular and nervous elements supplying structural additions. Thus, if the holostylic condition were to follow from the autodiastylic shift and the original mechanical stresses are thereby lost, then the lamina orbitonasal wall may be expected to be retained if (a) it's presence acts to minimize existing stresses, (b) it now acts to accommodate newer stresses or (c) to allow subsequent modifications within the rostro-orbital zone. I refer to the accounts of a laterally flaring orbitonasalis in Helodus to demonstrate how it is possible for this condition to persist in the holocephalic state. From these discussions on the formation of an ethmoid canal it is apparent that this trait need not be considered a recent acquisition for Holocephali. It is, however, a unique holocephalan character which supports a cladistical arrangement which would depict a close association between chondrichthyans and paraselachians and this collective unit

as having arisen from an "early autodiastyletic form".

In reference to previous studies, what has been described under the conditions of interorbital compression is in agreement with Holmgren's note on a vascular space extending from the ethmoid canal, over the holocephalan interorbital septum to the main brain cavity. Allis' description of the selachian condition agrees with my contention that orbitonasal canal formation occurs as the palatoquadrate becomes more intimately apposed to the rostro-orbital zone. That is, the region of continuity between the selachian ectoethmoid chamber and orbitonasal canal can be correlated with the extensive orbitonasal canal found extending between the holocephalan orbit and nasal capsule. The features highlighted in the posterior cranial remodeling explains the different pathway taken by the chimaerid postorbital compared to the selachian jugular (lateral head) vein. As is shown in the transition model, the lateral head vein (originally the largest tributary of the orbital sinus) is forced into a lower posterior margin of the orbit due to the reduced otico-occipital dimensions. With the subcranial positioning of the branchial arches the lateral head vein is subsequently found in closer proximity to that region of the orbit containing the foramina of the orbital artery, hyomandibular and palatine nerves. Furthermore, in reference to a vessel which is ignored in analyses of a selachian/holocephalan relationship, with

complete "subduction" of the arches beneath the cranium, this transition sequence suggests the maxillofacial vein develops as the branchial arches take on a nested arrangement. With regard to the fossil evidence, the transition model would suggest that the laterally flaring orbitonasalis cartilages of Helodus are actually the medial walls of the precerebral canals as found in Het2.

**The Cranial Anatomy of Extant Forms in Relation to
the Fossil Data**

Many of the observations made from the fossils are reinforced by observations made on the crania of extant forms (Figures 35-37). In comparing the crania of specimens from each of the three extant chimaerid families, it became apparent that the greatest cranial variation concerns the labial cartilages, the placement and extent of rostral cartilage development, and the expanse of the "ethmoidal" crest cartilage in relation to the position of the anterior opening of the ethmoid canal and the development of the median rostral cartilage. In the transition from the cranial anatomy of Callorhynchus to Chimaera the following trends were observed;

- (a) a shortening of the lower jaw,
- (b) a shortening of the apparent upper jaw region,
- (c) a closer association of orbital and nasal capsule cartilages as the length of the upper jaw and rostro-orbital

Figure 35: The Cranium of Callorhynchus

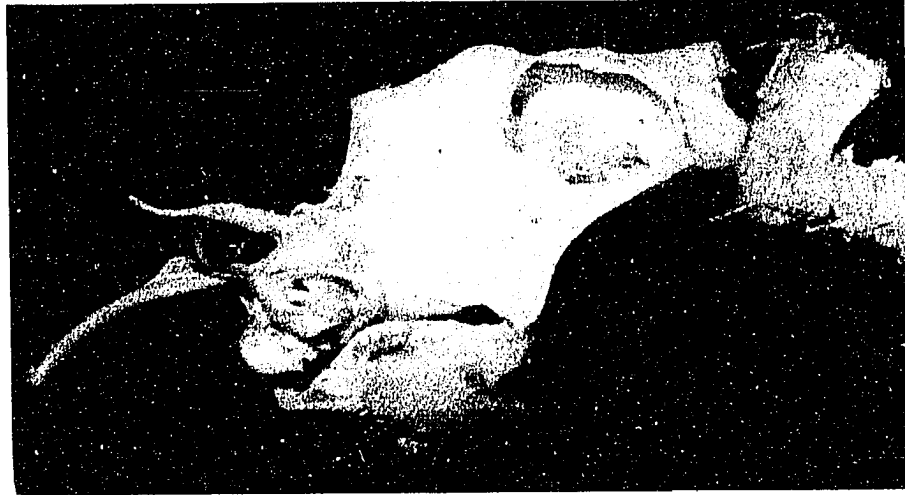


Figure 37 : The cranium of Chimaera

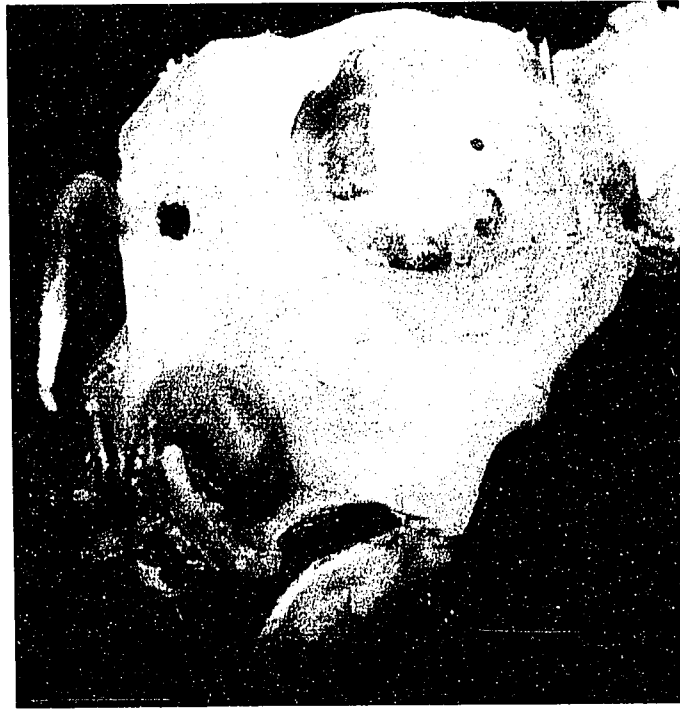
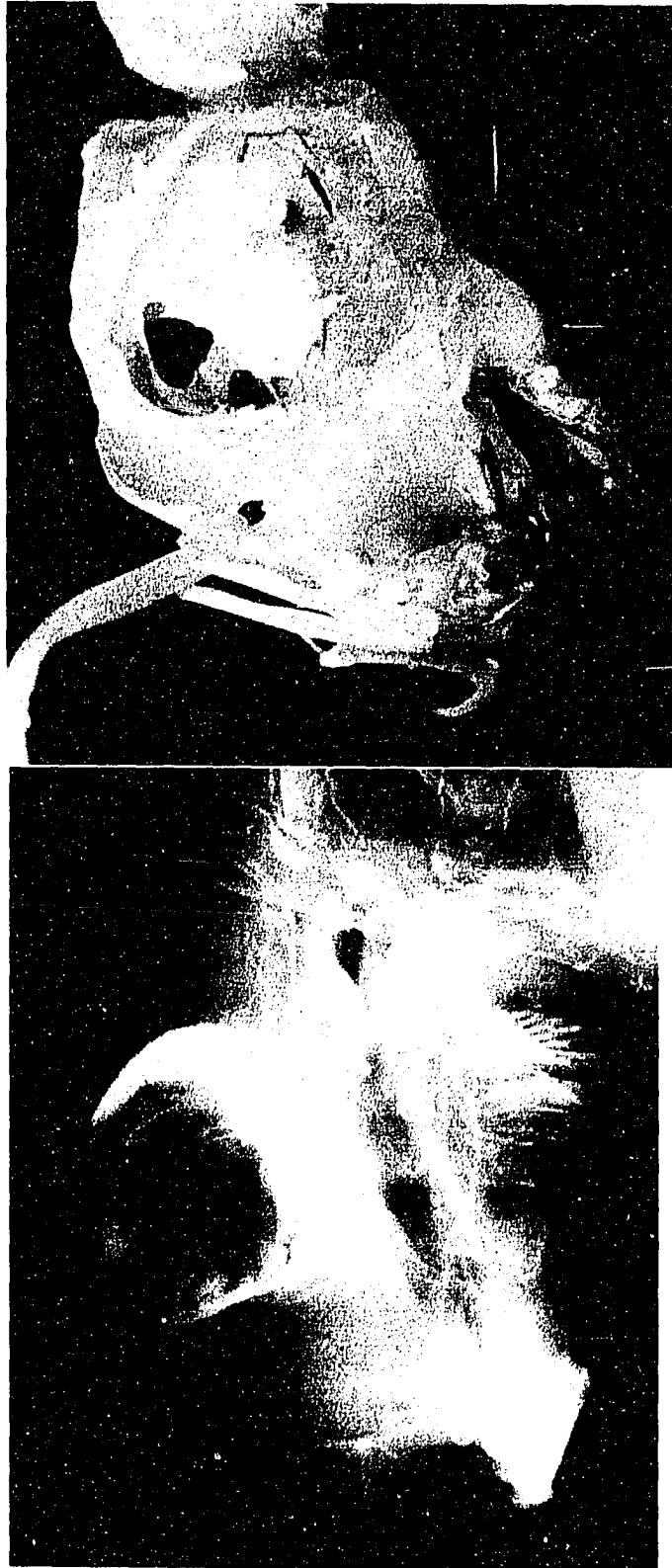


Figure 37 : The Cranium of *Rhinochimaera africana*



are reduced,

(d) a dorsad shift in the position of the median rostral cartilage as the length of the ethmoid canal shortens,

(e) a thinning and greater surface area of the interorbital septum, and

(f) reduced expanse of the "ethmoid" crest cartilage versus an increased span of the laterally directed supraorbital crest cartilage. In view of the paraselachian morphocline, it would appear that the striking difference in the orbitonasal and ethmoid dimensions represent successive stages of holocephalan cranial remodeling subsequent to the paraselachian shift if Callorhynchus is considered the least derived of the extant forms. The interpretation of this interfamilial relationship is also supported by Dean. From a comparison of the of the 60mm Callorhynchus and 51mm Chimaera preorbital cartilage, postorbital ridge, cranial proportions, interorbital cavity, and rostral cartilages he concluded that Callorhynchus's embryonic development more closely resembles the development of the selachian cranium than Chimaera. Furthermore, my observations on the orientation of the posterior ethmoid canal openings, the expanse of the ethmoid canal cavity, and features of the interorbital septum agree with Holmgren's comparative serial information which figures Callorhynchus with the least interorbital compression, Chimaera with the most and Rhinochimaera being intermediate. A comparative synopsis of

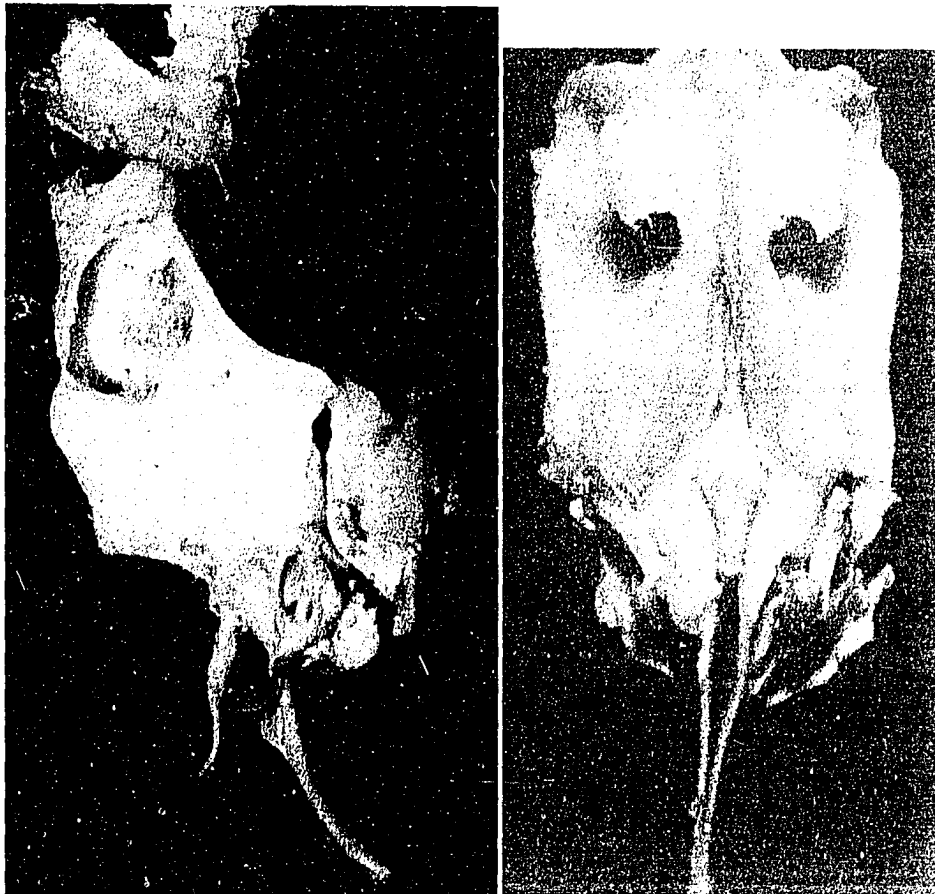
these extant features is presented in the following discussion with comments on the ethmoid canal and a relational analysis to paraselachian data.

In Callorhynchus, the angle of the ethmoid canal relative to the orbit and the dimensions of the canal itself are quite different from what is seen in either Rhinochimaera or Chimaera. The same can also be said for the relative length of the palatoquadrate and the appearance of the "ethmoidal crest cartilage" which extends vertically along the canal. Compared to the cranial structures exhibited by rhinochimaerid and chimaerid species, the length of the preorbital region is greater in Callorhynchus and, in overall cranial proportions is closer to the condition described for either Sup1 or Het2. The ethmoid canal of Callorhynchus is elongate and narrow, more reminiscent of Het2's rostro-orbital features than any other paraselachian which fits into the morphocline leading to ethmoid canal formation. What is most unusual in this extant form is that, anteriorly, at the level of the nasal capsule and for a short distance posterior to this point the canal is bilateral. A medial cartilage partition is found below and fused to the base of the median rostral cartilage. This cartilage wall persists backwards to that point where the ethmoid canal attains its greatest dimensions; a point anterior and approximately midlevel to the anterior orbital margin. Thus, the canal seems to be united for most of its

length but divided anteriorly where the median rostral cartilage arises from the internasal zone, and in doing so emphasizes the divided nature of the ethmoid canal anteriorly.

This region is particularly interesting, not only for the divided appearance of the ethmoid canal anteriorly but also for the features of cranial and nasal capsule cartilages (Figure 38). At the point where the median rostral cartilage narrows and extends anterodorsally from its more bulbous base, there are "prongs" of cartilage which appear to flare dorso-anteriorly from the lateral wall of the nasal capsule and, in doing so, come to lie alongside the lateral edges of the median rostral cartilage. DeBeer has obviously also noted this cartilage in relation to the anterior opening of the ethmoid canal for although he does not describe them in his paper he does diagram them for the 95 mm Callorhynchus. These extensions appear to arise with a posterior and dorsal expansion of the side and hind wall of the nasal capsules, i.e. that cartilage known as the lamina orbitonasalis. (In Selachii it appears to be associated with the cartilage separating the precerebral fontanelle from the epiphysial foramen.) The two lateral rostral rods give all indications of having developed from the medial wall cartilage (and some contribution from the roof) of the nasal capsules before extending and eventually fusing anteriorly. These observations suggest an internasal

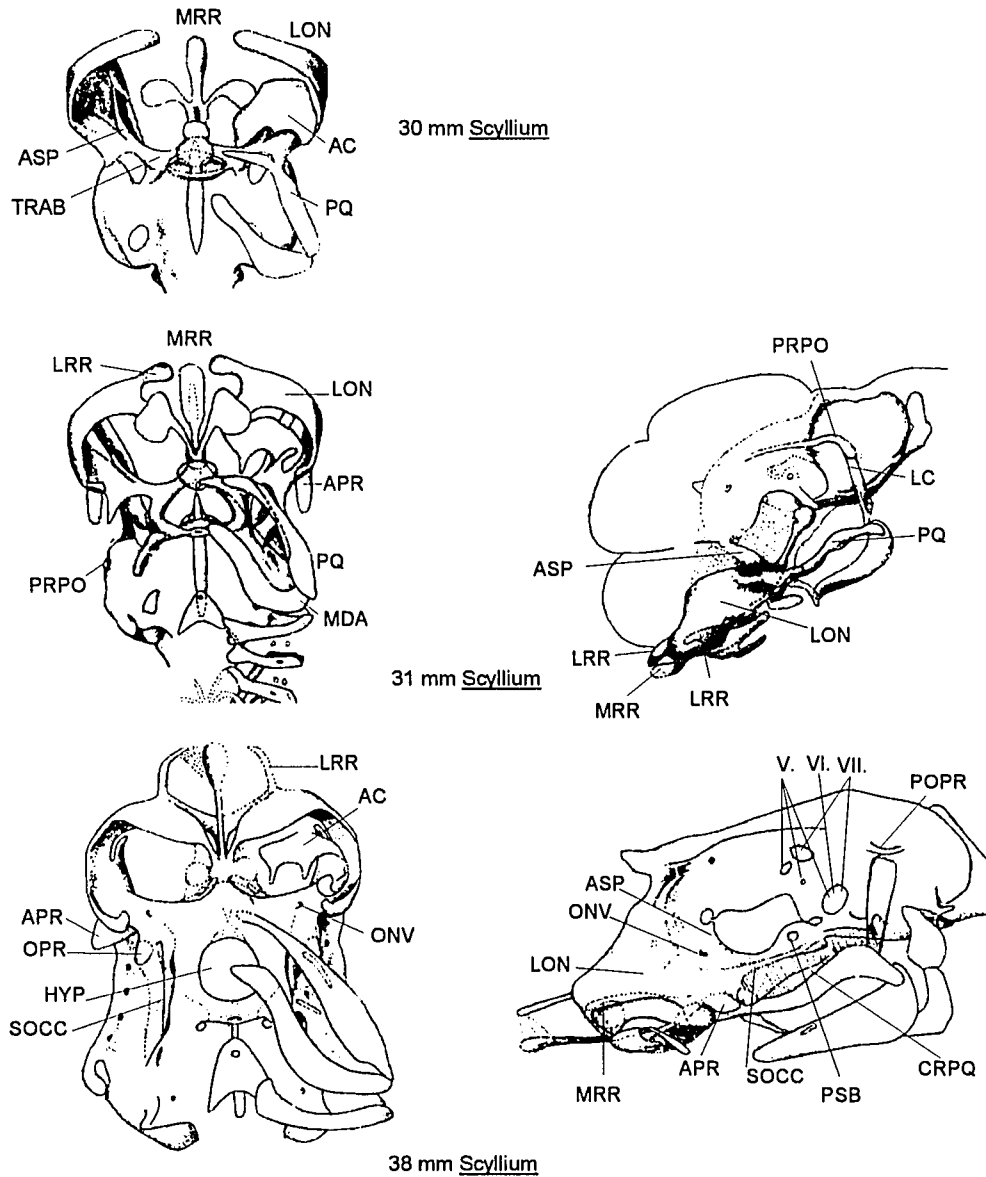
Figure 38: Various Cranial Features of Callorhynchus



cartilage partition gives rise to the median rostral rod and both of these structures either occlude the anterior opening of the ethmoid canal or induce the forward bifurcation of the canal. This appears to have forced the nasal capsule roof cartilage up and around the occlusive median rostral rod.

