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## Phylogenetic Systematics of Extant Chimaeroid Fishes (Holocephali, Chimaeroidei)

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## ABSTRACT

This investigation analyzes generic- and familial-level phylogenetic relationships of extant Holocephali using morphological characters. The six genera studied—*Callorhinchus*, *Rhinochimaera*, *Harriotta*, *Neoharriotta*, *Chimaera*, and *Hydrolagus*—belong to the suborder Chimaeroidei and are the only living representatives of the class Holocephali. Details of relationships among the Recent taxa have not been considered in any phylogenetic hypothesis. This comparative anatomical analysis, combined with developmental information, offers a new approach. The comparative morphology of the lateral line canals, skeleton, tooth plates, secondary sexual characters, and musculature of all six living genera of chimaeroid

fishes is described and compared with living elasmobranchs, the nearest Recent outgroup. Development of the jaws, hyoid arch, and ethmoid canal is briefly described for *Callorhinchus milii* of the family Callorhynchidae. *Callorhinchus* is the most primitive living chimaeroid, and the superfamily Chimaeroidea is erected to include the remaining five genera: *Rhinochimaera*, *Harriotta*, *Neoharriotta*, *Chimaera*, and *Hydrolagus*. A phylogeny of higher-level chimaeroid relationships is hypothesized on the basis of anatomical characters, and a new classification of chimaeroid fishes is proposed to reflect this phylogenetic interpretation.

## INTRODUCTION

The chimaeroid fishes (order Chimaeriformes in this work) belong to the class Holocephali and are regarded as an obscure lineage of mostly deep-water cartilaginous fishes. Holocephali and Elasmobranchii are widely considered to belong to a monophyletic Chondrichthyes, a relationship supported by numerous skeletal and soft tissue characters (Schaeffer, 1981; Maisey, 1984, 1986: table 1). Nevertheless, the early evolution and relationships of holocephalans are still poorly understood. My primary objective in this introduction is to condense a vast and complicated history of systematic research and to briefly discuss the history of holocephalan classification.

Numerous studies have focused on the description and classification of Holocephali (Müller, 1834, 1844; Newberry and Worthen, 1870; Saint John and Worthen, 1883; Zittel, 1887; Garman, 1901, 1904, 1908, 1911; Dean, 1906, 1909; Woodward, 1889, 1921; Hussakof, 1912; Nielsen, 1932; Moy-Thomas, 1936a, b, 1939; Obruchev, 1967; Berg, 1965; Arambourg and Bertin, 1958; Ørvig, 1962, 1980; Stensiö, 1963; Patterson, 1965, 1968; Saint-Seine, Devillers and Blot, 1969; Lund, 1977, 1986a, b; Zangerl, 1973, 1981; Zangerl and Case, 1973; Maisey, 1984, 1986). Historically, the focus of this research has been on fossil taxa, and there has been no prior systematic study focusing on the relationships of extant holocephalans. My pur-

pose is to examine the interrelationships of living forms through detailed comparative anatomical studies. Once monophyletic groups are established, the classification of fossil taxa, side by side with living forms, in a modern phylogenetic context will be facilitated.

There are two hypotheses on the origin of Holocephali. The first and most generally accepted scenario is that holocephalans have evolved from some lineage of bradyodont sharks (Woodward, 1921). The second hypothesis suggests that holocephalans are most closely related to placoderms (Stensiö, 1925, 1936; Ørvig, 1962). Because of the historic significance of this question, these two hypotheses warrant review.

Woodward (1921) originally erected the order Bradyodonti to include five families of Paleozoic chondrichthyans: Petalodontidae, Psammodontidae, Copodontidae, Cochliodontidae, and Edestidae. These families are referred to casually as the "bradyodont taxa," an assemblage of cartilaginous fishes that possessed tooth plates with a crown of hypermineralized tissue and had slow replacement of the teeth (Woodward, 1921). Nielsen (1932) recognized the inconsistency of Woodward's definition of the Bradyodonti because some bradyodonts had rapid replacement of teeth. Despite this problematic definition, the Bradyodonti remained in the literature as a convenient taxonomic group. It

**TABLE 1**  
**Characters That Support a Monophyletic Chondrichthyes**

- 
1. Prismatic calcification of cartilage (Schaeffer and Williams, 1977; Schaeffer, 1981; Zangerl, 1981; Maisey, 1986)
  2. Labial cartilages (Schaeffer and Williams, 1977)
  3. Ceratotrichia in paired and unpaired fins (Schaeffer and Williams, 1977)
  4. Dermal skeleton represented by denticles with a particular pattern of enameloid, dentine and basal tissue (Schaeffer and Williams, 1977)
  5. Rectal salt gland in living forms (Schaeffer and Williams, 1977)
  6. Mixipterygial claspers in males (Schaeffer and Williams, 1977; Maisey, 1986)
  7. Precerebral fontanelle and fossa (Schaeffer, 1981)
  8. Efferent pseudobranchial artery over trabeculae (Schaeffer, 1981)
  9. Occipital arch between auditory capsules projecting behind the capsule with separate foramina for occipitospinal nerves (Schaeffer, 1981)<sup>a</sup>
  10. Otico-occipital proportions less than ethmo-orbital portion (Schaeffer, 1981)<sup>a</sup>
  11. Scales with neck canals (Maisey, 1986)
  12. Posteriorly directed median basibranchial copula (Maisey, 1986)
  13. Dorsal fin with basal cartilage (Maisey, 1986)
  14. All premetapterygial radials of pectoral fin articulate with basals (Maisey, 1986)
  15. Pelvic basipterygium articulates with all but the anteriormost few radials (Maisey, 1986)
  16. Metameric suprarenal ganglia (Maisey, 1986)
  17. Multiple jointing of pectoral radials (Maisey, 1986)
  18. Anterior median sinus between anterior and posterior cardinal veins (Maisey, 1986)
  19. Endolymphatic duct (Maisey, 1986)
  20. Mesoadenohypophysis with ventral lobe detached from main body of the pituitary (Maisey, 1986)
  21. Nidamental gland secretes horny egg case (Maisey, 1986)
  22. Replacement tooth rows attached to mesial surface of jaws by basement membrane; linguo-labial tooth replacement (Maisey, 1986)<sup>b</sup>
  23. Teeth with specialized nutritive foramina in basal plate (Maisey, 1986)<sup>b</sup>
- 

<sup>a</sup> May be primitive; see discussion in Maisey (1983).

<sup>b</sup> Secondarily modified in Holocephali (Maisey, 1986).

has since been established that the micro-structure of teeth is not a useful character for systematics (Radinsky, 1961; Ørvig, 1967). As a result, *Bradyodonti* is no longer accepted as a valid taxonomic group (Romer, 1966; Bendix-Almgreen, 1968; Patterson, 1968; Lund, 1986a) and the relationships among Woodward's five bradyodont families have remained obscure.

Complete or partial skeletal material of holocephalans is extremely rare and almost all fossil holocephalans are known from teeth, denticles, or spines (e.g., Zittel, 1887, 1932; Newberry and Worthen, 1870; Saint John and Worthen, 1883; Woodward, 1889, 1891; Reis, 1895; Dean, 1909; Hussakof, 1912; Chapman, 1918; Nielsen, 1932; Patterson, 1965; Obruchev, 1967; Ward, 1973; Ward and McNamara, 1977; Lund, 1982, 1986b; Duffin,

1984). As a result, holocephalans have been classified primarily on the basis of tooth plate characteristics. Because holocephalans have tooth plates that are not shed, with a micro-structure like that of bradyodont teeth, most workers have allied them with at least one of the bradyodont taxa (e.g., Moy-Thomas, 1939; Obruchev, 1967; Berg, 1965; Arambourg and Bertin, 1958; Patterson, 1965, 1968; Lund, 1977; Zangerl, 1981).