These interpretations on chimaerid rostral rod cartilage derivation from that of the nasal capsule are important in determining the nature of ethmoid canal cartilages but, more importantly, to the questioned homology between holocephalan and selachian rostral rods. Gegenbauer (1872) and Allis (1917) both assume the holocephalan rostral processes correspond to the three rostral rods of galeoids despite the reversed position of medial versus lateral cartilages. Holmgren disagrees with this assumption based on the embryological evidence he interprets from Schauinsland's 85mm Callorhynchus. At this stage he notes that the three rostral processes are either supported by the internasal septum or at least embryologically inserted onto it. In contrast to this he then refers to the state in Scyliorhinus where the medial rostral rod appears as an anterior extension of the internasal septum and is derived from "the superficial section of the medial cartilage". In contrast, the lateral rods are derived from an early rudiment of the nasal capsule (Figure 39). Thus, he argues, "the only way the medial processes of selachians and

Figure 39 : Embryogenesis of Selachian Cranial Cartilages



Figures and abbreviations are modified from Holmgren 1940. AC: annular cartilage; APR: antorbital process; ASP: anterior side plate; CRP: cranioquadrate connection; HYP: hypophysial fenestra; LC: Lower labial cartilage; LON: lamina orbitonasalis; LRR: lateral rostral rod; MDA: mandibular arch; MRR: median rostral rod; ONV: orbitonasal vein; OPR: orbital process; PRPO: postorbital process; PSB: efferent pseudobranchial artery; PQ: palatoquadrate; SOCC: subocular cartilage; SOS: subocular shelf; TRAB: trabecula; V.: Trigeminal; VI.: Abducens; VII.: Ophthalmic Branch of Facial.

chimaerids may correspond to each other is through a shifting of the nasal capsule from the selachian position" (ventrally directed and with vertically oriented nasal capsules) "to a holocephalan orientation" (rotated frontally and upwards). In the process of this transformation, "the ventral border of the internasal septum rotates to a frontal position and the the median rostral process is rotated into a dorso-frontal position. This shift in the orientation of the nasal capsules is demonstrated in my observations of the extant families and correlated with a more dorso-posterior positioning of the nasal capsules; a trend which also reflects transitions in the state of the ethmoid canal and position and development of rostral rod cartilages. Figure 40 shows the typical relations of the rostral rods to the nasal capsule, and these in relation to the precerebral fontanelle in selachians or the anterior ethmoid canal openings of holocephalans. Comparison of the two photographs reveals, if one were to imagine a medial compression, frontal rotation, and dorsoposterior shift in nasal capsule orientation, the direct shift from a selachian to holocephalan condition is achieved (Figure 41). Again, the flaring processes from the nasal capsule cartilage ("prongs") provide the clearest landmarks for judging the apparent shift of cartilages; initially flanking the postero-dorsal margin of the precerebral fontanelle, subsequently flanking the reoriented median rostral

Figure 40 : A Comparative View of the Preorbital Region of Squalus and Callorhynchus

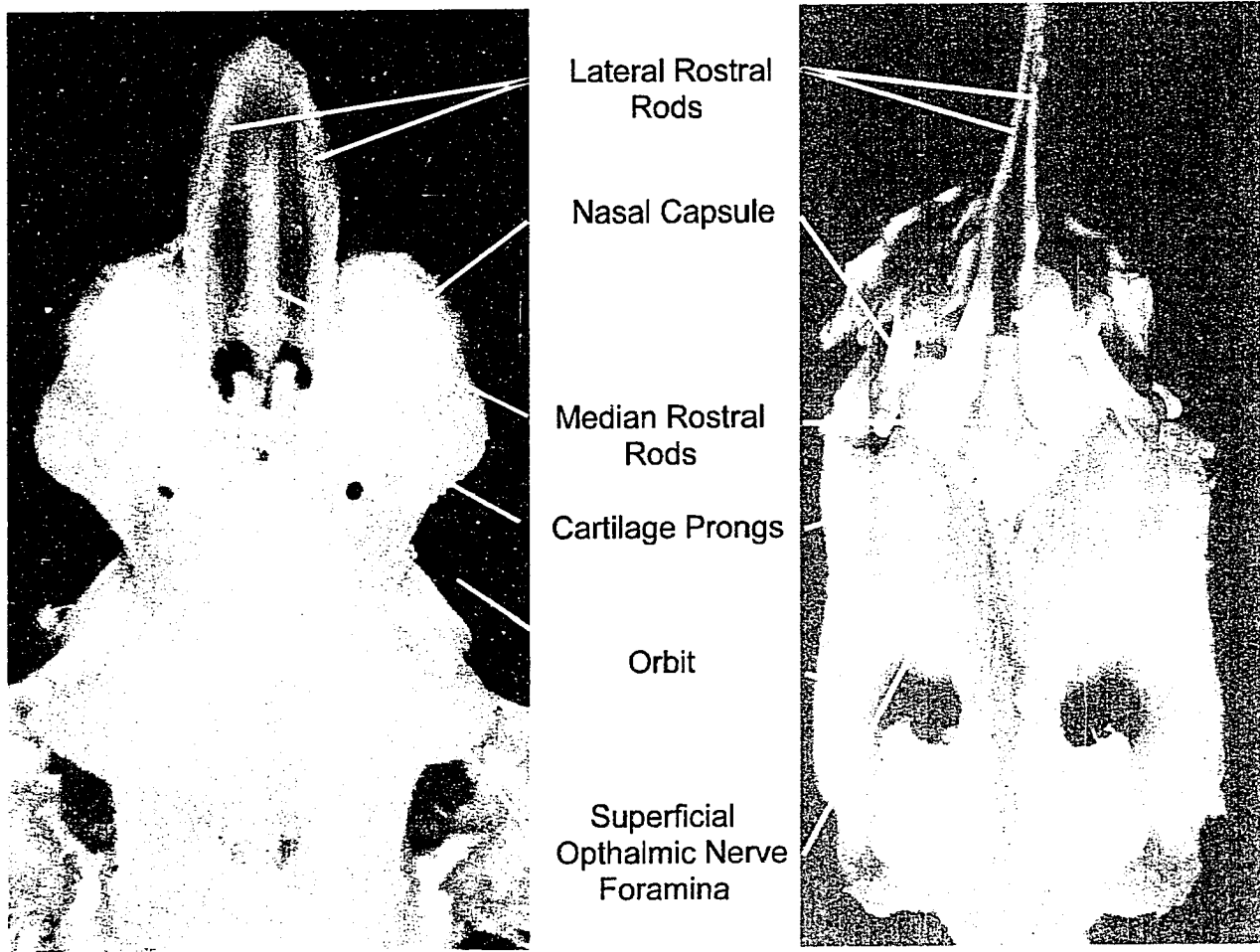
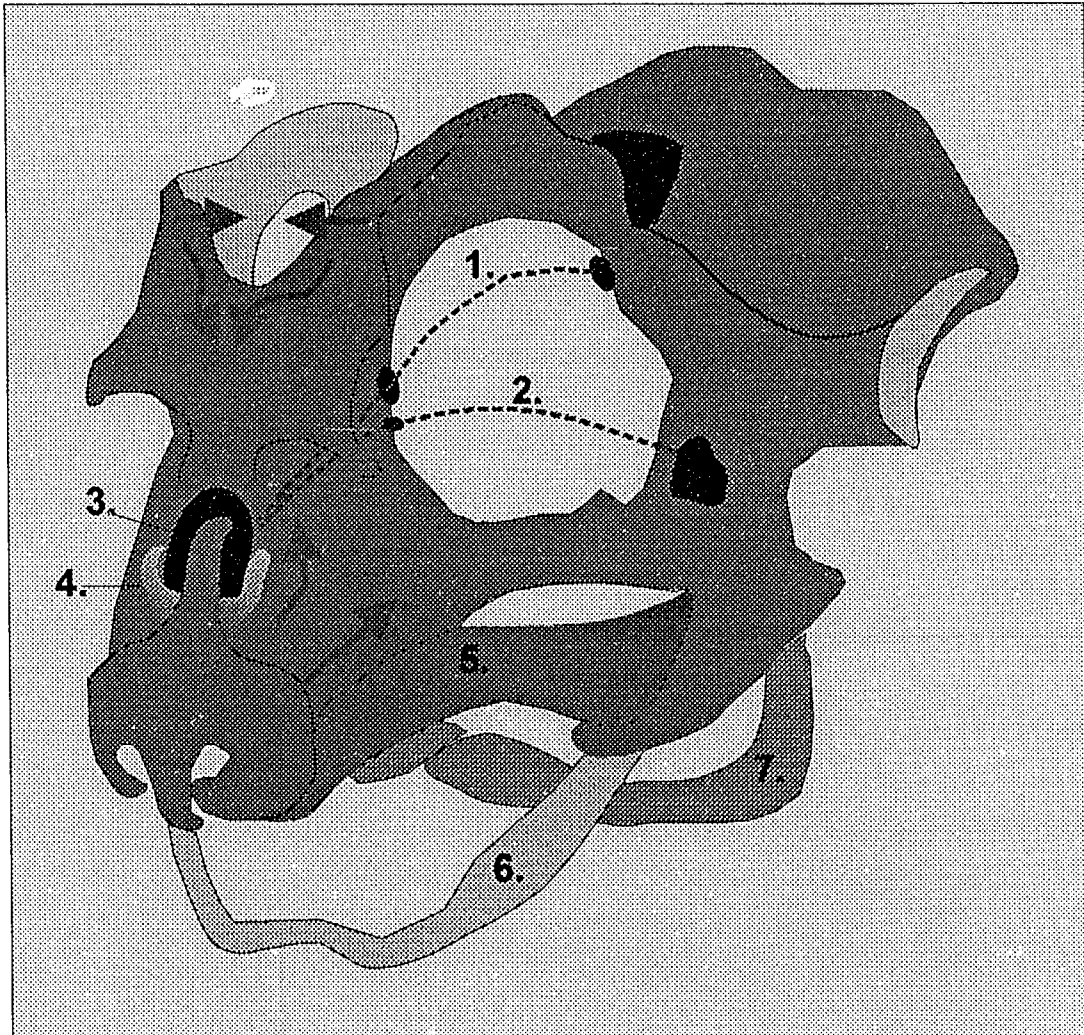


Figure 41 : The Shifting of Cartilages Required for Ethmoid Canal Formation



The arrows indicate the direction of cartilage growth or distortion. As elucidated in the text, the ethmoid canal is formed by contributions from the roof, hind and side walls of the nasal capsule cartilage (lamina orbitonasalis). More posteriorly the canal is formed in part from the anterior displacement of the medially compressed supraorbital cartilage. The nasal capsule "prongs" serve as landmarks for comparing the remodeled chimaeroid cartilages with those of the nasal capsules and ethmoidal region for the selachian chondrocranium. Numbered elements are; 1,2: superficial ophthalmic and profundus nerves, 3: precerebral fontanelle, 4: displaced nasal capsule cartilages ("prongs"), 5: partially fused palatoquadrate, 6: Meckel's cartilage, 7: Hyoid arch components

cartilage and anterior to the forward ethmoid canal openings.

From these notes I have concluded the ethmoid canal is, as DeBeer argues, not neurocranial in origin. However, it appears to be associated with the position of a precerebral fontanelle to the degree that the hind margin of the nasal capsule marks the anteriormost limit of both the fontanelle and the forward opening of the ethmoid canal. This is further emphasized by the persistence of the "pronged" processes of the nasal capsule which serve as landmarks for this point in both chimaerids and selachians and also serves as a landmark for the epiphysial (pineal) foramen.

In summary of the extant data, the condition of Callorhynchus, as the least derived genus among extant forms, provides the evidence needed for a clear interpretation of the nature of ethmoid canal cartilages. It is the dorsal and posterior distortion of the hind wall of the nasal capsule which generates the floor of the ethmoid canal while the extension of the lateral nasal capsule wall cartilage caudally to the preoptic root cartilage and posterior-dorsally to the supraorbital cartilage which forms the side wall of the canal. The roof of the canal is formed from the anterior extension of that supraorbital crest cartilage which was impinged upon during compression of the interorbital space. The limits of the supraorbital and lamina orbitonasalis cartilages are evident

in Figures 35-37. The margins of the respective cartilages is determined by those contours of cartilage growth and the implied suture lines which become more apparent as the alcohol evaporates from preserved specimens under examination. Within this analysis, both the fossil and extant data lead to the conclusion that the form ancestral to holocephalans most likely possessed an anterior precerebral fontanelle. This cranial feature is subsequently occluded by the development of the rostromethmoidal region and preorbital canals as the nasal capsules undergo reorientation.

**Contributions of Helodus and Squaloraja Information to the
Ethmoid Canal Controversy**

Patterson (1965) has addressed the feature of an ethmoid canal within the context of the sistergroup debate. In contrast to the embryologically based analyses discussed earlier Patterson has primarily relied upon data from the fossil record and concluded the ethmoid canal is cranial in nature and a recent acquisition to holocephalans. This determination has been based on examinations of Helodus and Squaloraja. In Patterson's analysis the Carboniferous Helodus is considered to represent a new order, Helodontiformes, within the subclass Holocephali. This species was compared with the Jurassic Squaloraja. This form is a member of the Chimaeriformes, that group to which extant forms are aligned. Following comparison of these forms he argues, "The form of the ethmoid canal in the laterally compressed chimaeroids and the absence of the structure in the dorsal-ventrally flattened Squaloraja suggest that the canal arose as a consequence of the formation of the interorbital septum, by the compression of an originally broad-headed form." The Bear Gulch paraselachian data would indicate this comparison deserves reexamination for the information revealed by the Helodus appears to be incomplete and certain features of Squaloraja may have been misinterpreted.

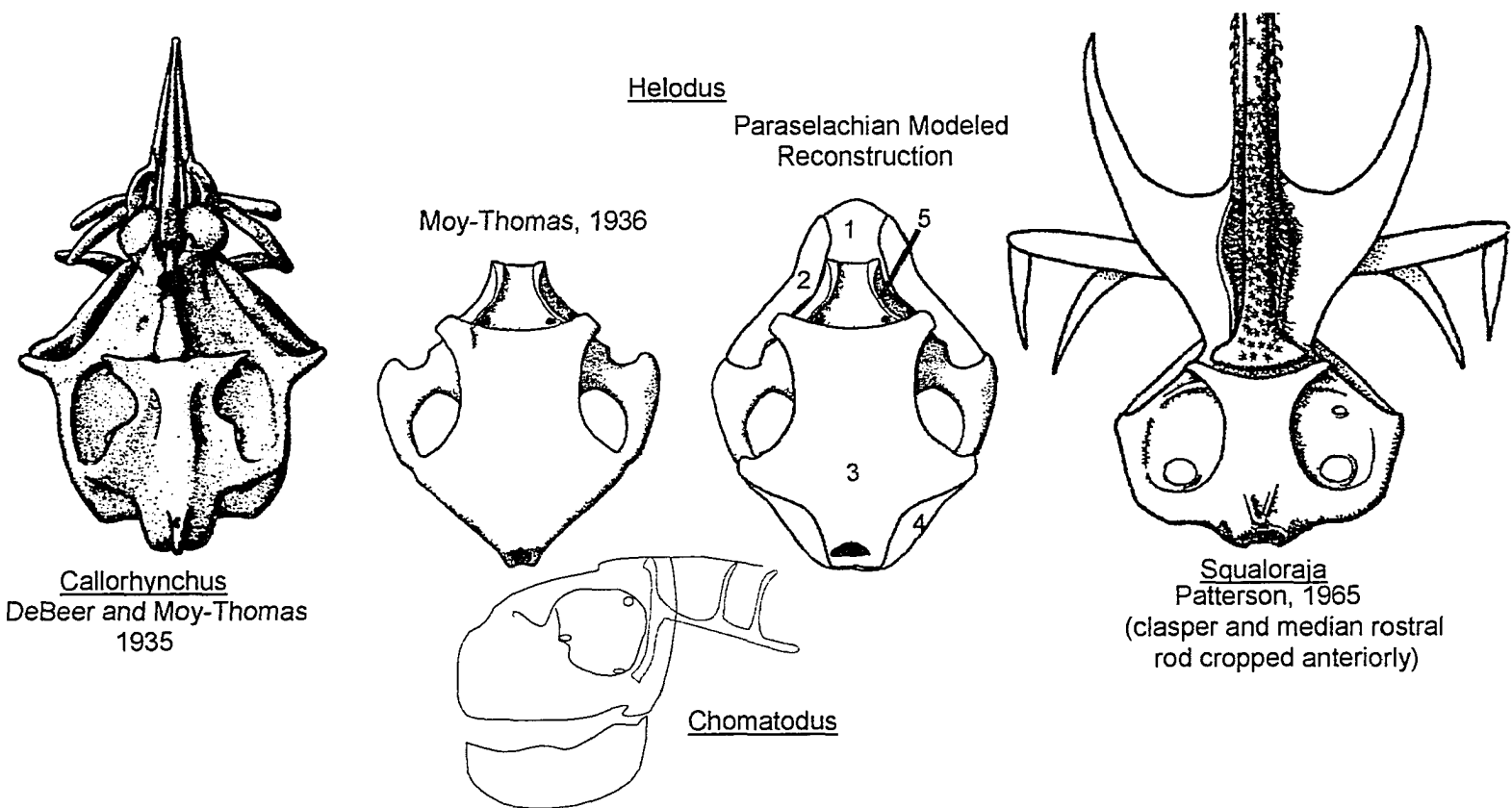
Helodus' cranium, as described by Moy-Thomas (1936) and referred to by Patterson, is broad, dorsoventrally flattened, holostylic, and underlain by the branchial skeleton. It is also characterized by a wide interorbital cranial cavity, the absence of an ethmoid canal, and the presence of vertical laminae on the preorbital segment of the skull roof. These laminae are seen to enclose what have been interpreted as the efferent foramina for the superficial ophthalmic nerves which, like the selachian equivalent, would proceed forward onto the snout external to the cranial cartilages.

With regard to the paraselachian data presented earlier, it is striking that the description of Helodus' "cranial roof" closely approximates certain rostro-ethmoidal features of Het2. In comparing the the crania of paraselachians (Het2, Chomatodus, Harpacanthus, Orodus) and Helodus it would seem most likely that the preorbital "skull roof" laminae noted for the latter specimen are actually equivalent to the Het2's preorbital passage walls. The proximity of these laminae to the orbit suggests that these walls, like the preorbital passages of Sup1 and Het2, probably enclosed the rostro-ethmoidal vessels and nerves. Therefore, this fossil is actually preserved without the cranial roof. What is diagrammed by Moy-Thomas is likely to be an incomplete portion of the internal rostro-ethmoidal cranial structure. Other cranial evidence which fits

Helodus into the early stages of the paraselachian morphocline are the apparent posterior limit of the palatoquadrate cartilage relative to the orbit, the general cranial dimensions, interorbital dimensions and branchial arch position.

Squaloraja's cranial dimensions have been compared to that of Callorhynchus by DeBeer and Moy-Thomas (1935). Figure 42 presents these crania and supplements the comparison with the inclusion of Chomatodus and Helodus. In the parallel examination of these heads the Jurassic holocephalan is reported to display labial cartilages, rostral processes, and a frontal clasper which closely resemble the corresponding features in Callorhynchus. Thus, it would seem most appropriate to depend upon this comparative analysis when assessing the formation of an ethmoid canal with respect to the evolution of the lineage. In keeping with this philosophy, Patterson states that the canal of extant fish opens into the orbit just below and behind the insertion of the frontal clasper. Anteriorly, it opens immediately lateral to the base of the median rostral process. Therefore, he predicts if such a canal were present in Squaloraja it should also be lateral to the base of the median rostral process. Since he considered the anterior canal opening "larger in the long snouted Callorhynchus, and Rhinochimaera" than in Chimaera he anticipated that the anterior opening would be comparatively

Figure 42 : A Comparison of Squaloraja, Chomatodus, Helodus, and Callorhynchus Heads



Helodus reconstruction reflects the cranial dimensions of Chomatodus and Harpacanthus. Numbered elements are 1: Anterior limit of skull roof, extending from the preorbital ridge; 2: lower jaw, 3: supraorbital process, postorbital process and otico-occipital cartilage; 4: posterolateral cranial wall, 5: lamina orbitonasalis.

large and easily found if the longer snouted Squaloraja were to have such a canal. However, his examination of the species did not reveal any foramen at the fused base of the medial rostral process. Rather, he reports a parallel series of small rostral cartilage foramina in the region of the frontal clasper attachment and considers these unlikely representatives of ethmoid canal openings. Further posteriorly, he reports finding the superficial ophthalmic nerve foramen at the base of the lateral extension of a "transverse ridge" of the skull roof. In Patterson's view these are to be homologized with the superficial ophthalmic nerve foramina of Helodus and not the anterior opening of an ethmoid canal. Thus he summarizes, "there can have been no ethmoid canal in Squaloraja" and "Squaloraja gives support to no one of the theories concerning the origin of the ethmoid canal, but suggests that the canal arose late in holocephalan history." (p.121)

My observations from the extant and fossil crania of holocephalans and selachians and on the paraselachian cranial anatomy suggest a different interpretation of Patterson's data. Firstly, I concur with DeBeer and Moy-Thomas that the anteriormost foramen in the ventral orbital margin of Squaloraja is best defined as the orbitonasal passage, not the efferent pseudobranchial artery passage and that the posterior foramen is best termed the cranioquadrate passage. This nomenclature remains consistent with the

subcranial positioning of Squaloraja's branchial skeleton, holostyly, and the coursing of an orbitonasal canal in Selachii versus Holocephali. As for the ethmoid canal openings, in contrast to Patterson, I have not found the anterior ethmoid canal opening to be greatest in the longer snouted extant forms. In fact my observations suggest the reverse state; it is smallest in Callorhynchus with the long, thin ethmoid canal and largest in the short canalled Chimaera.

With regard to those serial foramina which Patterson uses to disavow the possibility of an ethmoid canal in Squaloraja, I suggest they should be compared to the superficial opthamic foramina of the shark cranial roof and the ethmoidal roof of Callorhynchus. The positioning of these foramina in Squaloraja agree with those found in Callorhynchus. Therefore, since Patterson has also noted these to occur on either side of a rostral cartilage ridge I propose that the serial foramina in question are most likely to be homologous to what is found in Callorhynchus and that these do suggest an ethmoid canal is possible in Squaloraja. Linking this to the earlier note on the relative size of the anterior ethmoidal opening, if Squaloraja were to possess an ethmoid canal I would anticipate small anterior openings may be found if one were to follow the ridge marked by the bilateral series of foramina.

Given so many similarities between the paraselachians

and Helodus and the conditions of Callorhynchus and Squaloraja the next question would be whether or not the data on Squaloraja and Helodus is consistent with the paraselachian morphocline. Helodus does fit into the paraselachian morphocline at that stage of cranial remodeling where the supraorbital crest cartilage is distorted and anteriorly displaced from the interorbital zone by a medial compression of the orbits. The overall cranial dimensions support the reconstruction which shows how the forward displacement of supraorbital crest cartilage results in establishing a continuous cranial roof from the orbit to the rosto-ethmoidal zone. This form may have had bilateral preorbital canals like Sup1.

The posterior end of Sup1's preorbital canal is considered to be in such close association with the well developed orbital roofing that the cartilage of the latter region helps to form both the exiting superficial ophthalmic nerve/preorbital vein foramen and the roof the the canal. According to the paraselachian morphocline then, it is not a coincidence that the appearance of this preorbital cartilage is so similar to the transverse ridge of Squaloraja's skull roof and its corresponding superficial head vasculature. Although Squaloraja is undeniably derived (extremely specialized within the Chimaeriformes) and far removed from either Sup1 or Het2 the features noted in this discussion agree most with DeBeer and MoyThomas' theory of ethmoid

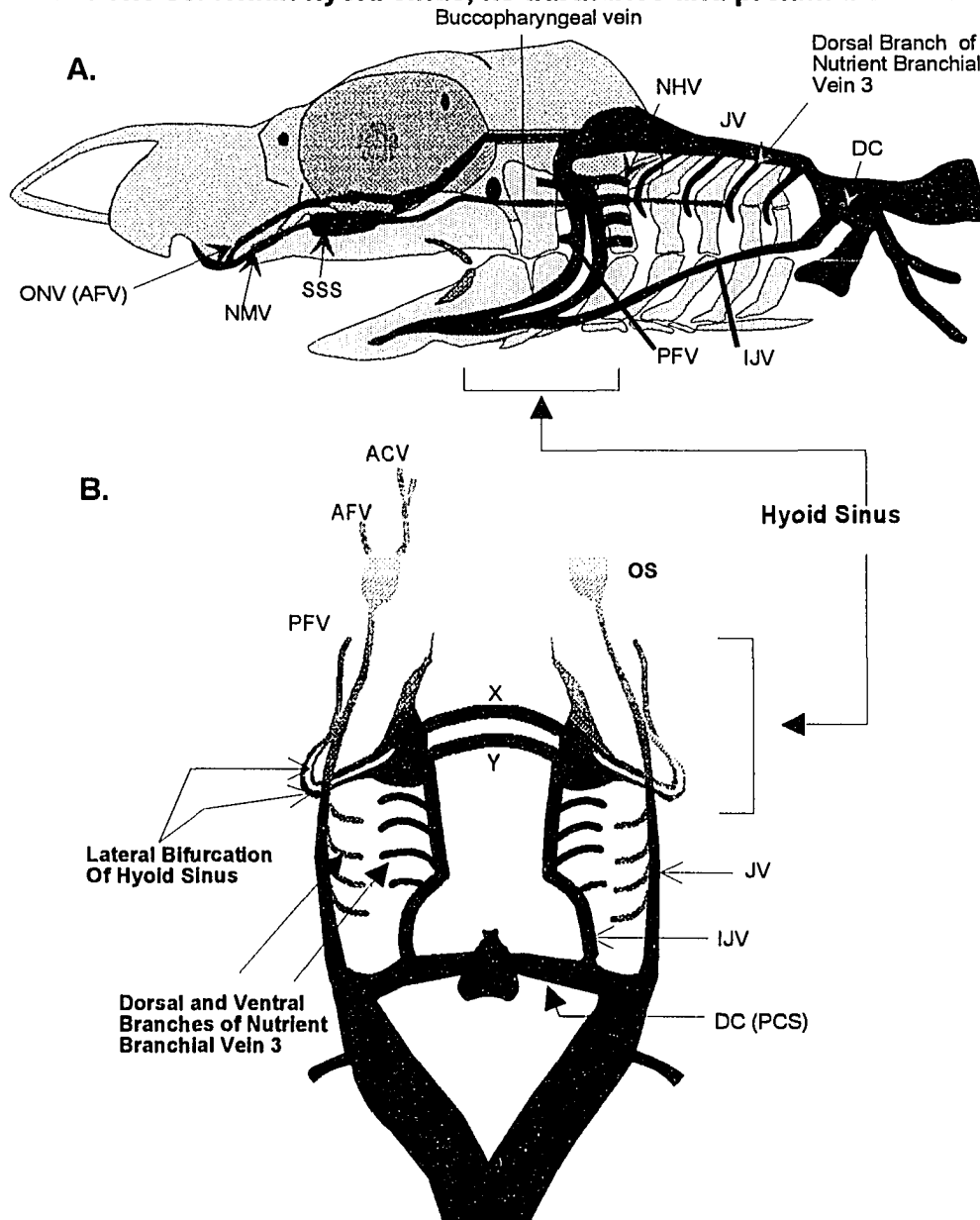
canal formation, my designation of ethmoid cartilages, and the development of a median ethmoid canal from originally bilateral preorbital canals.

What is a hyoid sinus?

The hyoid sinus is a spacious bilateral venous structure situated along the anterior margin of the first branchial arch in Selachii, parallel to the afferent branchial artery. As described for Mustelus by Parker (1886) and depicted in Figure 43, this sinus connects the dorsal jugular vein with the more ventro-mesial inferior jugular and has three chief drainages; mandibular, hyoidean hemibranch, and posterior facial. In its ventral-most orientation there are two symmetrically arranged interconnecting bridges between right and left halves of the sinus. The sinus of each side is further subdivided into 2 parallel lateral tracts between the level of the hypobranchial and the ceratobranchial cartilages. The intervening space allows forward passage of the mandibular artery and the dorsolaterally directed first afferent branchial artery which supplies the hyoid hemibranch.

The arrangement of the sinus suggests that it is formed from two originally separate veins; namely, mandibular and hyoid arch homologs of the serial holobranch "nutritive veins". Conditions under which specialization of the mandibular and hyoid arches occur, would favor vessel realignment such that merging and eventual fusion would

Figure 43 : The selachian hyoid sinus, its tributaries and proximal vasculature



A. Lateral View. B. Dorsoventral View after Parker (1886). Lighter shading indicates more dorsal plane of orientation; darker shading indicates a more ventral position. Abbreviated labels in parenthesis denote the nomenclature of Parker. ACV: anterior cerebral vein; AFV: anterior facial vein; DC (PCS): duct of Cuvier (precaval sinus); IJV: inferior jugular vein; JV: jugular vein; NMV: nasomaxillary vein; ONV (AFV): orbitonasal vein; OS: orbital sinus; PFV: posterior facial vein; SSS: submental symphyseal sinus; X,Y: ventral interconnecting hyoid sinus tributaries.

occur along the ventral to ventrolateral and dorsal to dorsolateral margins. The fusion points would subsequently develop into the more spacious sinus proper, while the unfused portions remain evident as parallel lateral tracts permitting passage of vessels.

Hypotheses for the rise of a hyoid sinus in reference to the origin and interrelationships of Chondrichthyes

In her arguments favoring coeliodont ancestry for Holocephali and separate evolutionary lineages for the latter and Selachii, Stahl (1967) proposed an explanation for the presence of a hyoid sinus in selachians and absence of the character in chimaerids. She argued the appearance of this sinus is specifically tied to "reduction" of the branchial basket and development of suspensorial jaws. More properly stated, "reduction" applies to the modification of those elements comprising the original premandibular and mandibular arches. [In the transition from agnathans to gnathostomes, the elements of the anteriormost arches are theorized to undergo modification into nonrespiratory structures (labial, rostral rod, and jaw cartilages), thereby reducing the total number of arches (see review by Thompson, 1971).] Within this paradigm, the selachian suspensorium is believed to develop as the epihyal is shifted and enlarged, forming a cranially articulating hyomandibula which functions as the securing mechanism of

the palatoquadrate. Forward displacement of the epihyal would generate a space in which a novel sinus could form. In contrast to the selachian condition, the holocephalan epihyal shows no departure from serial alignment with the remainder of the branchial elements and is argued to retain its four original elements. Therefore, Stahl concludes, no structure such as a hyoid sinus is present in extant chimaerids since there is no stimulus for its development and none is evident throughout the holocephalan lineage.

The obvious underlying assumption of this theory is that the nonsuspensorial hyoid arch is primitive and the sinus, when present, is a derived or secondary feature. This assumption must be clarified and in doing so, I will propose another interpretation for development of a hyoid sinus in select Chondrichthyes, an interpretation which coincides with a very different view on chondrichthyan derivation.

First, I concur that the original hyoid arch of gnathostomes was most likely nonsuspensorial, but, this condition of the suspensorium need not necessarily be holostylic, as Stahl invokes for her interpretation of chondrichthyan relationships. I specifically question to what degree pre-hyoidean arches are modified for jaw formation and what modes of jaw mechanics were possible in early gnathostomes. It must be noted from analyses of those early fishes for which a suspensorium is defined (eg

autostylic placoderms reconstructed with a hyomandibular) that there is little evidence as to the exact nature of the hyomandibular and branchial skeletal elements (Stensio 1945, 1959, 1965; Moy-Thomas and Miles 1971). Furthermore, Stensio deduced the nature of these elements through comparison with the elasmobranch condition, thereby, biasing the interpretation in favor of his theorized affinities of early vertebrates. Yet, with the recent discovery of new gnathostome species and interpretations of their relationships (reviewed by Forey and Janvier, 1993) it is clearly evident that the earliest vertebrates were significantly diversified by the Lower Ordovician, particularly in features of the cranial and branchial regions. Particular features of these areas must have influenced the organization and arrangement of premandibular and mandibular arches. I propose the earliest form of true jaws was most likely to depend upon some intimate connection between the exo- and endoskeletal elements in order to establish some form of mandibular suspensorium. This condition is certainly plausible for reports of fused and articulating exo- and endoskeletal elements have been made for agnathans and gnathostomes (e.g. Stensio's pariea-autostyly (1963) or Moy-Thomas and Miles' neurocranial articulating autopalatine and cheek bone-quadrates fusions (1971, illustrated in Figures 44 and 45), Parker's extrabranial (1878) or Holmgren's external

Figure 44 Pariea-Autostylic Quadrato-Spiracular

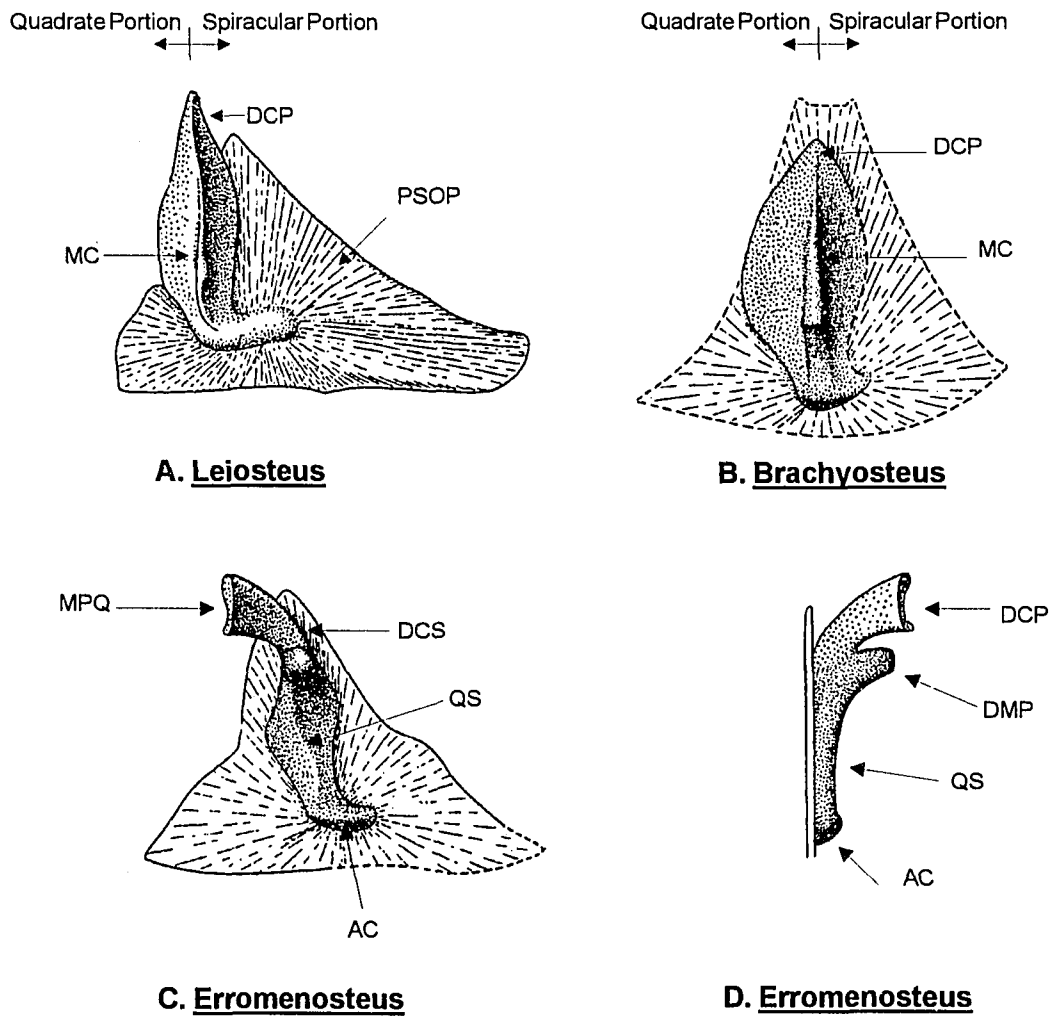


Figure taken from Stensio (1963); figure 116. A-C: Medial view of right quadrato-spiracular and Postsuborbital plate (Ventral preopercular plate) of select arthrodires. D: Anteriorly directed view of connection between left endoskeletal and endocranial elements. The different morphologies shown for the quadrato-spiracular suggest distinctly different forms of suspensorial attachment and, therefore, different mechanics of action and stress accommodation. AC: Articulating Condyle. DCP: Dorsal Connecting Process. DMP: Dorsomedial Process. MC: dorsoventrally directed Medial Crest. MPQ: Medial fraction of Palatoquadrate. PSOP: Postsuborbital Plate. QS: Quadrato-spiracular

FIGURE 45: Brachythoracid Arthrodires

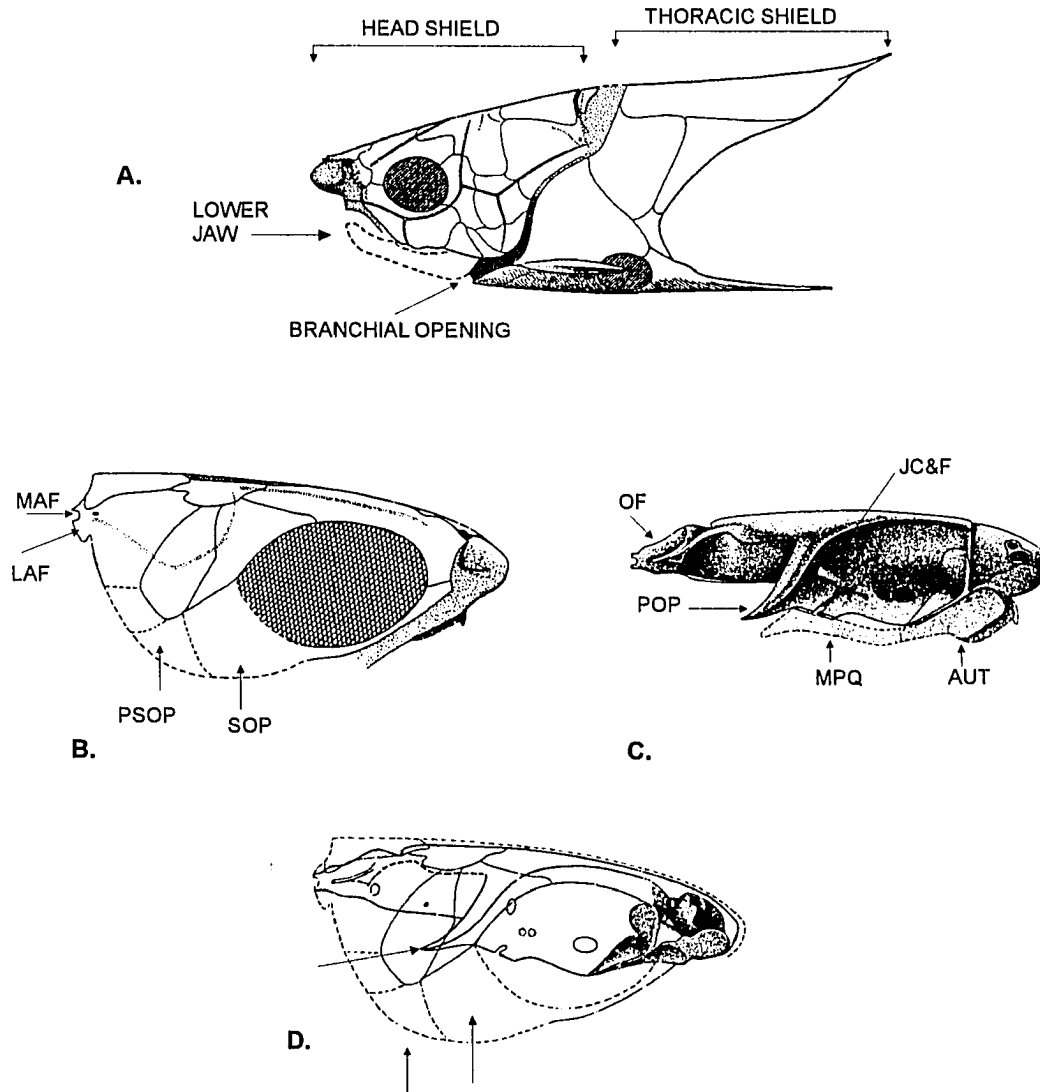
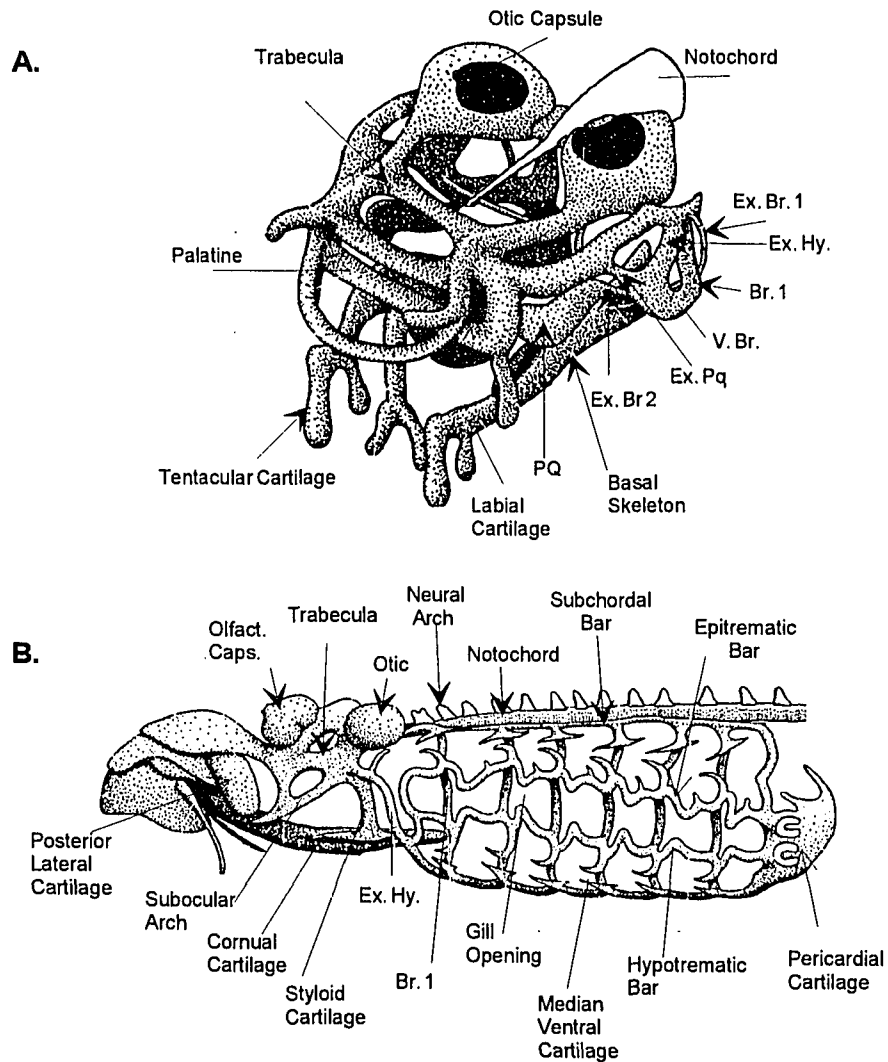


Figure modified from Stensio (1963), figure 91. (A) *Millerosteus*. Generic anatomy of placoderm with cranio-vertebral joint. (B-D) *Trematosteus*. Exoskeletal, endoskeletal, and combined anatomies respectively. Arrows in figure D indicate elements which may be involved in intimate connections between the endocranium and exoskeleton. APP: anterior postorbital process AUP: Autopalatine JC&F: Jugular Canal and Foramen LAF: Lateral articulating fossa of Cranio-Thoracic Joint MAF: Medial articulating Fossa MPQ: Middle Section of Palatoquadrate OF: Occipital Face PSOP: Postsuborbital Plate SOP: Suborbital Plate

visceral arch supporting mechanism for internal (branchial) arches (1942, illustrated in Figure 46). In these conditions the endoskeletal and exoskeletal anatomy appear to be inextricably linked, most likely in a cooperative effort to dissipate mechanical stresses while establishing a suspensorium functioning independent of a hyomandibular-type element. From this state one may derive the hyostylic selachian condition upon reduction of the exoskeleton itself or its role in dissipating intrinsic cranial stresses. Subsequently, the characteristic holostyly of chimaerids may also be derived from this initial condition. [It is imperative to note, the main points of this argument are to (1) establish that holostyly is not necessarily equivalent to autostyly and (2) to consider what is absolutely required in the earliest anatomical transitions if gnathostomes are to be derived from agnathans. This argument is not intended to specifically advocate the derivation of Chondrichthyes from Placoderms. A membranous or hydrostatically stabilized integument would serve the same purpose as a placoderm-type exoskeleton in this argument.]

As a second objection, if the precursor suspensorial condition for Chondrichthyes was holostylic it could not have been of the holocephalan form for the chimaerid hyoid arch is clearly modified. In Callorhynchus the efferent hyoidean artery lies medial to the tip of the pharyngohyal. This is in contrast to the efferents of the remaining arches

Figure 46 : Extrabranial / External Visceral Arch Architecture in Relation to "Jaw Cartilages" and Branchial Arches



From Parker and Haswell, (1963) A. Myxine embryonic skull B. Petromyzon adult skull and branchial basket. Br. 1: First Branchial Arch.; Ex. Br. 1: first extrabranial arch.; EX. Br.2: second extrabranial arch.; Ex. Hy. : Extrahyal Arch.; PQ: palatoquadrate, V. Br.: Ventral Branchial Bar.; Developmental Interpretation of Noted Petromyzon Features: Styloid Process believed to be extra-mandibular cartilage of gnathostomes, the cornual representing the mandibular cartilage. Note the arrangement of the nine visceral arch elements: the first (homologous with the extra-hyal) is immediately posterior to the styloid, the second lies immediately *in front* of the first gill cleft, and the remaining seven are located *behind* their respective gill clefts.

wherein each efferent artery is found lateral to its respective pharyngobranchial element (Watson 1937). This variation is attributed to holocephalan holostyly being secondary and, as such, it can not represent an original state.