In 1925, Stensiö proposed that holocephalans were closely related to placoderms. This suggestion was supported by his observation that some placoderms, particularly the ptyctodontid arthrodires (e.g., *Ctenurella*), shared certain anatomical similarities with holocephalans, which include: the joint between the head and vertebral column, an operculum, the shape of the pectoral girdle,

an autostylic jaw, tooth plates, gill arches concentrated underneath the neurocranium, a well-developed rostral portion of the neurocranium, first dorsal fin with a basal cartilage and fin spine, and the general body shape. Ørvig (1962) discovered several additional characteristics present in both holocephalans and pttyctodont arthrodires: a synarcual, prepelvic spines, pelvic claspers, the position and shape of the mandible, and paired rostral processes. Detailed comparative morphological investigations have prompted others to consider a relationship between holocephalans and arthrodires on the basis of these and other anatomical similarities (Holmgren, 1942; Westoll, 1962; Stahl, 1967; Jarvik, 1980). Based on evidence presented by Stensiö (1925, 1936) that chondrichthyans were related to placoderms, the group Elasmobranchiomorphi was erected by Jarvik (1955) to include elasmobranchs, holocephalans and placoderms. The implication of this grouping was that placoderms and chondrichthyans are closely related and may share a common ancestry.

Miles and Young (1977), in a study of placoderm relationships, dismissed the anatomical evidence for a close relationship to holocephalans on the grounds that placoderm characters have been interpreted based on a holocephalan model. It was therefore concluded that the characters presented by Stensiö (1925) and Ørvig (1962) appear to be convergent features. Recent studies of the systematics of placoderms support a closer relationship between placoderms and osteichthyans than between placoderms and chondrichthyan fishes (Forey, 1980; Gardiner, 1984; Forey and Gardiner, 1986). This evidence against a relationship between placoderms and holocephalans is reflected in a recent redefinition and classification of Elasmobranchiomorphi (Jarvik, 1980: 324) that excludes holocephalans.

In a thorough analysis of holocephalan relationships, Patterson (1965) focused almost exclusively on the fossil chimaeroids, including squalorajoids, myriacanthoids, and menaspoids. The goal of Patterson's (1965) analysis was to examine the evidence for a placoderm-holocephalan relationship as suggested by Stensiö (1925, 1936) and supported by Ørvig (1962). Patterson (1965: 213) con-

cluded that holocephalans are not derived directly from placoderms, but he cautiously suggested that holocephalans may share a common ancestor with arthrodires. This conclusion is reflected in his grouping of Holocephali within the superclass Elasmobranchiomorphi, which by his definition includes all Selachii and Arthrodira (Patterson, 1965: 105).

As a complement to paleontological investigation it is important to approach the problem of holocephalan evolution through neontological studies. Many workers have contributed to our understanding of holocephalan relationships through studies of extant taxa (Vetter, 1878; Garman, 1888, 1904; Dean, 1895, 1904a, b, 1906; Cole, 1896a, b; Jungersen, 1899; Schauinsland, 1903; Cole and Dakin, 1906; Luther, 1909; Burlend, 1910; Reese, 1910; Allis, 1912, 1917, 1926; Shann, 1919, 1924; Leigh-Sharp, 1922, 1926; Rabinerson, 1925; Kesteven, 1933; de Beer and Moy-Thomas, 1935; Edgeworth, 1935; Holmgren, 1940, 1941, 1942; Patterson, 1965; Stahl, 1967; Ribbink, 1971; Raikow and Swierczewski, 1975; Jarvik, 1980). Embryological material of chimaeroids has historically been difficult to obtain, and only *Hydrolagus colliei* and *Callorhinchus milii* inhabit relatively shallow near-shore waters, making it possible to obtain developmental material for these two species. Four studies have focused on aspects of development (Schauinsland, 1903; Dean, 1903, 1906; de Beer and Moy-Thomas, 1935; Kemp, 1984). Of these studies Schauinsland (1903, *Callorhinchus milii*) and Dean (1903, 1906, *Hydrolagus colliei*) have studied a series of embryos. Kemp (1984) described tooth plate development in *Callorhinchus milii* and de Beer and Moy-Thomas (1935) studied the development of the head in a single 95-mm *Callorhinchus* embryo.