My third objection to Stahl's analysis concerns the progression of suspensorial forms and how this relates to data on the soft anatomy. I question, on mechanical and physiological grounds, the plausibility of transition from chimaeroid holostyly to selachian hyostyly. The reverse transition or separate development of the conditions is more logical, unless the former condition were some other type of autostyly, eg autodiastyly. In either case, a shift from the fused or suspensorial form of autostyly to a hyomandibular based suspensorium would generate a milieu of new mechanical stresses, the ramifications of which would certainly affect the circulatory system. Elaborate changes in the arterial and venous system would have to arise in conjunction with true functioning jaws to accommodate the demands of an enhanced musculature and endoskeletal elements. (If the ancestral condition were indeed represented by a cooperative, exo- and endoskeletally sustained suspensorium then there must also be a concomitant reduction in exoskeletal elements originally participating in the "autostylic" suspensorium.) Therefore, vessel repositioning, proliferation, and expansion into sinus-type

reservoirs is likely to be favored by this transition.

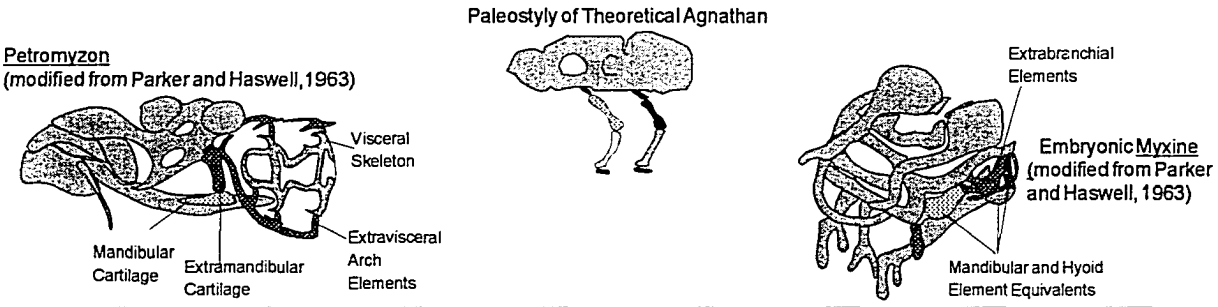
In this analytical approach one must consider what vessel (a) of a suitable agnathan or early gnathostome ancestor or (b) of the classical, unmodified arch is most likely to give rise to the hyoid sinus. Stahl did not address this in her analysis and, as such, this presents some difficulty when examining the evidence for variation in early vertebrate suspensorial design (Figure 47).

I have already offered a likely answer to my question regarding the unmodified arch vasculature; i.e. identifying vascular elements the hyoid sinus may develop from. The other criticism concerning the vasculature of a suitable ancestor is addressed in my phylogenetic interpretation of sinus development. This is one which considers the variation in early gnathostome and chondrichthyan suspensoria as well as the relationships of early Chondrichthyes.

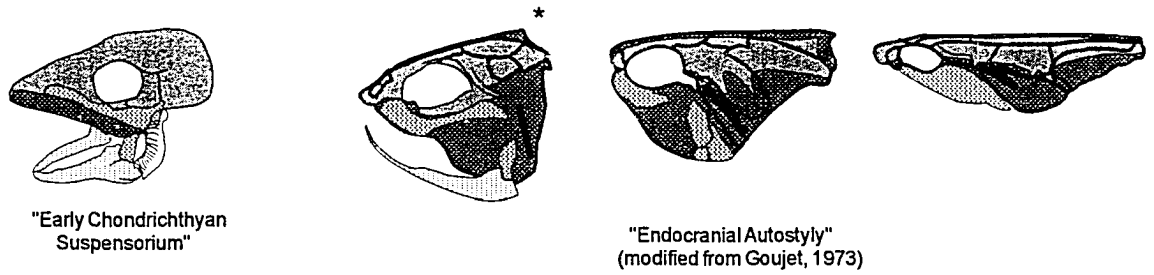
I propose sinus formation is linked to establishing distinct cranial and thoracic regions in the early gnathostomes; although elemental transformation of the branchial elements may have been initiated in early agnathans (akin to the arrangement of Petromyzon's exo- and endoskeletal "hyoid" elements; see Figure 46b). For example, using the armored fish analogy, separation of the placoderm armor into cranial and thoracic components via formation of a cranio-vertebral joint would influence both the jaw and hyoid structure and, consequently, the nature of

FIGURE 47: SUSPENSORIAL FORMS AND PROPOSED LEVELS OF ORGANIZATION

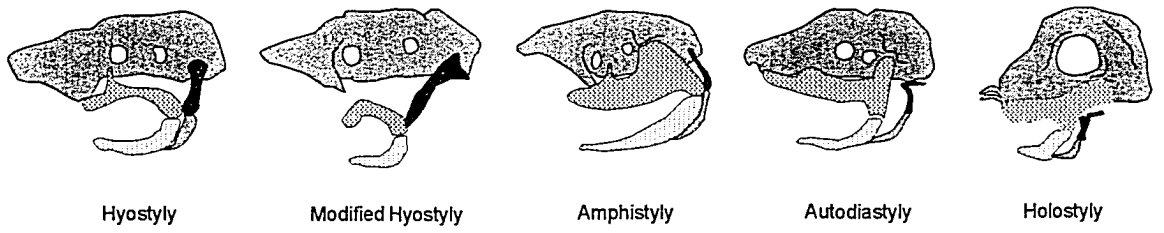
LEVEL 1
 Jawless condition
 Nine or more visceral arches
 Branchial skeleton composed of exoskeletal



LEVEL 2
 Specialization of arches into suspensorial and respiratory elements
 Exoskeletal Elements provide the supportive mechanism for true jaws
 Hyoid arch may or may not be modified. If so, the function may relate to either respiration or suspensorium (*Form in



LEVEL 3
 Various suspensorial forms
 Suspension with or without the involvement of the hyoid arch
 Articulating, Ligamentous Attachment, or Fusion of Palatoquadrate to



the hyoid arch vasculature. Remodeling of the original hyoid arch (particularly the epal segment) into a connecting element would be favored by the subdivision of an originally larger, complete head shield. In forms with a relatively short otico-occipital region the angular nature of the posterior margin of the head shield and the anterior margin of the thoracic shield would favor the forward displacement of the epihyal so that it can be propped between the hind margin of the jaws and the posterior end of the head (Figure 45a). Remodeling of this element may also be favored in those forms possessing a strong postorbital process against which the dorsal aspect of the epihyal may brace (Figure 45c; Figure 47, level 2). Direct connection(s) of the palatoquadrate with exoskeletal elements may be established to secure the upper jaw while also dissipating cranial stresses but need not accompany development of a suspensorial hyomandibula. As an alternative hypothesis for hyoid arch modification it is possible for both of the conditions just described to arise in tandem. Hyomandibular development may have transpired for a purpose other than maxillary suspension (eg as a part of the respiratory mechanism) while the suspensorial function was fulfilled by an exoskeleton-assisted or labial cartilage-sustained mode of autostyly. In either event, major stresses for structural modification would be placed on the hyoid region.

With increasing delineation and specialization of

cranial and thoracic regions the intervening space generated between the two regions would accommodate the acquired capacity for cranio-vertebral flexion while also providing the spatial impetus for sinus formation. The muscles necessary for carrying out the cranial flexure provide the physiological impetus for sinus development by virtue of their need for a blood supply. Furthermore, the action of this flexure may act as a vascular pump for a thin-walled sinus much like the relationship between the first dorsal fin and movable fin spine of Holocephali and the dorsal fin sinus. This hypothesis is in agreement with the common philosophy that a joint chondrichthyan ancestry is possible.

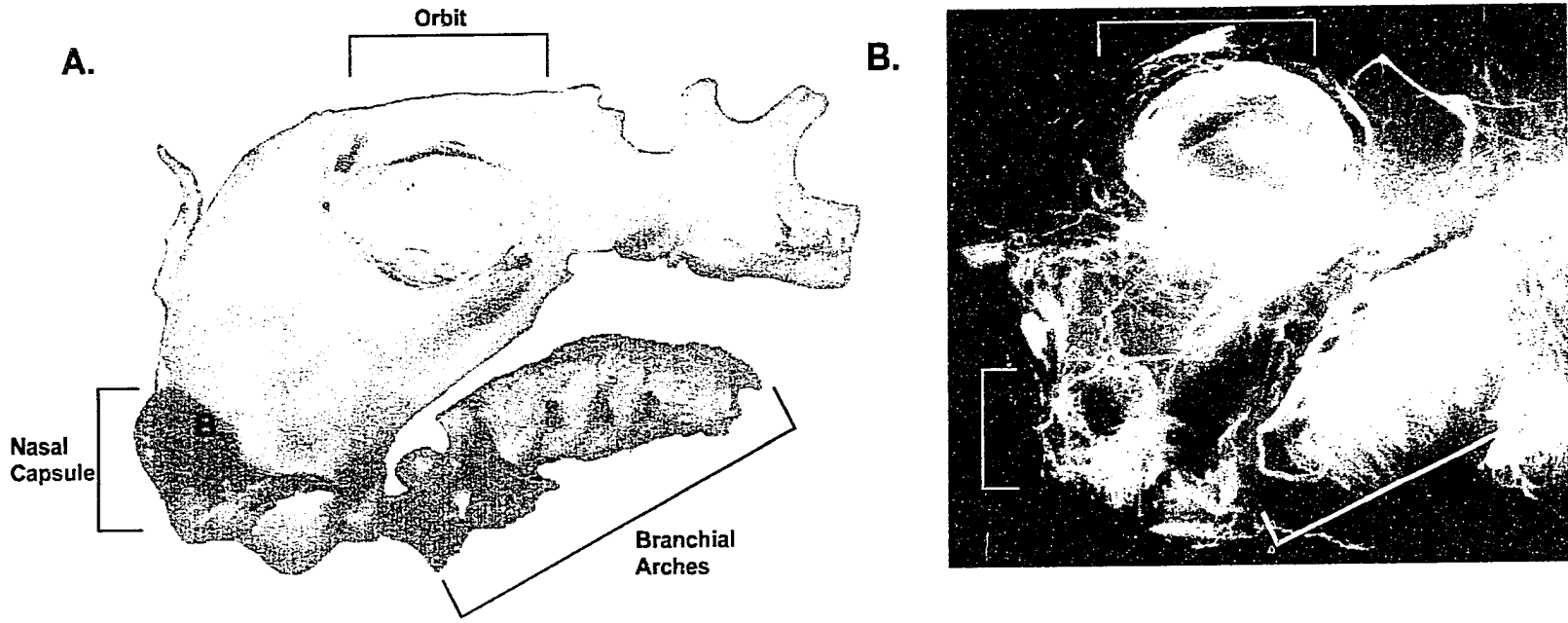
**The Contribution of Data from Extant Forms to the Origin and
Phylogenetic Status of a Hyoid Sinus**

As a separate approach to the question of a hyoid sinus a comparative examination of extant selachian and holocephalan vasculature was undertaken. The objective was to obtain information on the origin of the hyoid sinus through analyses of venous pathways, function, and the association of the sinus with other anatomical structures. The primary function of the shark hyoid sinus is drainage of the upper jaw (via mandibular symphysis/submental vein), the lower jaw (via the inferior jugular), the hyoidean hemibranch (directly via "nutritive hyoid vessels"), the four holobranchs (via the inferior jugular collection from

each holobranch's "nutritive branchial vessel") and to connect the jugular vein (i.e. lateral head vein) with the inferior jugular. In the holocephalan there is no appreciable span between the lower jaw and the subcranial branchial arches (Figure 48). So, as Stahl has correctly noted, there is no space for an equivalent sinus to form. There is, however, a major cranial vessel responsible for drainage of the lower jaw region, the anterior portion of the branchial basket, and muscles of the preorbital region (Figure 49). This vessel, the maxillofacial vein, is the largest tributary of the main venous space of the head (the orbital sinus) and is in close proximity to the other main tributary of the orbital sinus, the lateral head vein (i.e. postorbital or jugular). From this comparative examination of the holocephalan maxillofacial vein and similar drainages in the shark (Figure 43), I propose this chimaerid structure is, despite its more superficial placement, the equivalent of the selachian hyoid sinus on the basis that it assumes the same drainage functions.

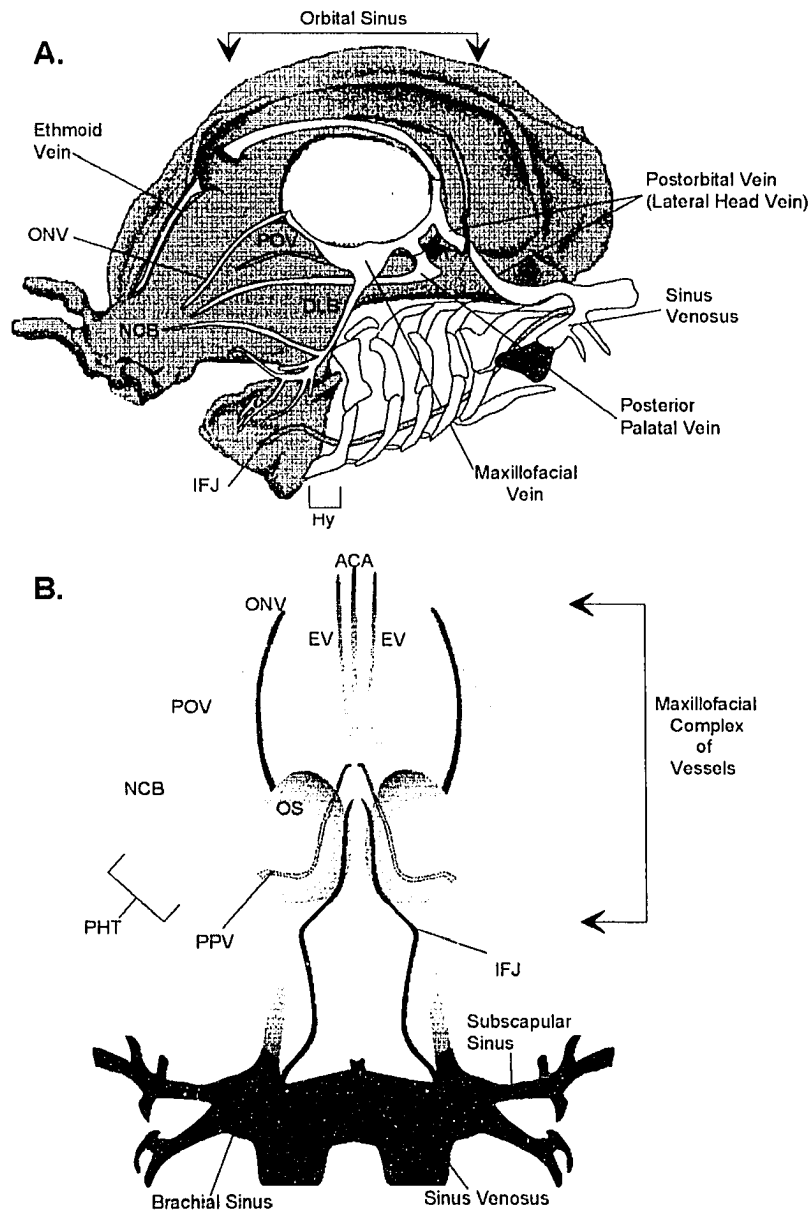
This proposition is, in general, consistent with the sole comparative description of the holocephalan venous system in the literature (Stahl 1967). A point by point comparison of select selachian and holocephalan vessels is presented here with reference to Stahl's work in order to evaluate this proposed homology. The postorbital vein is the holocephalan link between the orbital and anterior

Figure 48 : Holocephalan Cranium and Branchial Arches



A. Photograph of *Chimaera* sp. B. Radiograph of barium injected *Chimaera* sp. Regions labeled in A are also depicted in B.

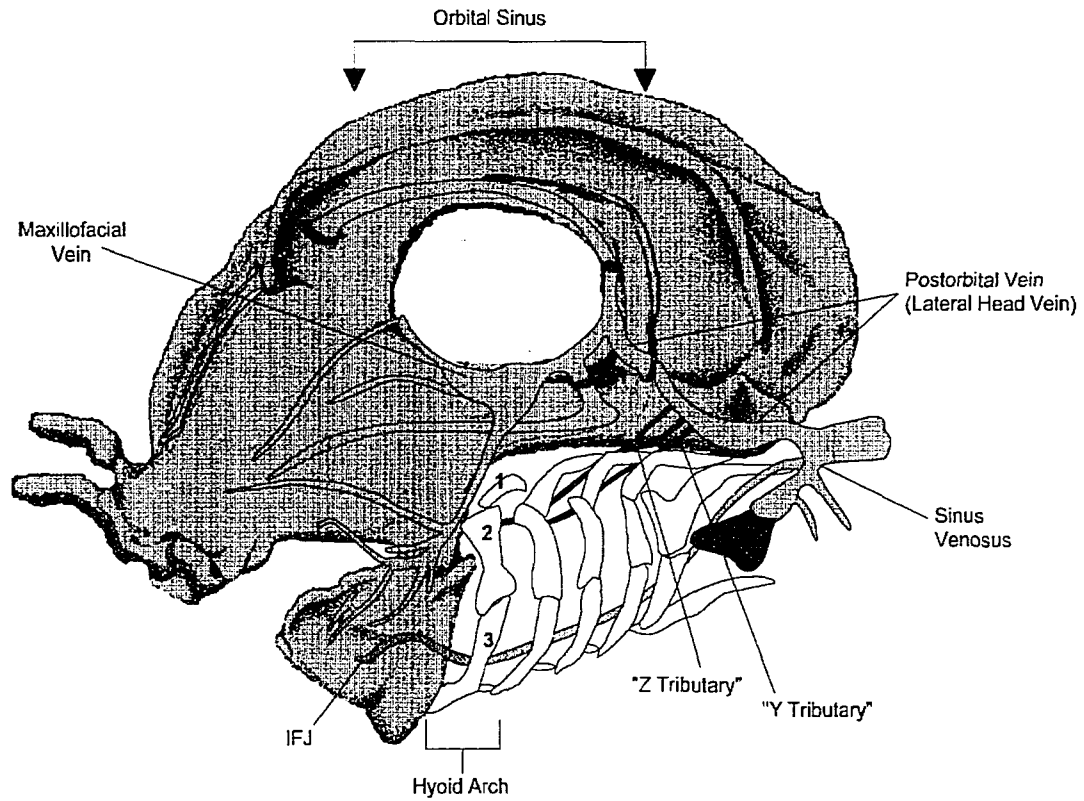
FIGURE 49 : The holocephalan maxillofacial, its tributaries, and proximal vasculature



A. Lateral View of *Callorhynchus* B. Dorsoventral View. (After Schauinsland, 1903; Stahl, 1967) Components of the maxillofacial complex; DLB: deep labial branch, NCB: nasal capsule branch, PHT: posterior tissue draining and probable hyoid tributaries, POV: Preorbital vein. Other features: ACA: anterior branch of the anterior cerebral vein, Hy: hyoid, first branchial arch, IFJ: Inferior jugulars. OS: orbital sinus. PPV: Posterior palatal Vein.

cardinal sinuses. It was noted on one occasion by Stahl, there may be postorbital vein drainage of gill septa nutrient veins, albeit via a common stem vessel. It is clearly evident these overall features of the postorbital drainage are reminiscent of the selachian jugular. Thus, acting on this similarity, Stahl searched for a possible connection between the postorbital and vessels of the chimaerid hyoid region; i.e. searching for an equivalent of the hyoid sinus. She found no evidence for a major vessel on either side of the ceratohyal but identified a "probable hyoid tributary" (Figure 50). This determination, i.e. labelling the vessel as hyoidean in nature, was made on the basis that this small vessel emanated from the dorsal ceratohyal region and drained into the postorbital vein. Stahl suspected both this "tributary" and the postorbital vein to connect with the suprapalatal tissue by a series of veins anastomosing within the tissue mass. This supposition was, tautologically, used to back up the interpretation of this vessel as a hyoidean tributary. My dissections offer no support for such observations nor the interpretations cited here. It seems Stahl, while emphasizing the distinction between the selachian and chimaerid hyoid architecture, was attempting to explain development of the uniquely holocephalan suprapalatal tissue as a consequence of a failure to develop a true hyoid sinus; that the "tributary" was somehow connected with the establishment of this tissue.

Figure 50 : Stahl's "Hyoid Tributary" in Relation to Other Cranial Vessels



"Y" and "Z" are those vessels described by Stahl (1967) as probable hyoid tributaries. The numbered elements represent the pharyngo-, epi-, and ceratohyal cartilages. In the selachian condition, the hyoid sinus is found just anterior to the cerato- element of the hoid arch. As described in the text, these vessels are more likely to represent the residuals of the jugular vein drainage for the dorsal branch of each nutrient branchial vein.

If the presence of this vessel is verified it is more likely to be a neomorph than having anything to do with the original hyoid vasculature. The position of confluence with the postorbital vein and forward placement of the arches indicate a corollary between these tributaries and features of the selachian-type vascular plan. These structures may be vestiges of the selachian plan link between the jugular and dorsal nutrient vessels of more posteriorly placed visceral arches.

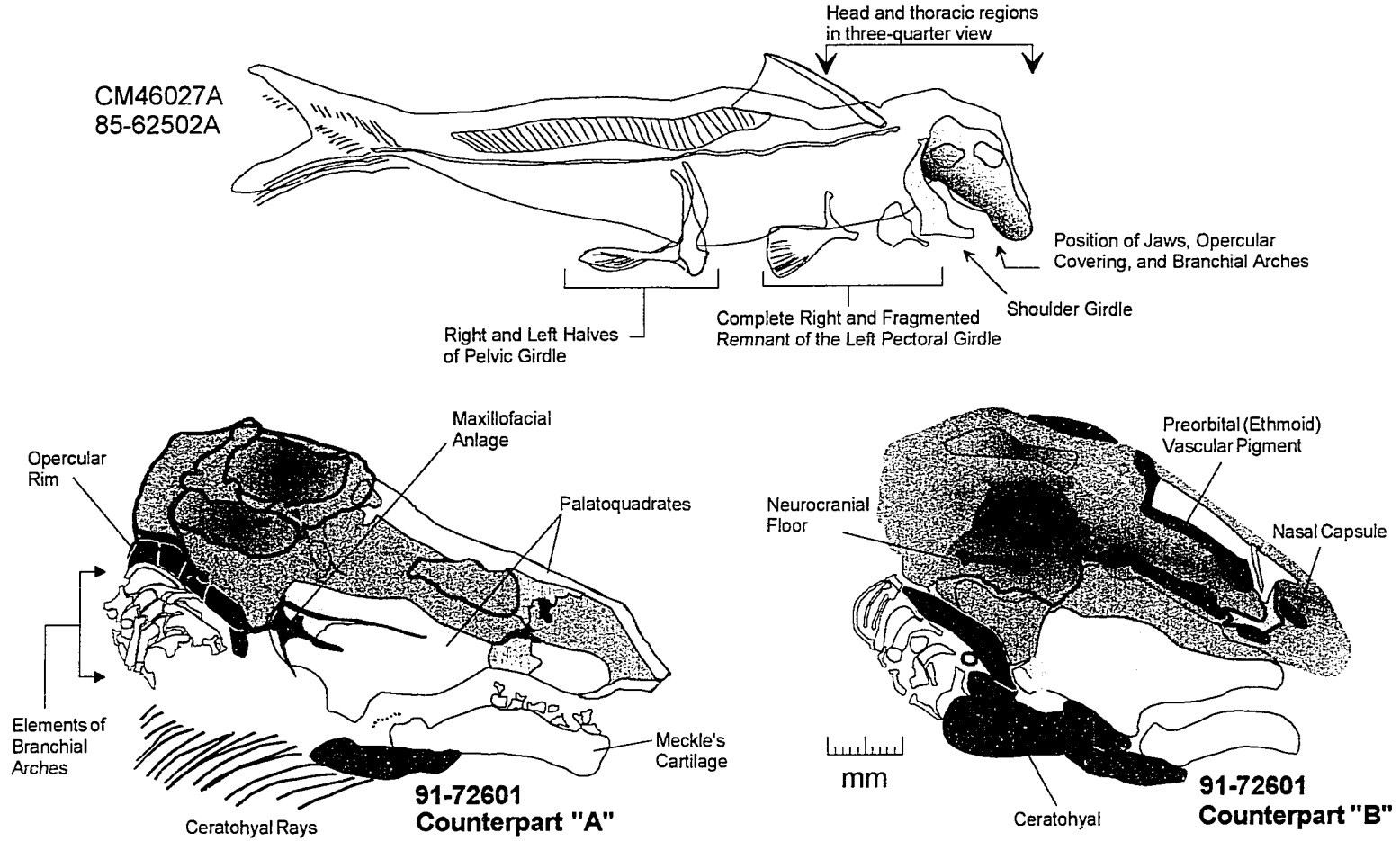
A second vessel which Stahl identifies as a "posterior palatal vein" is also professed to run forward from the dorsal aspect of the ceratohyal but this runs alongside the efferent pseudobranchial artery towards the ventral orbital cartilage. In its anterior position the posterior palatal vein is known to drain the suprapalatal tissue before piercing the suborbital cartilage and entering the orbital sinus. If one were to seek an analog of the selachian hyoidean sinus this vessel would serve as a "landmark" vessel on the basis of its pathway alone and drainage functions. This posterior palatal vein is most likely to be specialized for draining the, likewise novel, suprapalatal tissue and may represent the equivalent of the selachian buccopharyngeal vein. Given the close proximity of this vessel to the maxillofacial and similar relations of these vessels to the orbital sinus would lead one to propose an original association between these structures. Thus, if the

maxillofacial is, as previously argued, the vestige of the chondrichthyan hyoid sinus then the posterior palatal vein would represent the proximal buccopharyngeal vessel which is responsible for draining the dorsal symphyseal sinus. (As it has been used in this discussion, the nomenclatorial distinction between sinus and "major vessel" is strictly based on the size of the structure and is consistent with published descriptions of the structures.)

The Contribution of Data from Bear Gulch Chondrichthyes to the Origin and Phylogenetic Status of a Hyoid Sinus

If the Selachii are remotely or directly related to autostylic (autodiastylic and holostylic) chondrichthyans, one would also need to trace the vascular features of the latter groups for phylogenetic and developmental analyses. To this end, the specimens of Bear Gulch Selachii, Paraselachii, and Holocephali were examined for evidence of branchial and cranial vasculature. Vascular pigmentation was most abundant and clearly preserved in paraselachians, particularly Het2 which has been tentatively placed at the holocephalan end of a selachian:paraselachian: holocephalan morphocline. In this species, a large pigment mass is consistently preserved at the level of juncture between the posterior limit of the palatoquadrate, the anterior limit of the branchial basket and the lower anterior arc of the orbit (Figure 51). The main body of the vessel appears to be

FIGURE 51: HET 2 MORPHOLOGY

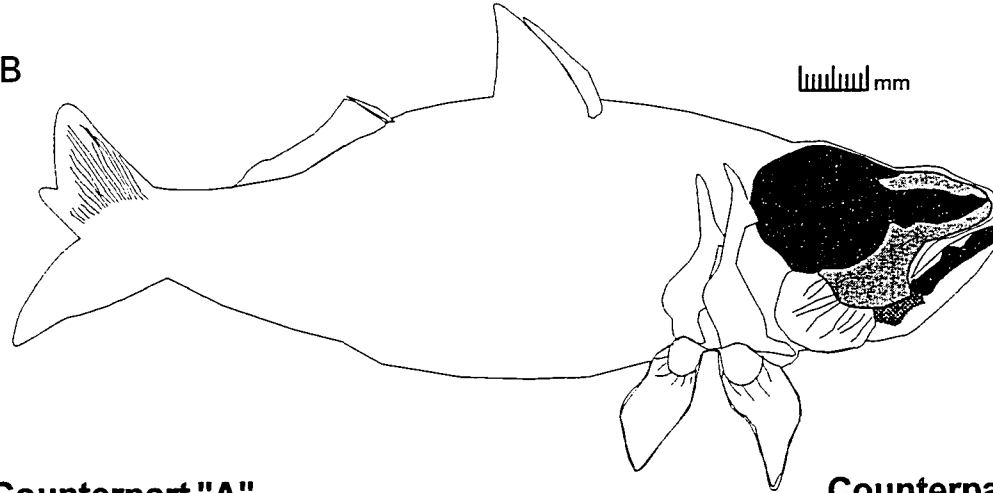


moderately deep at the level of the first branchial arch and the hind limit of the palatoquadrate. More superficial tributaries travel towards the rostrum, lower jaw and the extremities of the branchial basket. This arrangement is strikingly similar in placement and design to the holocephalan maxillofacial (Figure 49a) and, given Het2's proposed close affinity to Bear Gulch holocephalans, this data supports my interpretation of the nature of the hyoid sinus and maxillofacial vein.

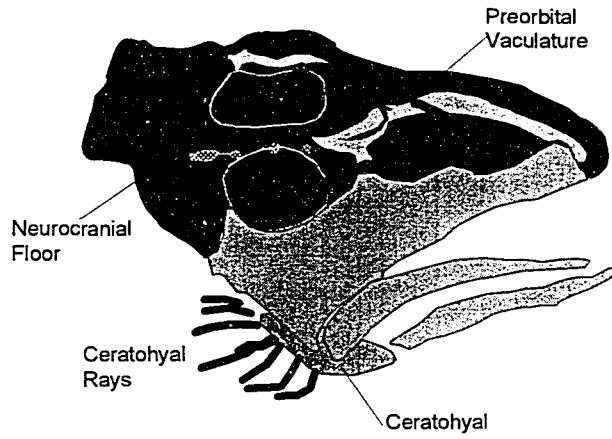
Sup1, which is at the selachian end of a selachian/paraselachian/holocephalan morphocline shows no overt evidence of a hyoid sinus or maxillofacial vein (Figure 52). The branchial arches are shunted forward but it is questionable to what degree nesting occurs for the arches. The relatively long autodiastyltic upper jaw, moderately sized otico-occipital region, and position of the shoulder girdle suggest no appreciable pressure for forward displacement of hyoid vasculature. The presence of the long ceratohyal rays and accompanying well developed vasculature may have something to do with (a) the lack of evidence for a hyoid sinus-type of vascular element or (b) the absence of the structure itself. The fact that this animal was autodiastyltic may have also influenced this condition but no definitive rationalization can be presented without knowledge of the respiratory mechanism used by these fish. If this fish possessed a "hyomandibular-type" element whose

FIGURE 52 : RECONSTRUCTION OF SUPERFISH 1 CRANIUM

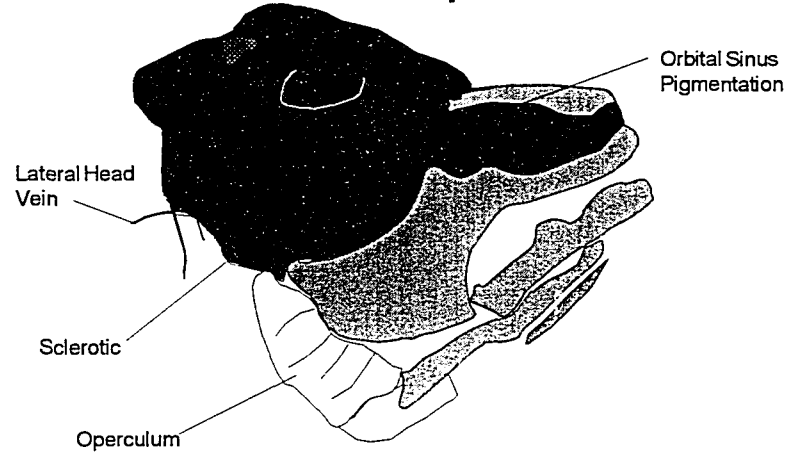
CM41036A&B
80-71209



Counterpart "A"



Counterpart "B"



main purpose was respiratory in nature and not suspensorial then the lack of evidence for a hyoid sinus in these individuals may represent a "trade off" or shift in vascular plans to accommodate the hyoid gill cover and extensive ceratobranchial rays.

**The Application of the Hyoid Sinus Analysis to
Chondrichthyan Phylogenetic Theory**

Certain phylogenetic conclusions can be drawn from this discussion of the hyoid sinus. Irrespective of what the original inducing mechanism was for sinus development (ie whether my cranio-thoracic demarcation theory is the mechanism or not) an organism with an unmodified hyoid arch (and concomitantly, an unmodified series of hyoid and branchial arch vessels) must represent the condition ancestral to a selachian-type suspensorium and hyoid sinus. The condition immediately antecedent to that of the selachian would involve remodeling of the hyoid arch for a suspensorial or related role but, if the purpose were suspensorial in nature, the hyoid element was not the sole agent in this endeavor (i.e. condition was not true selachian hyostyly). Once developed, the hyoid sinus is derived for the cervically-mobile gnathostomes and plesiomorphous within Chondrichthyes. The holocephalan maxillofacial is derived; being a homolog of the selachian hyoid sinus and maintaining all original drainage functions

of the latter structure with the exception of deep portions of the upper jaw or palate. (The holocephalan posterior palatal vein achieves this latter function.) Autodiastylid paraselachians exhibiting (1) a maxillofacial-type vascularization of the cranial and branchial regions, reminiscent of the extant holocephalan condition, and (2) an anteriorly shifted upper jaw would be more closely aligned with Holocephali than Selachii.

These data and observations have been compiled to generate an early chondrichthyan morphocline and to formulate a theory of transition which explains the apparent dichotomy in hyoid vasculature for Chondrichthyes. The hyoid sinus arose in the gnathostomes; most likely favored by pivotal conditions under which innovative suspensorial and respiratory specializations occurred. This vascular feature persisted or was more completely developed with the rise of the chondrichthyan form of hyostyly. In the transition from the selachian-type cranial and branchial element configuration to that of the paraselachian the dimensions and position of the selachian hyoid sinus were altered as the branchial basket is relocated anteriorly. The sinus is impinged upon as the gills are shifted forward and the hyomandibula is relieved of its suspensorial function.

From Paraselachii to Holocephali the changes in vasculature are further enhanced. The "modified hyoid

sinus" assumes a more superficial position to accommodate the reduced lower jaw and increased crowding of gill arches beneath the posterior cranial region. Furthermore, as this severe nesting of branchial arches proceeds, the otico-occipital region undergoes relative foreshortening and these structures come to lie in such close proximity to the shoulder girdle as to disrupt the original connection between the hyoid sinus and the lateral head vein. The lateral head vein now continues anteriorly to the orbit without direct communication to the novel hyoid sinus anlage. This anlage, as the sole superficial tributary, subsequently drains directly into the main cranial vascular space, the orbital sinus. The epal element of the hyoid arch, no longer functioning in a suspensorial mode, appears unmodified with respect to its cartilaginous elements due to regressive remodeling.

The Physiological Role of a Hyoid Sinus in Chondrichthyes

Before concluding this analysis one should consider why a sinus would develop at all, anywhere in the body of these fish. In order to address this it is important to realize that the venous system of extant Chondrichthyes is unusual within Vertebrata; and is assumedly plesiomorphous. There is no appreciable muscle layer(s) contributing to the vessel wall. Without this investiture the vessel must depend upon some other means for maintaining local pressure and movement

of blood. The same mechanical result may be attained by establishing a system wherein the vessels are not free but loosely to intimately associated with nearby, physically active, structures. As described by Satchell (1971) the elasmobranch sinuses "...are large blood spaces wherein the vein wall has disappeared except for the endothelium which spreads over the surface of adjacent organs. The pressure within these structures are determined by the movement of structure adjacent to it." Having closely examined the vascular elements of my specimens during dissection, it is clear this description also applies to chimaerids.

Pertaining to the impetus for sinus formation and its spatial designation, the immediate function needs to be defined for such a structure in order to answer where and why it forms. If the immediate function of a thin walled sinus is to act as a reservoir for the collection of blood at key points in the system, then it is logical, and consistent with the earlier physiological and mechanical arguments, to expect the development or localization of such a structure in a region characterized by some form of pumping action and for the sinus to be valved where it drains into a central vessel. I have concluded from observations made during dissections that all sinuses mentioned in relation to the hyoid question are dependent upon the motion of local structures for blood flow. As data in support of this "pumping mechanism" approach to my

analyses, I offer the following observations: the orbital sinus depends upon the actions of orbital muscles; the selachian mandibular symphyseal on the relative movements of the palatoquadrate and adjacent neurocranial sites; the holocephalan dorsal fin sinus on the dorsal fin and fin spine action. I surmise the selachian hyoid sinus must depend upon the respiratory actions of the branchial arches, the motion of the hyoid and mandibular arches, and contractile jaw muscle actions to pump the blood draining into this reservoir. The parallel in mechanics is clearly evident between this condition and that observed in chimaerids. The maxillofacial also seems to depend upon the muscular actions of the respiratory and suspensorial regions (i.e. the regions it drains) to set up a current or pumping mechanism to maintain a directed flow of blood. The only distinction between the former and latter conditions is that the maxillofacial pumping mechanism would be limited to the action of the massive facial muscles in holocephalans where no relative motion is possible between the upper jaw and neurocranium. Consequently, this analysis provides additional support for my propositions on the evolution of a hyoid sinus and homology between the selachian hyoid sinus and the holocephalan maxillofacial vein.

**The Origin, Nature, and Variation of Lymphomyeloid Tissues
Within Chondrichthyes**

This chapter focuses on the fourth point of divergence between Selachii and Holocephali addressed in this research; that is, the distinct arrangement of the hematopoietic tissues central to the chondrichthyan immune system. I have found the patterns of localization distinctive to the subclasses are correlated with the other points of divergence discussed earlier, namely, the features of suspensorium, cranial dimensions, and patterns of vascularization. Therefore, this discussion also recalls the paraselachian transition model to explain points of divergence (pertaining to the organization of the immune system in this case) while advocating a close relationship between the two groups.

A General Description of the Chondrichthyan Immune System

The basic description of the selachian immune system also applies to the chimaerid condition. Distinct erythropoietic red and lymphopoietic white pulp regions have been noted for the shark spleen while thymic tissue may be found in association with the gills. Although this tissue

is typically involuted with age in the elasmobranchs, "primitive" forms such as Heterodontus are said to possess this tissue throughout life (Fange, 1987). Primitive forms may also exhibit lymphomyelogenous renal tissue, but this condition is rare for the overall chondrichthyan grouping. All forms possess gut-associated lymphoidal tissue, best described as Peyer's patches lacking an enveloping sheath.

Concurrent to possessing a cartilaginous skeleton, both elasmobranchs and holocephalans lack bone marrow and distinct lymph nodes of the mammalian form. Thus the hematopoietic tissue of chondrichthyans is distinctly different from the mammalian form. In these vertebrates there is no regional separation of multi/pluripotential lymphoidal and myelogenous elements. Rather they exhibit lymphogranulopoietic tissues which are the chondrichthyan equivalent of bone marrow. In elasmobranchs, this tissue may envelop the gonads as an epigonal organ or invest the esophageal submucosa as Leydig's organ. That this tissue is essential to the immune system is reflected by the fact that any member of Elasmobranchii can be found to possess either or both of these organs; no member lacks both.

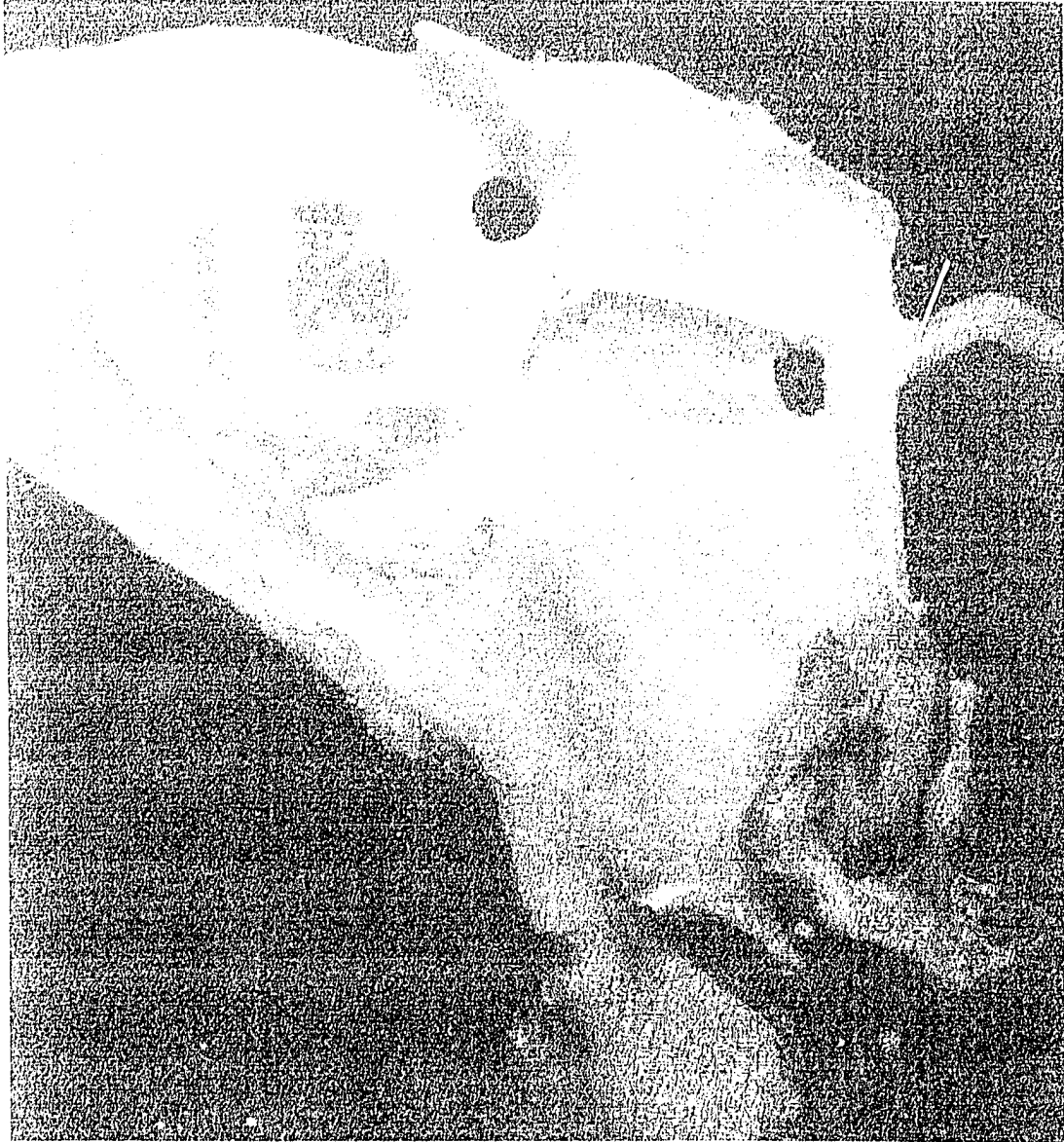
As previously stated, this general description of immunological organs or tissues may also be ascribed to the holocephalan condition. These fish, like the less derived sharks, possess a thymus through adulthood (Chimaera, Hydrolagus) and the spleen features, albeit less distinct,

red and white pulp compartments (Mattisson and Fange 1986, Fange 1987). Histologically, the cellular composition of these tissues is also consistent between the two groups. The thymus is populated by lymphocytes in various stages of differentiation, monocytic cells and morphs identified as reticuloendothelial cells. The splenic tissue is primarily comprised of granulocytic cells with minor populations of lymphocytes, monocytic/macrophage, and blast cells. However, the similarity ceases between immune systems of the two groups when one considers that holocephalans possess neither Leydig's nor an epigonal organ and they do not exhibit, as the less derived sharks do, any immunologic tissue in their renal zone (Stanley, 1963). Rather, Chimaeriformes uniquely exhibit lymphomyeloid tissues within the chondrocranial ethmoid canal, the pectoral girdle and along the anterior and ventral orbital margins (Stahl 1967, Mattisson and Fange 1986). By virtue of their localization within or in association with cartilaginous cavities these tissues are often referred to as white marrow.

My dissections of Rhinochimaera, Hariotta, Chimaera, and Callorhynchus support what has been described above as the distribution pattern for these tissues and supplement Stahl's description of the orbital mass such that, not just the margins, but the entire orbital sinus is invested with lymphogranular tissue. Furthermore, interfamilial variation was noted in the mass of orbital, ethmoidal and suprapalatal

lymphomyeloid tissues and this appears to correlate with divergence in features of the rostral-ethmoidal and interorbital regions. Irrespective of the age of the specimen, the volume of each of these tissues was greatest in Chimaeridae and lowest in Callorhynchidae, with Rhinochimaeridae being intermediate. In fact, the ethmoidal tissue in Callorhynchus was limited to that portion of the ethmoid canal immediately anterior to the orbit while the greatest proportion of the suprapalatal mass was restricted to the hind margin of the tooth plates where a space can be found between the dentition and telencephalic floor. These conditions are clearly the result of the specialization, in relatively derived species, of the ethmoid canal to harbor lymphomyeloid tissue. This specialization is reflected in the increased diameter and shortened length of the canal in Chimaera (Figure 53) compared to the long, narrow and anteriorly divided space of Callorhynchus' canal. Upon comparison of the cranial anatomy of specimens from each family, it appears that the only feature which may correspond to variation in the mass of the suprapalatal tissue is the length of the preorbital region. In Callorhynchus, where the preorbital length is greatest, the triangular shaped suprapalatal mass is thin and concentrated anteriorly at the posterior limit of the tooth plates and within a concavity created on either side of a median ridge. From this point posteriorly the lateral margins of the mass

Figure 53 : The Ethmoid Canal of Chimaera sp.



The lateral wall of the canal has been dissected from the right side to demonstrate the great expanse of the canal in the more derived Chimaeriformes.

are delimited on the opposite side of the cranial cartilage by the orbits (Figure 54). In contrast Chimaera, which exhibits a reduced or anteroposteriorly compressed preorbital span, a comparative thickening of the suprapalatal mass is evident. Since the ethmoidal and suprapalatal tissues are continuous with that of the orbit (via foramina for the superficial ophthalmic nerve and posterior suprapalatal vein) it is not surprising to find the orbital mass of Chimaera significantly exceeds that found in Callorhynchus.

My comparative selachian and holocephalan dissections also offer a refinement of the positional description of the Chondrichthyan thymus. Stahl (1967) has referred to this tissue as situated in the roof of the pharynx, posterior to the suprapalatal lymphogranulopoietic mass. My dissections have revealed this tissue is located in a position which is identical for both selachians and holocephalans; i.e. dorsal to the first three branchial arches. In sharks this is superficially evident between the cucullaris muscle and dorsal constrictor muscles of the branchial arches. In chimaerids, this is compressed between the pharyngobranchials and the pharyngeal lining and therefore upon first glance appears to be in a position distinct from the selachian equivalent. Yet, as mentioned earlier if a positional description is given with regard to the branchial arches, it maintains the same position as the selachian

Figure 54 : The Suprapalatal Region of Callorhynchus and Chimaera



B. Chimaera

Area where principal mass
of the suprapalatal tissue
is found



A. Callorhynchus

thymus. Therefore, it is due to the relocation of the branchial basket under the holocephalan cranium that the thymus is not found posterior to the cranium as in selachians.

Collectively then, the primary immunologic tissues of chondrichthyans are consistent in both position and in cellular composition. In contrast, however, there is a distinct pattern of distribution for the hematopoietic tissues for selachians and holocephalans. What of the cellular makeup of these masses? Are they similar in their morphologic and immunologic nature as well as their spatial character? My histological survey of the selachian epigonal and chimaerid cranial "white marrow" tissues indicate that the cellular composition of chondrichthyan lymphomyeloid tissue is generally consistent. The cells are predominately those of the granulocytic series (eosinophilic and heterophilic) although small lymphocytes, monocytic, blast and occasional nucleated red blood cells are also present. Therefore, aside from the positional distinction the greatest variation between selachian and holocephalan lymphomyeloid tissue concerns the types of granulocytes found within the masses and the enzymatic staining character of these cells relative to their degree of maturation (Mattisson et al. 1990, Hine and Wain 1987, 1988). Yet, as the latter researchers have found, this is not a variability which is limited to the two sistergroups for there is ample

evidence that this phenomenon is widespread among genera and species of the same Class.

These observations have been interpreted to suggest that if the divergence between selachian and holocephalan immunologic tissues distribution is to be explained while also advocating a sistergroup relationship then the vascular plan is the most likely determinant effecting the different tissue localizations. I have sought an answer to the question of analogy versus homology in the circulatory plan because neither of these groups exhibit a lymphatic circulation typical of bony vertebrates. The only other means of establishing a body-wide distribution of stem and pluri- or multipotential cells is through the vascular system; a conclusion which is supported by my analyses of elasmobranch peripheral blood cell morphology, histochemistry, and select reactivity analyses (Grogan and Lund 1990, 1991).

To determine if the circulation is the crucial element permitting this body wide distribution, I conducted a comparative analysis of the venous circulatory plan of holocephalans and selachians and superimposed these on similar comparative plans of immunologic tissue. The results of this study strongly endorse the notion that a common pattern of immunologic tissue distribution exists for Chondrichthyes and this suggests the divergence between selachian and holocephalan plans is minimal. Furthermore,

the basic patterning of tissue distribution is determined by the organization of venous pathways, and the specialization of the major chondrichthyan blood sinuses (gonadal, orbital, brachial, or renal) to support those hematopoietic cords responsible for producing and infusing the various regions of the body with immunocytes.

The Chondrichthyan Venous Circulation Relative to Immunologic Tissues

Figure 55 presents the major features of the selachian superficial and deep venous circulation. Figures 56 and 57 show the distribution of chondrichthyan immunologic tissues relative to the selachian and chimaeroid venous circulation. In the selachian condition the precaval sinus, gonadal sinus, and the vena profunda arising from the first dorsal fin sinus are correlated with Leydig, epigonal and nephrogenic lymphohematopoietic zones respectively. The inner wall of the precaval sinus is closely applied to the esophagus (Parker, 1886) and is believed to give off a network of tributaries to the cardiac region of the esophagus where Leydig's organ may be found. The gonadal sinus forms an extensive network of nutritive capillaries as this structure completely envelops the reproductive tract. These venules are proposed to be responsible for establishing the extensive infiltrating mass of lymphogranulopoietic tissue. As noted in the description of

Figure 55 : Superficial and Deep Venous Circulation of Selachii

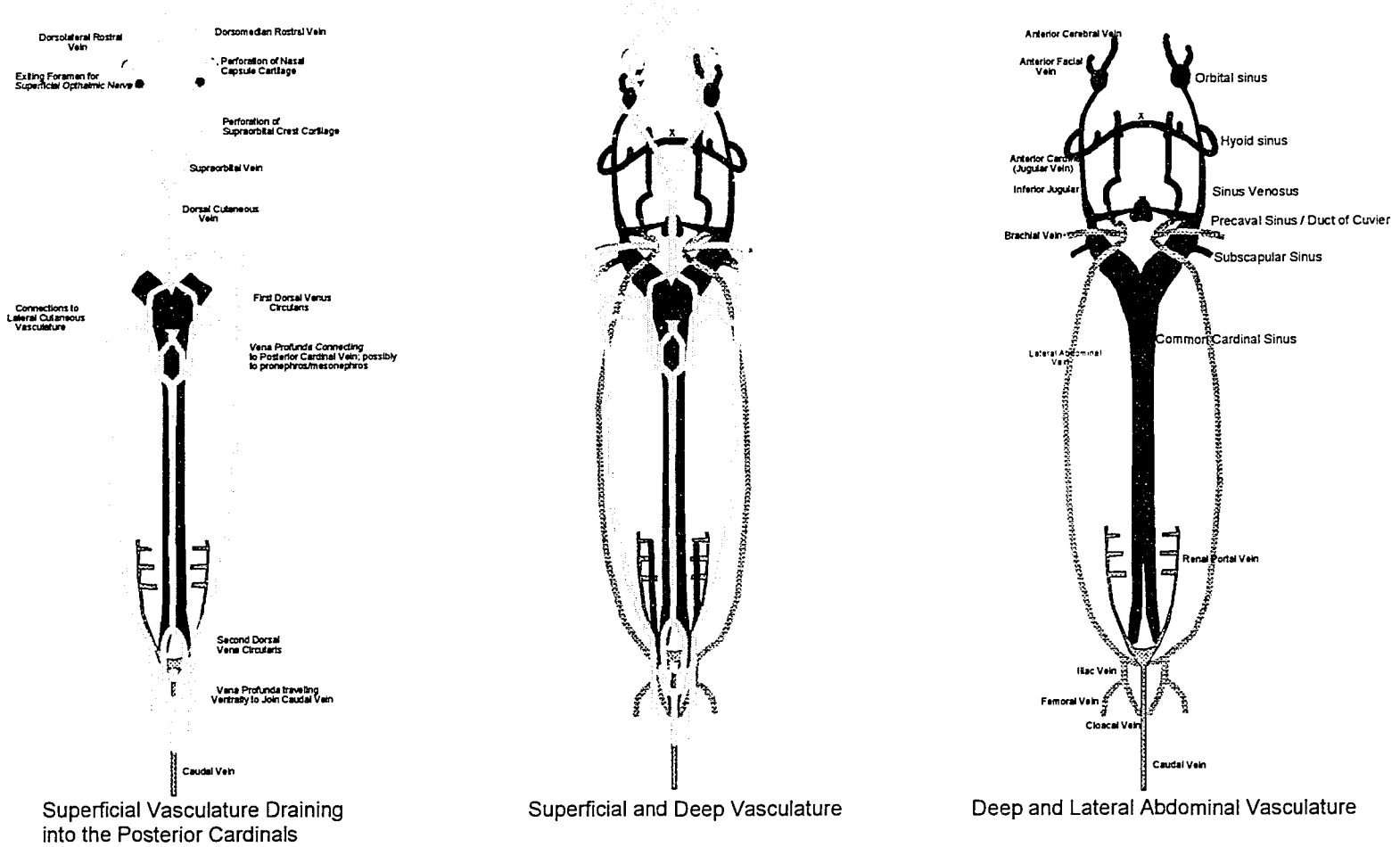
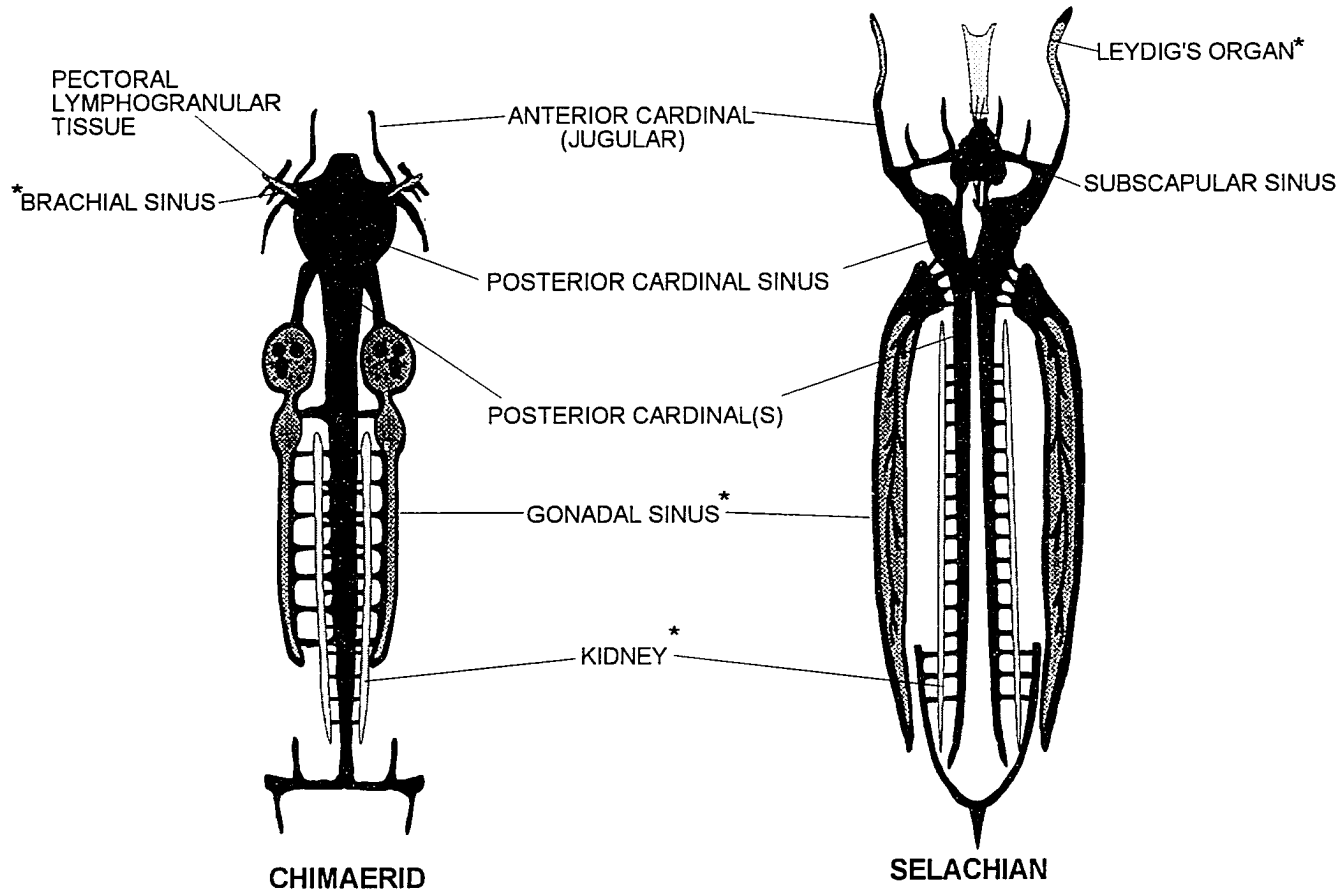
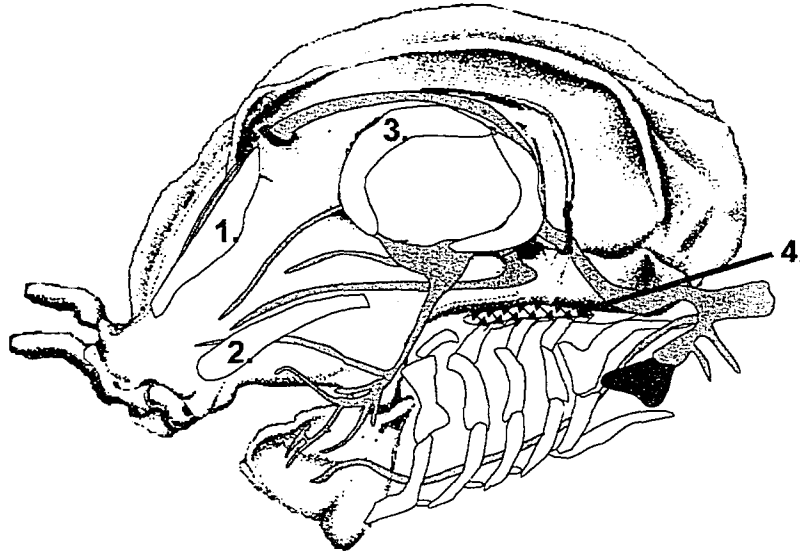
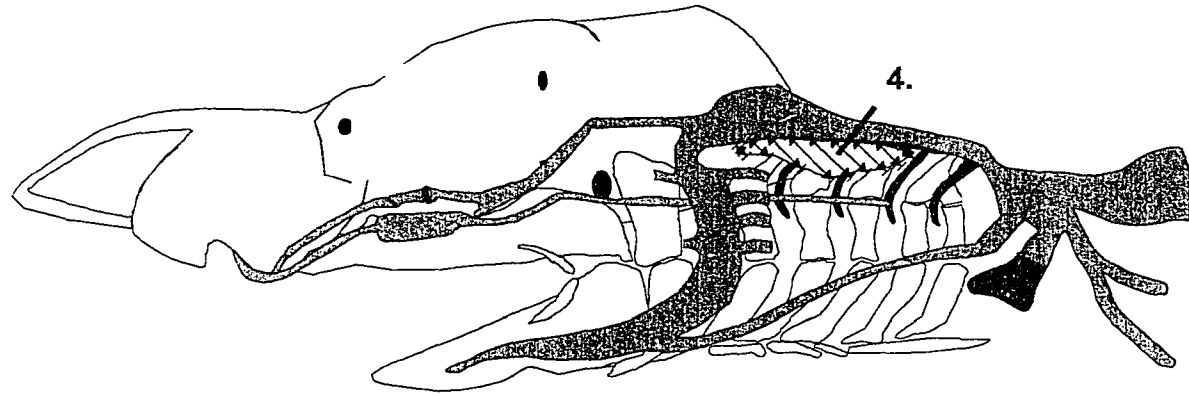


Figure 56 : Comparative Cardiac and Postcardiac Venous Circulation of Chimaerids and Selachians



Note: The hepatic sinus is omitted for each drawing and neither diagram is intended to reflect the actual dimensions of the circulatory system. Labels with an asterisk indicate the venous elements associated with lymphohematopoietic tissues.

Figure 57 : A Comparative Distribution of Precardiac Venous Vasculature and Associated Immunologic Tissues



- 1: Ethmoidal Tissue
- 2: Suprapalatal Tissue
- 3: Orbital Tissue
- 4: Thymus

selachian immunologic tissues, the rarest tissue is that associated with the kidney. Therefore, it is not surprising to note that the pathway taken by the vena profunda, as it courses ventrally from the first dorsal fin sinus, is highly variable among selachii. I propose that those selachians which possess renal hemopoietic tissue are most likely to exhibit the type of vascular pattern exemplified by Mustelus (Daniel and Stoker, 1927; Daniel and Bennett, 1931). In this selachian the vena profunda sends off tributaries and subbranching venules to the pro- or mesonephros before the main branch joins the renal portal vein. Since the abdominal viscera of holocephalans is comparatively less developed it is not surprising to find an absence of lymphogranulopoietic tissues in this region. Rather, the only postcardinal evidence of such tissue in the chimaerids is in the pectoral girdle, a region supplied by a brachial sinus which is more complex in terms of its branching pattern than the corresponding subscapular sinus of selachians. The strictly lymphoidal thymic mass of both Selachii and Holocephali appears to be associated with the jugular (postorbital) vein and its collecting venules which extend from the dorsal aspect of the gill arches. The remaining holocephalan lymphomyeloid tissues; ethmoidal, orbital, and suprapalatal, are found within cartilaginous enclosures and intimately associated with the ethmoid veins, orbital sinus, and posterior palatal vein respectively. The maxillofacial vein

is proposed to drain the suprapalatal and orbital tissues (Stahl, 1967; Fange and Sundell, 1969). I have found no evidence of this in my dissections, however, nor do the radiographs taken of barium injected specimens indicate such a relationship to these tissues. Rather, my observations suggest the posterior palatal and postorbital veins drain the orbital and suprapalatal tissues and the ethmoidal mass is principally a forward extension of the orbital aggregation.

**The Venous Vascular Plan as the Determinant for Localization
of Lymphopoietic Tissues**

My analysis of the origin of lymphohematopoietic tissues and spatial divergence of these masses within the sistergroups is based on the stipulation that the plesiomorphous vascularization plan must be of the selachian form. This determination is based on assessing the selachian as the more primitive condition according to a classification consistent with the embryogenic phases of vertebrate hemopoiesis. That is, the selachian mode of hemopoiesis is viewed as intermediate between the hepatic and myeloid phases. The holocephalic condition of "white marrow" would correlate with more of a myeloid phase with the exception that endochondral ossification does not occur and, like the selachians, hemopoiesis remains intravascular. Since all chondrichthyan hemopoiesis is intravascular in

contrast to mammalian extravascular hematopoiesis it is clear that, irrespective of the bony or cartilaginous endoskeletal environment, the nature of chimaerid "white marrow" is not equivalent to the bone marrow. Thus, it is unlikely that this feature of the Holocephali is a vestige of a hematopoietic organ restricted to this Class of chondrichthyans (Stahl, 1967) nor is it the phylogenetic anlage of bone marrow.

Having established (a) the histological equivalence of all forms of chondrichthyan lymphopoietic tissues and (b) the distinction between chondrichthyan "white" and mammalian bone (red) marrow in terms of its nature of promoting cell development and the evolutionary lineage, one must now consider how the divergence in chondrichthyan immune system organization may have arisen. In examining the distribution of chimaerid lymphomyeloid tissues relative to the endoskeleton I was struck by the observation that all "white marrow" is found in or associated with those cartilages which embody endoskeletal divergence between the sistergroups. From this, I surmised that a phylogenetic model which would account for the development of the cranial lymphomyeloid tissues must require (i) transition from a suspensorial to fused association between the upper jaw and neurocranial cartilages (ii) and remodeling of the original preorbital cartilages so they may, subsequently, come to be associated with lymphomyeloid tissues of the holocephalan

head. It is no coincidence that these requirements are the same tenets behind a selachian/paraselachian/holocephalan morphocline.

In the simplest application of this theory, one may begin to understand how a holocephalan suprapalatal lymphomyeloid tissue may develop if one were to envision the effect of a transition from an autodiastylitic to holostylitic state, as described in chapters two and three. The acquisition of fusion sites rather than palatoquadrate/neurocranial articulations which result in the nearly complete unification of relevant cartilages would provide the type of encasement identified for the chimaeroid suprapalatal tissue mass. Similar remodeling of the rostroethmoidal cartilages which accompany the increased jaw/neurocranial association and development of an ethmoid canal would provide the space in which an ethmoidal mass may form. It is apparent, therefore, that the validity of such a theory would depend upon the vascular data and how a selachian-type plan is affected by endocranial remodeling. Thus, in its design this model also requires the caveat that venous structures in close proximity to or traversing the preorbital and pharyngeal regions become isolated and eventually enclosed by the neurocranial and/or palatoquadrate cartilages under the remodeling exemplified in the paraselachian/chondrichthyan transformation. In reconstructing such a transition I am forced to rely upon

the vascular data available from extant forms. Yet, this should not be considered as a weak point in this paradigm for, as has been indicated in earlier chapters, there is sufficient data in the Bear Gulch fossil record to argue the general features of selachian and holocephalan circulation have been conserved over time.

Comparing the cranial vascularization plans in Figure 57 it is obvious that the selachian dorsal symphyseal sinus, located below the orbit and dorsal to the anterior symphysis, corresponds to the position occupied by the holocephalan suprapalatal tissue. Thus, in accordance with the transition paradigm, the symphyseal sinus would be enclosed between the neurocranium and upper jaw as the autodiastyletic cartilages progress towards the holostyletic arrangement. This sinus would subsequently provide the basis for establishing a suprapalatal tissue.

In order to assess all ramifications of the rostro-orbital cartilage remodeling accompanying jaw/neurocranial fusion, the superficial as well as deep cranial vasculature of sharks needs to be considered. The vessels which are relevant to the paraselachian/chondrichthyan transition and chimaeroid tissue formation are detailed in Figure 55. With the dorsomedial compression of the orbits, anterior displacement of supraorbital crest cartilage, and extensive growth and realignment of lamina orbitonasalis the selachian supraorbital vein and its anterior connections would be

forced into a chimaeroid structural plan.

In its original state, the superficial supraorbital vein would proceed forward of the orbit via medial and dorsolateral rostral tributaries. After having pierced the nasal capsule cartilage the dorsolateral tributary would give rise to the nasomaxillary, connecting with the dorsal symphysial sinus. However, shifting cranial dimensions which accompany the transition would force the supraorbital to drain directly into the orbital sinus; any connections to anterior tributaries would be severed. Consequently, the dorsolateral rostral vein would establish an independent connection to the orbital sinus if it is to be preserved. In this latter case, it may be initially retained as dorsolateral preorbital and, in subsequent stages of the morphocline, as parallel, medial ethmoid veins. The nasomaxillary ventral connection would either be lost with the shifting of nasal capsule cartilages, or incorporated into the suprapalatal plexus as the lamina orbitonasalis develops posteriorly and laterally. The orbitonasal/facial vein, originally connecting anteriorly to the origin of the nasomaxillary before continuing to the nasal capsule and posteriorly to the orbital sinus, is not disturbed by shifts in the ventral and medial aspects of the lamina orbitonasalis. Therefore, this vessel is left, more or less undisturbed, and is represented by the orbitonasal vein in chimaeroids. If the orbitonasal vein does provide anterior

drainage of the suprapalatal tissue then it does so as a vestige of the original connection between the nasomaxillary and the selachian orbitonasal vein.

The holocephalan posterior palatal vein is responsible for draining the posteriormost region of the suprapalatal tissue. The corresponding vascular element(s) of the shark system would be the posterior continuation of the symphyseal sinus, the buccopharyngeal veins. By comparison, it would appear that the buccopharyngeal veins represent the plesiomorphous condition of those vascular elements which are responsible for suprapalatal tissue drainage. Thus, all vessels found in association with holocephalan "white marrow" have been accounted for in the transition paradigm by comparison with the (assumedly plesiomorphic) selachian plan.

In a critique of this theory, one may ask, even if these conditions are met why would these changes be accompanied by a shift in the localization of hematopoietic tissues? I have reasoned that the fundamental principals governing formation of lymphoidal aggregates at one site versus another are most likely to be regulated by those variables of temperature, space, and the essence of the stromal microenvironment. These have been identified as the critical variables based on general knowledge of the developmental and regulatory phenomena governed by (a) the three dimensional architecture and composition of

hematopoietic stroma (Fawcett, 1986; Fliedner et al. 1985), (b) yellow and red marrow reversal dynamics, and (c) that feature of chondrichthyan blood tissues which permits extramedullary hematopoiesis as a rule; intravascular immunocyte development (Tavassoli, 1986; Grogan and Lund, 1990, 1991). Any remodeling of cranial cartilages would satisfy the first two requirements; space, as described by the fusions or reassociation of cartilages and temperature, by virtue of the heat exchange vascular plexuses concentrated in the cranial and cardiac/branchial regions. The third stipulation, however, is a trait which need not be achieved within the transition but represents the distinctive essence of the chondrichthyan condition. The intravascular fating of immunocytes is that feature of the chondrichthyan immune system which makes the vascular plan the link required for understanding lymphohematopoietic tissue distribution. These tissues develop within the constraints of the vascular system in contrast to the mammalian or teleostean conditions where the lymphatic and circulatory systems are distinct.

Ultimately, the major venous structures which directly infuse or traverse the rostro-orbital and pharyngeal regions provide the optimal environment for reticuloendothelial specialization essential to formation of an immunologic tissue mass. The establishment of lymphomyeloid aggregates is thereby promoted as the venous structures become

relatively privileged sites through stromal cell expression of the homing protein receptor necessary for selective localization of hematopoietic progenitor cells (Hardy and Minguell, 1993) and the enclosure of the vessels within protective cartilages. Phylogenetically, the transition in immunologic tissue distribution would have to proceed from that typified by a selachian vascularization plan to the more derived holocephalan plan which involves cartilage contained tissues.

In terms of the sistergroup relationship, it is also critical to consider if cavities were to develop within the selachian endoskeleton would "white marrow" form? To answer this, I refer to a note made by Holmgren (1942) wherein he reported the presence of lymphomyeloid tissue in the wide carotid foramen which pierces the subotic cartilage of Sphyrna. This appears to be the only account of selachian lymphomyeloid tissue being found at a site other than the major blood sinuses supplying reproductive, digestive or renal tissue. Thus, it appears as though both elasmobranchs and holocephalans have the capacity to form lymphomyelogenous aggregates within cartilaginous inclusions, but, it is the latter group which is commonly associated with this phenomenon. This, in turn, has been predicated on the greater propensity of holocephalans to develop cavities within or between those cranial cartilages subject to remodeling over the evolution of the lineage.

In conclusion the vascularization plan has been identified as the main determinant for the placement and cellular composition of chondrichthyan immunologic tissues. It is due to shifts in the endoskeletal anatomy which concomitantly or secondarily induce the development of alternative pathways of vascularization between Selachii and Holocephali. Thus a consequence of endoskeletal remodeling is a relocalization of vascular elements. It is this remodeling which underlies any organizational divergence in the immune system of chondrichthyan sistergroups even though both selachians and holocephalans possess the ability to develop "white marrow". Table 4 presents a summary of the cranial selachian vessels equivalent to the holocephalan elements found in association with "white marrow".

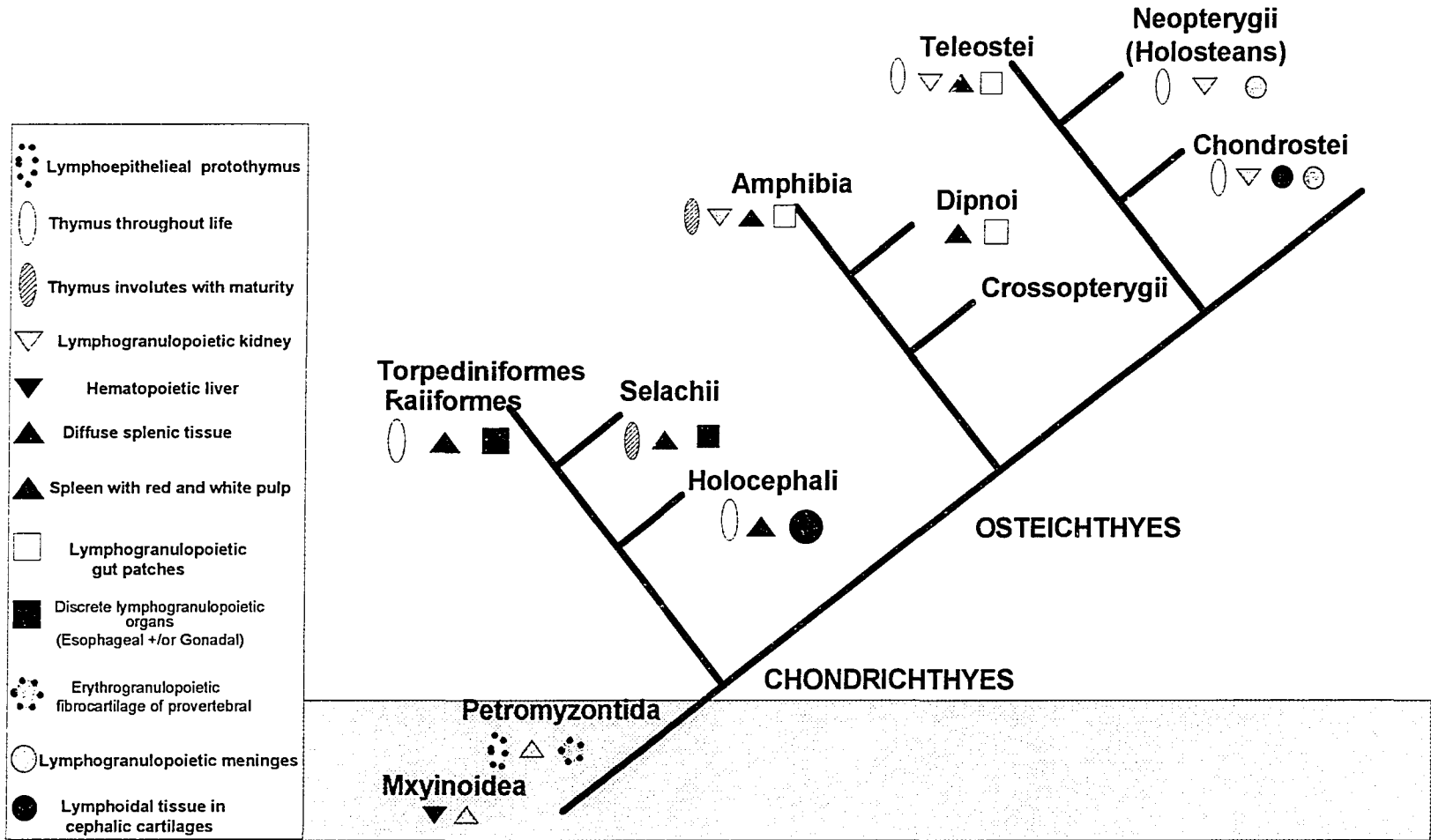
Table 4: Equivalent Cranial Vessels of Chondrichthyes

Selachians	Holocephalan
jugular (lateral head) vein	postorbital vein
supraorbital vein (superficial vasculature)	dorsal cephalic vein (superficial vasculature)
dorsolateral rostral vein	ethmoid (preorbital) vein
nasomaxillary vein	none
orbitonasal vein	orbitonasal vein
dorsal symphysial sinus	anastomosing venules of the suprapalatal tissue
buccopharyngeal veins	posterior palatal vein

How Does This Paradigm Fit into the Evolutionary Scheme of Immune System Development Within all Vertebrate Classes?

The type, combination, and distribution of chondrichthyan immunologic tissues fits a paradigm for the evolution of vertebrate immune systems and immunologic capacity (Figure 58). Within this model I have identified Selachii and Holocephali as representing the prelymphatic state, a condition which is necessary if all vertebrate immune systems are to be developed from a common plan. My analyses on the progressive staging in vertebrate immune system development are supported by data generated at the cellular level. For example, I have argued that the chondrichthyan condition is primitive within Vertebrata to the degree that it is characterized by an intravascular versus extravascular hematopoiesis. Based on this condition I have suggested it is best to describe chondrichthyan hematopoiesis as intermediate between the hepatic and myeloid stages of mammalian prenatal hematopoiesis. Aside from my current and previous research, is there any study which supports this interpretation? The answer is yes. Firstly, McKinney (1992) has compiled the results of her leukocyte characterization studies and those transplantation, mitogenic, and morphological analyses of earlier workers to present a description of the elasmobranch

Figure 58 : An Evolutionary Analysis of Vertebrate Immune Tissue Types



immune system which explains the immunologic capacity of the group in view of ontological shifts in the mammalian immune system. By analogy, the selachian immunocytes were labelled as embryonic-type cells (gamma delta T-cell receptor bearing T lymphocytes and neonatal and newborn primary B cells). This description follows what I have identified as the stage of immune system development attained by Chondrichthyes in my evolutionary model. Moreover the combined ultrastructural and cytochemical characterization of holocephalan leukocytes also supports my phylogenetic hierarchy of comparative immunologic capacity (Hine and Wain 1988, Mattisson et al. 1990). It has been concluded, "holocephalan enzyme cytochemistry more closely resembles agnathan than elasmobranch enzyme cytochemistry" while "in granulocyte ultrastructure and lymphocyte alkaline phosphatase, the dogfishes (Squaliformes) more closely resemble holocephalans than any other elasmobranch groups" (Hine and Wain, 1988). Mattisson et al. agree with this and specify Chimaera heterophils are to be histologically correlated with squaliform neutrophils; Hydrolagus' heterophils being viewed as "modified" heterophils of Etmopterus.

Thus, in conclusion, all these data support my morphocline determination of lymphogranular tissue character polarity. This form of tissue is plesiomorphic for establishment of a vertebrate immune system and is the

consequence of the specialization of blood sinuses which permits the attraction and promotes the proliferation of hematopoietic progenitor cells. The selachian-type organization exemplifies the initial state of vertebrate lymphatic system development wherein the tissue is found in association with organ masses specialized for other activities. The "white marrow" of Holocephali is derived, following from the selachian state as anatomical remodeling transpires and both the vasculature and its stromal network become specialized to support hematopoietic activities. This approach is consistent with Tavassoli's theory of a "patrimonial relationship" between marrow and bone (1986), a theory which advocates the origin of marrow outside bone as evolutionary pressures forced marrow to merge with bone and extend into the bone cavities where the microenvironment is more suitable for hematopoiesis.

**A Cladistical Analysis of the
Selachian/Paraselachian/Holocephalan Data**

All analyses up to this point have been centered around the concept of a morphocline. This has proven to be the easiest way of organizing the plethora of anatomical data from extant and fossil fishes and for envisioning probable relationships using variations in the appearance of cranial, branchial, and vascular features. However, this type of examination offers no rigorous means of comparing my results to any systematic examination of Chondrichthyes. Nor does it assist in determining the appropriateness of a paraselachian grouping nor the systematic relationship of individuals within this classification to either Selachii or Holocephali. Therefore, to permit these comparisons and to test the implied phylogenetic conclusions of my morphocline a series of seventy eight characters was compiled for a cladistical analysis. These characters included traits used in generating my morphocline (i.e. cranial, branchial, vascular, and pectoral girdle features) as well as morphocline-independent traits. Table 5 lists these characters and the conditions possible for each character. The character matrices which were used as input data for the Hennig '86 cladistical analysis program, having been

individualized for each species or fish grouping, are presented in Table 6. In defining the program constraints all characters were identified as nonadditive. Acanthodians and actinopterygians identified as outgroups, Callorhynchus was included as the token representative of extant holocephalans and Sup2 was included as the token elasmobranch. Hennig 86 generated only one tree from the analysis (Figure 60). Elasmobranchii emerge as the sister group of Stethacanthidae plus a clade virtually identical to my morphocline. This latter clade suggests autodiastylic forms are more closely related to the holocephalans than to the other Bear Gulch chondrichthyans. The tight grouping of Bear Gulch holocephans is emphasized and it is noteworthy that Callorhynchus (and modern Chimaeriformes) arise as the plesiomorphous sister taxon of Echinochimaera and the cochliodonts. Upon evaluating the bifurcations at nodes 22, 21, and 15, if autodiastily is proven to be plesiomorphous for all true gnathostomes, then I am led to the conclusion that autodiastily, amphistily, and holostily have all arisen more than once in vertebrate phylogeny.

To further scrutinize the cladistic significance of the morphocline the data was rerun in Hennig '86 and Macclade (PAUP) for all thirteen taxa. However, the characters were limited to those upon which the morphocline was generated. These represented twenty-five characters (concerned with head or head-associated traits) out of the original seventy-

50	LARGE DORSAL SCALES	C-O	SCAL	0	UNDIFFERENTIATED	1	DI CAUDAL	2	BETWEEN FINS	N
51	SCALATION/SEX	C-O	SCAL	0	MONODORPHIC	1	SEXUALLY DIMORPHIC	2	ONE SEX ONLY	Y
52	CANAL SCALES	C-O	SCAL	0	SMALL SAMPLE	1	RINGS	2	THRU SCALES	Y
53	PECTORAL GIRDLE	C-O	FNS	0	UNFUSED ACROSS MIDLINE	1	FUSED ACROSS MIDLINE	2	NO RADIALS ON GIRDLE	Y
54	PECTORAL RADIALS	C-O	FNS	0	MOST RADIALS ON GIRDLE	1	>50% ON METAPIERGIUM/AXIS	2	TREBASAL	N
55	PECTORAL BASALS	C-O	FNS	0	MULTIBASAL	1	METAPIERGIUM	2	ABSENT	N
56	PECTORAL AXIS	C-O	FNS	0	SMALL	1	LONG	2	ABSENT	N
57	PELVIC GIRDLE	C-O	FNS	0	UNFUSED ACROSS MIDLINE	1	FUSED ACROSS MIDLINE	2	ABSENT	Y
58	REPRODUCTION	C-O	FNS	0	EXTERNAL FERTILIZ	1	INTERNAL W/ CLASPERS	2	ABSENT	Y
59	PELVIC DIMORPHISM	C-O	FNS	0	MONODORPHIC	1	REDUCED/ABSENT IN FEMALES	2	ABSENT	Y
60	PELVIC DORSAL PROCESS	C-O	FNS	C	ABSENT	1	S-OBT	2	TALL	Y
61	PELVIC RADIALS	C-O	FNS	0	MOST ON GIRDLE	1	NEAR HALF ON METAPIERY	2	MOST ON METAPIERY	Y
62	PREPELVIC TENDACULUM	C-O	FNS	0	ABSENT	1	POSTERIOR EDGE OF GIRDLE	2	ANTERIOR EDGE OF GIRDLE	Y
63	CLASPER GLANDS	C-O	FNS	0	ABSENT	1	PRESENT	2	ABSENT	Y
64	CLASPER SCALES	C-O	FNS	0	BONE	1	PRESENT	2	ABSENT	N
65	ANAL FN	C-O	FNS	0	ABSENT	1	PRESENT	2	ABSENT	N
66	DORSAL FIN MEMBERS	C-O	FNS	0	TWO FNS	1	ONE FN	2	NO FNS	Y
67	DORSAL SPINES	C-O	FNS	0	FIRST FN ONLY	1	TWO SPINES	2	NO SPINES	N
68	DORSAL FN BASE	C-O	FNS	0	ALL RADIALS	1	BASAL PLATE & RADIALS	2	ALL BASAL PLATES	N
69	FIRST DORSAL SPINE	C-O	FNS	0	S-OBT SUPERICIAL	1	LONG FIRED	2	LONG MOBILE	N
70	FIRST DORSAL PRESENCE	C-O	FNS	0	PRESENT BOTH SERIES	1	ABSENT BOTH SERIES	2	SEXUALLY DIMORPHIC	N
71	FIRST DORSAL DEVELOPMENT	C-O	FNS	0	AT BIRTH	1	AT PUBERTY	2	FORWARDLY CURVED	Y
72	FIRST DORSAL SHAPE	C-O	FNS	0	POSTERIORLY DIRECTED	1	VERTICAL	2	ABSENT	Y
73	SPINE ORIENTATION	C-O	FNS	0	PRESENT	1	EXTENDED HETEROCERICAL	2	HOMO CERICAL	N
74	CAUDAL FN	C-O	FNS	0	HETEROCERICAL	1	EPICERICAL COMPONENT	2	FUSION OF RAYS	N
75	CAUDAL ENDOSKELETON	C-O	FNS	0	SERIAL HYPOCERICAL	1	CEROCENTRA	2	COMPLETE CENTRA	Y
76	VERTEBRAL CENTRA	C-O	ALS	0	UNCALCIFIED	1	PRESENT	2	ABSENT	Y
77	SYNURACULUM	C-O	AMS	0	ABSENT	1	PRESENT	2	ABSENT	Y

Table 6: Character Matrices According to Taxa

Actinopterygians

1000000100020230000010000000000013010000003000000000200020000000
011203100?0000

Acanthodians

10000001??02023?20001????00????????????000100000000000002?000?00
01002100000000

Falcatus falcatus

0110000000000011120011000000000200000000000111002001101110100000
00011121212010

Stethacanthus altonensis

0110000010000011120011000000000200000000000111002001101110100000
10011121110000

Superfish 2

011000001000001121001100010000000????0000000000000000?2220100?00
01222300000000

Heteropetalus elegantulus

011000001010001010000000201202202100010001012000003000002320100200
10110020103100

Het2

0100110111112101312000001002201000010002112000000000102120100200
10001100000000

Superfish 1

010011010011121013110001010001100????001101000000000002120100?0?
?0011100000100

Erismacanthus

0100120101111233231200321210233332311121211032111011?002120102211
00002200201111

Coch1

010012011111233231200321210233332311121211032122011000212010221?
00002200101111

Echinochimaera meltoni

010012101111123323120032132030333231011?21?0101101131002120102210
01002200101111

Elweirdo

0101009011?102002?010000000020000????0021?20000030020021201002?0
00023000013100

Callorhynchus

01011211111112332312003213102333323101122112000002110102120102221
10001200101111

Figure 59: Bear Gulch and Related Chondrichthyans

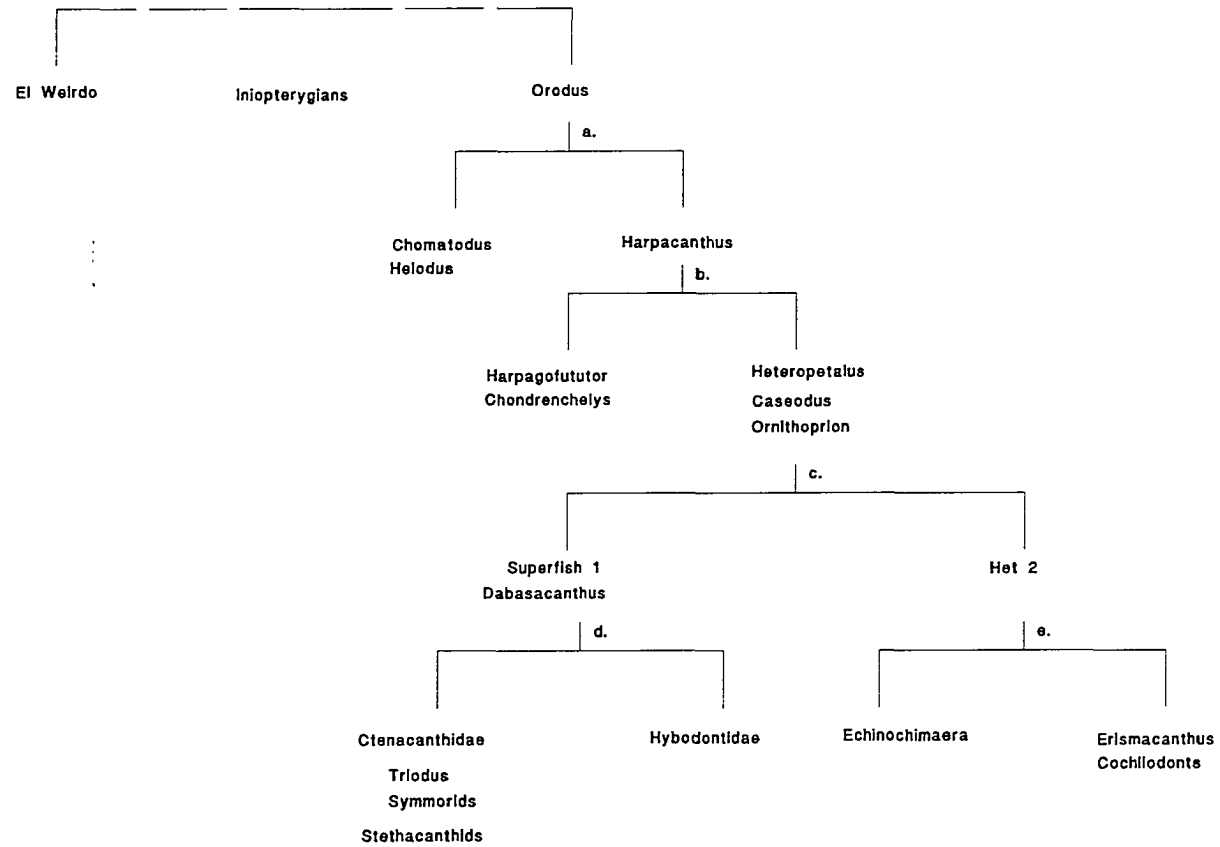
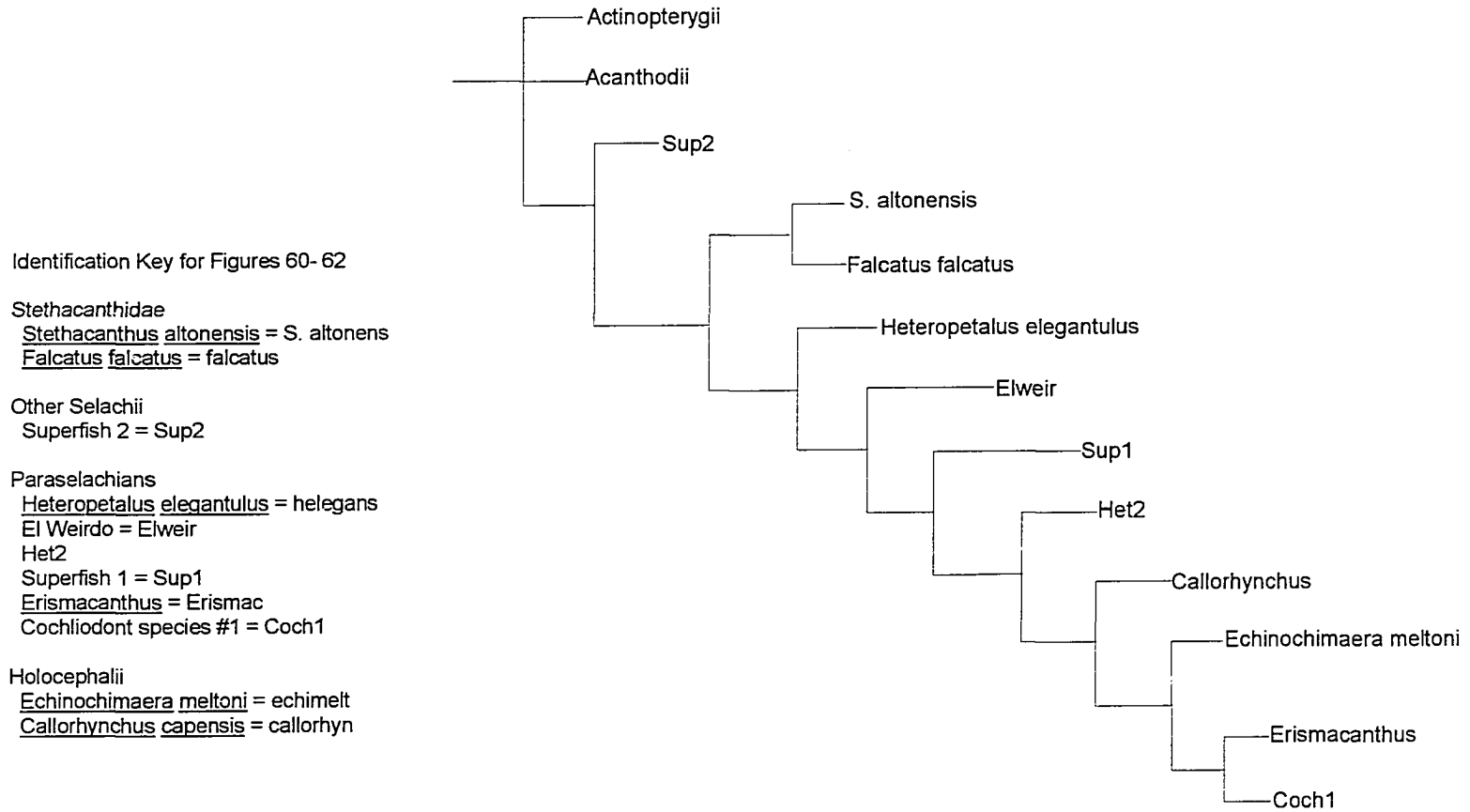


FIGURE 60 : The "Hennig '86" Cladogram of Bear Gulch Chondrichthyans



seven. In both programs, four trees resulted from this analysis (Figures 61 and 62) and, again, they reflected minor variations from my original morphograde. The retention index indicates the (1) interorbital span, (2) preorbital length and ampullary state, (3) dimensions and relative points of upper jaw articulation, (4) the possession of a frontal clasper, and (5) the position of the jugular vein are the most critical characters for establishing the relatedness of these taxa.

FIGURE 61. "Hennig '86" Cladograms based on Head and Head Associated Characters

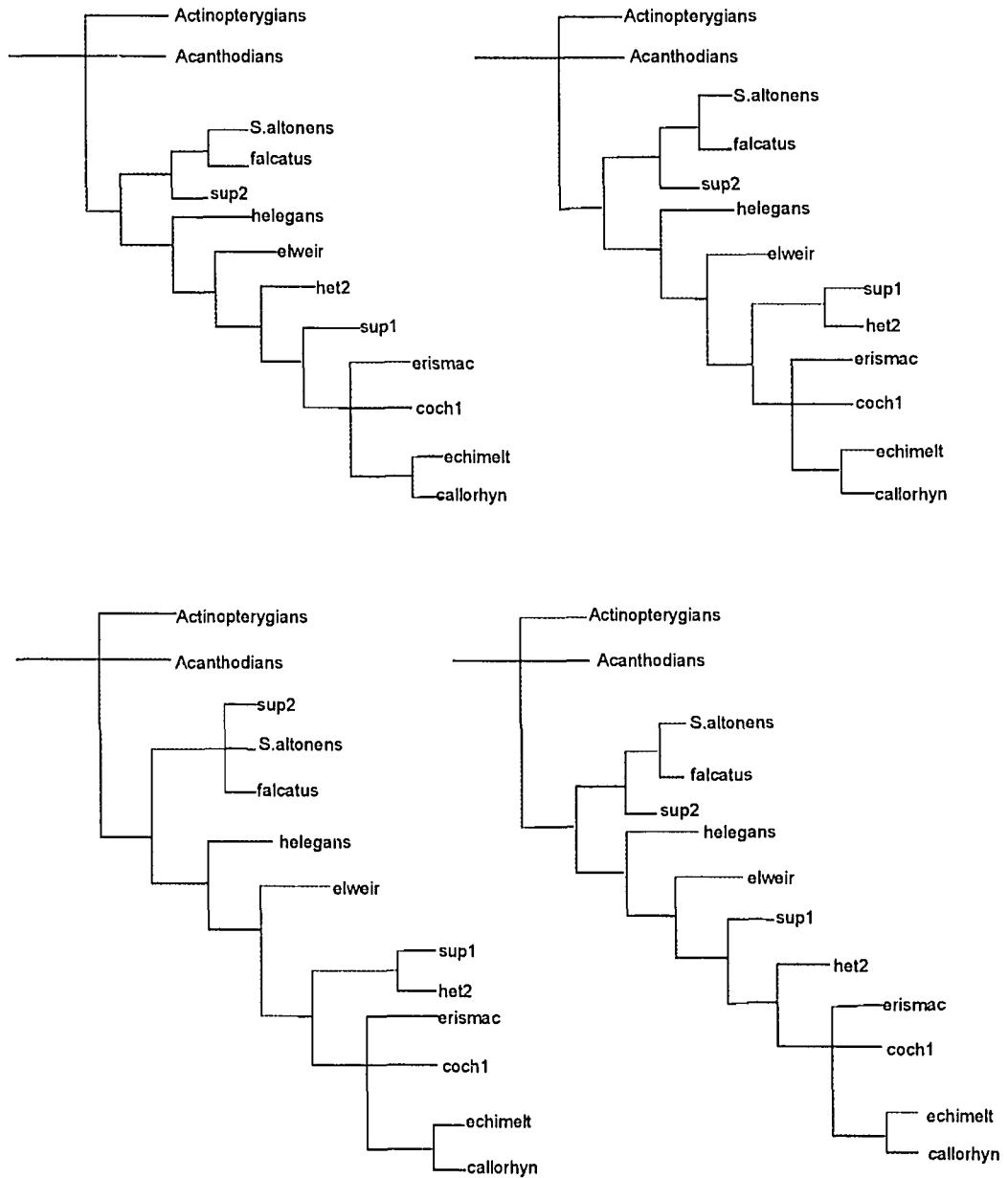
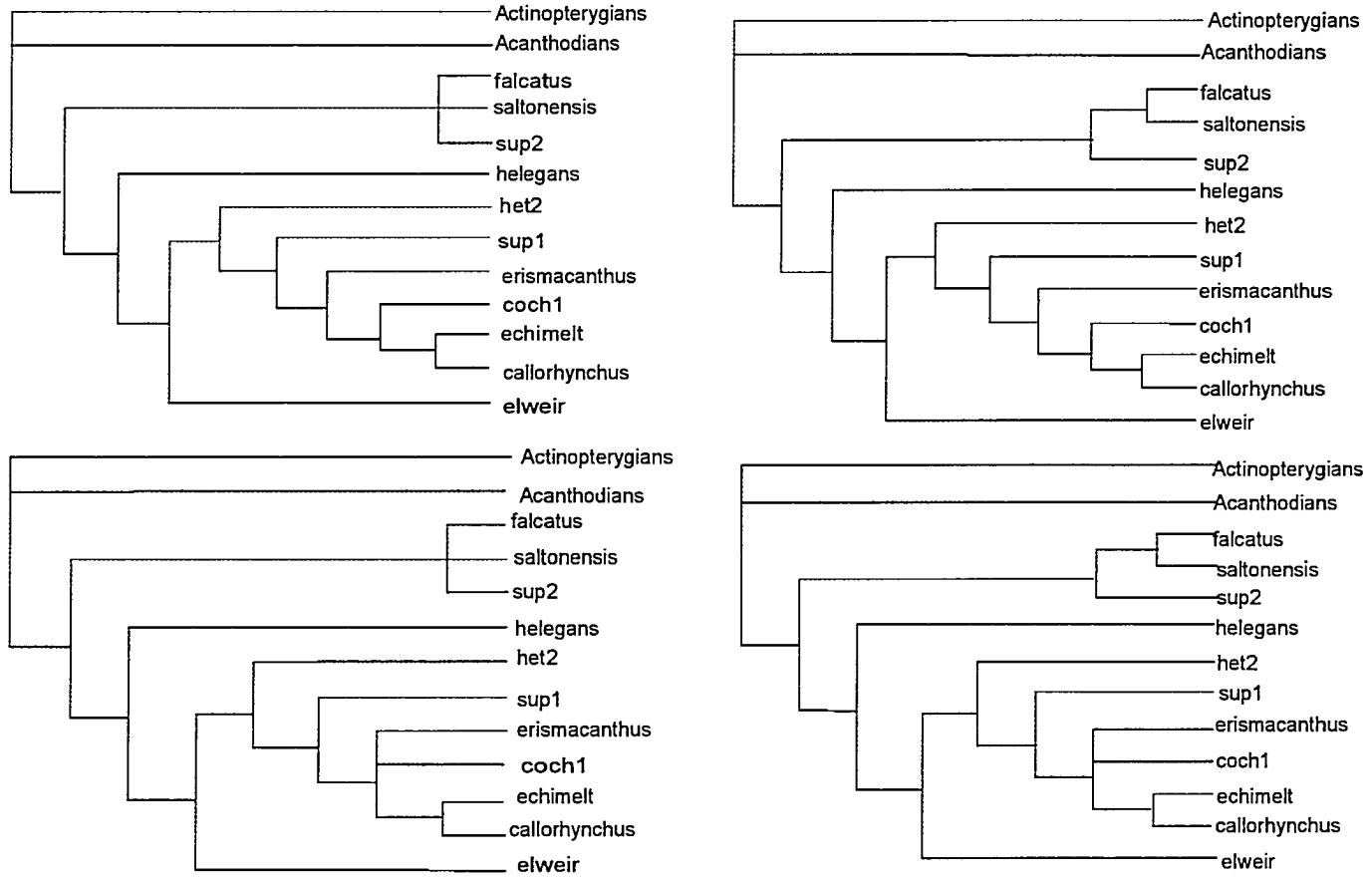


FIGURE 62. The PAUP Cladograms Based on Head and Head Associated Characters



SUMMARY

All the data resulting from this research on the four points of divergence supports the concept of selachian and holocephalan sister groups within a chondrichthyan classification. The Chondrichthyes were highly diversified within the Carboniferous, an observation which is supported by the morphological data on Bear Gulch selachians, paraselachians, and holocephalans. Yet, both the morphoclinical and cladistic analyses clearly support the view that the cochlodonts are the most likely representatives of an ancestral stock for extant holocephalans.

Autodiastyly is an irrefutable feature of Bear Gulch paraselachians and is, to the knowledge of the author, confirmed for the first time as a valid condition rather than a theoretical construct. In the autodiastylic state the hyoid arch is primitively responsible for the support of an opercular covering. If autodiastyly proves plesiomorphous for all gnathostomes then the operculated condition is as well. In terms of suspensorial development, the hyoid arch is not initially modified for a support of the mandibular arch.

Other conclusions pertinent to the interrelationships and evolution of Chondrichthyes are:

1. The paraselachians provide the critical data for establishing a morphocline between the selachian and holocephalan conditions. The resulting transitional series has proven to be tenable in terms of a cladistical analysis.
2. A precerebral fontanelle is plesiomorphous for Chondrichthyes, and is similarly likely for all gnathostomes. The holocephalan ethmoid canal is not a recent acquisition but forms with a shifting of the nasal capsule and supraorbital cartilages. The preorbital remodeling of cartilages which generate an ethmoid canal is also responsible for the roofing over of the precerebral fontanelle.
3. "White marrow", or the localization of lymphohaematopoietic tissue within cavities of the endoskeleton is an autapomorphic character of Holocephali, although Selachii may have the capacity to exhibit white marrow. The development of the "white marrow" condition is solely attributed to the reorganization of endoskeletal and vascular elements.
4. The hyoid sinus vasculature is most likely to be retained from an ancestral state and has probably developed with an increased capacity for cranial flexure. It is lost within holocephalans due to the forward encroachment of the branchial arches and development of a synarcuum. In the latter state, the maxillofacial vein is formed.

APPENDIX NOTES

1. In 1937, Watson proposed an aphetohyoidean condition, which is based on the presence of a complete spiracular gill slit, as the state intermediate to paleostyly and hyostyly. This condition was originally ascribed to the Lower Permian Acanthodes bronni but the suspensorial nature of this species was redescribed in 1968 by Miles as amphistylic (in Huxley's terms) or more specifically as nonsuspensorial amphistyly (amphystly in Gregory's 1904 terms). The aphetohyoidean condition remains purely theoretical as no extant or fossil form has been found to comply with this description.

2. DeBeer's definition of an otic process: Postorbital articulation of the pterygoquadrate, directed toward the auditory capsule, fused in the Holocephali and failing to meet the auditory capsule in Heterodontus. The otic process always lies laterally to the head vein and dorsal and anterior to the palatine branch of the facial nerve.

3. On the identification of the selachian Processus Oticus Internus and Processus Oticus Externus:

a) The "internus" is only found in selachians with a

suspensorial hyomandibula. It is represented by the lateral commissure (the commissure is the consequence of the mandibular gill slit being reduced to a spiracle and therefore the reduction is correlated with the formation of a suspensorial hyomandibula). "By the development of a spiracle the upper portion of the mandibular (branchial rays) was transformed into spiracular cartilages and their support, the lateral commissure, inside of which the hyomandibular nerve and jugular vein run." p167

b) The processus oticus externus lies outside the processus oticus internus' hyomandibular nerve and jugular vein , but outside the palatine nerve, orbital artery, and pseudobranchial artery as well. It is located in front of the spiracular cleft and posterior to the trigeminal.

4. It is apparent from the descriptions of Chondrichthyan conditions that suspensoria are defined according to the extent of hyoid arch modification. The focus of the description is placed on hyomandibular development and this interpreted as the primary mechanism responsible for achieving the jawed state. Less attention is given to the non-hyoid factors of the suspensorium; e.g. the shape of the elasmobranch palatoquadrate which varies with suspensorial type. This variation is most apparent when a comparison is made of the palatoquadrate process of articulation in extant forms versus fossil forms described as having an identical suspensorium.

The classical description of hyostyly does not agree with that which is found in the heterodonts. These selachians exhibit a suspensorium considered to be the typical example of paleo-hyostyly, i.e. that form of hyostyly found in the early fossil record of selachians. Described as antorbital hyostyly by Glickman (1967) this form of hyostyly is said to feature an antorbital (ethmoidal) articulation rather than the palatobasal just described. Amphistyly is also exhibited by both extant and fossilized selachians. However, the amphistylic Bear Gulch cladodonts, as described by Lund (1977), have palatoquadrate articulations with (1) the ventrolateral surface of the ethmoid region and (2) with the posterior surface of the postorbital wall via a pterygoid expansion. These articulations follow the descriptions for ethmoidal and otic articulations rather than the otic and basal connections noted by DeBeer for neoselachians.

These examples demonstrate the discrepancy between the conceptual description of suspensorial articulations and that which is observed in specimens considered to be at an early stage in the evolution of the jawed condition. The primary confusion centers around a variation in the position of that articulation which is directed to the orbital region. This variation is considered so that the polarity of suspensorial characters and possible transitions

between suspensorial states may be clarified.

If it is generally agreed that the cranial regions are to be described, following Goodrich's interpretation, as

- (a) a posterior occipital region which connects with the vertebral column and surrounded by the foramen magnum
- (b) a otic region containing the auditory capsules
- (c) an orbitotemporal region and
- (d) an anterior ethmoid region with nasal capsules separated by a median nasal septum

then the palatoquadrate ethmoid articulation or fusion must occur between the anterior end of the pterygoquadrate and the ethmoid region of the cranium. This articulation is therefore distinct from what is described as an orbital articulation. Any variation in the placement of this latter articulation within the orbital region is attributed to different patterns of trabecular cartilage development, a condition which has been established by Holmgren in analysis of jaw/neurocranial connections in squaloid and galeoid development.

Consequently, the nature of both paleo-amphistyly and paleo-hyostyly can be explained as misidentification of an orbital or basal connection as ethmoidal. Otherwise, if these articulations are truly ethmoidal then the paleo-amphistylic attachment must be derived in accord with the directive there was no contact between the anteriormost visceral arches in pre-gnathostomes and that a basal

connection arose as the primary contact in the early gnathostome condition. The paleo form of the suspensoria can be explained as the basal articulation appearing to have migrated forward, but, in essence it is the differential growth of the trabeculae which, as in the squaloids, results in a more anterior connection some feel inclined to call the ethmoid connection. Yet, Huxley's definition of the initial attachment of upper jaw to the neurocranium describes it as between cranial nerves II and V, not at the site of V and VII. Thus, in the purest interpretation of Huxley's definition either of the articulations described to occur at the orbital level are basal connections and not ethmoidal. In application, then, the anterior orbital connection seen in Paleozoic Chondrichthyes and in paleoniscoids should be considered as plesiomorphous and identified as basal or orbital and not ethmoidal. These can only be considered derived given the development of the palatine segment in the preceding autodiastyle form.

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