Despite these efforts to describe and understand the anatomy of living chimaeroid fishes, there have been no comparative studies of all extant genera and none that has attempted to make broad comparisons with the expressed purpose of understanding phylogenetic relationships. Although the comparative anatomy of living forms was discussed in Patterson's (1965) publication, his focus was on fossil chimaeroids. Since then



the advent of cladistics along with new information and techniques have changed our approach to evolutionary morphological research and a reexamination of chimaeroid relationships is warranted. The goal of this comparative anatomical analysis, then, is to provide the first complete analysis of the morphology of all genera of living chimaeroids.

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#### ABBREVIATIONS *Institutional*

Institutional abbreviations follow Leviton et al. (1985), with the following additions:

MAF	Ministry of Agriculture and Fisheries
Fisheries	Wellington, New Zealand
UMA	University of Massachusetts, Amherst

#### *Anatomical*

ACC	anterior clasper cartilage of pelvic clasper
AF	anal fin
ama	<i>M. adductor mandibulae anterior</i>
amp	<i>M. adductor mandibulae posterior</i>
AN	angular lateral line canal
ANC	antorbital crest
AP	ampullary pore
APF	angular ampullary pore field
AR	anterior radial element of pectoral fin
BBR	basibranchial cartilage
BD1	basal cartilage of the first dorsal fin
BHY	basihyal cartilage
BT	basipterygium of the pelvic fin
BTP	basipterygial process of the pelvic fin
cb	<i>Mm. constrictores branchiales</i>
cbr	<i>Mm. coracobranchiales</i>
cd	<i>M. constrictor operculi dorsalis</i>
cda	<i>M. constrictor operculi dorsalis anterior</i>
ch	<i>M. coracohyoideus</i>
CHY	ceratohyal cartilage
cm	<i>M. coracomandibularis</i>
COR	coracoid region of the pectoral girdle
cp	<i>M. cucullaris profundus</i>
CP	chin process of Meckel's cartilage
cs	<i>M. cucullaris superficialis</i>
CT	connective tissue
CTB	ceratobranchial cartilage
cv	<i>M. constrictor operculi ventralis</i>
D2	second dorsal fin
DI	diencephalon
DL	descending lamina of tooth plates
DR	distal radial elements of the paired fins
E	eye
EAF	ethmoid ampullary field
EBR	epibranchial cartilage
EC	ethmoid canal
EHY	epihyal cartilage

EN	enameloid layer	OP	otic process
ep	<i>M. epaxialis</i>	OPC	opercular cartilage
EP	ethmoid process of the neurocranium	OPF	ophthalmic foramen
FT	frontal tenaculum	OR	oral lateral line canal
GB	growth base of tooth plate	OS	orbital septum
H	horizontal lateral line canal	OT	otic lateral line canal
HBR	hypobranchial cartilage	OTC	otic capsule
HD	hypermineralized rod (= compact pleromin of Ørvig, 1985)	PBR	pharyngobranchial cartilage
HOC	hyomandibular lateral line canal	PC	pulp cavity
HP	hypermineralized pad (= vascular pleromin of Ørvig, 1985)	PCC	posterior clasper cartilage of pelvic clasper
HR	cartilaginous hyoid rays supporting opercular flap	pdp	<i>M. protractor dorsalis pectoralis</i>
HT	hypermineralized tissue (= pleromin of Ørvig, 1985)	PHY	pharyngohyal cartilage
ih	<i>M. interhyoideus</i>	PL	prelabial cartilage
im	<i>M. intermandibularis</i>	PMD	premandibular cartilage
IMX	inferior maxillary cartilage	PMX	premaxillary cartilage
IO	infraorbital lateral line canal	PO	postotic lateral line canal
IOP	infraorbital ampullary pore field	POP	preorbital ampullary pore field
JJ	jaw joint	POR	postorbital ridge
K	dorsal keel of chimaerid egg case	PPT	prepelvic tenaculum
KN	tubercles on the snout of <i>Harriotta</i>	PQ	palatoquadrate cartilage
L	lymphoid tissue	pr	<i>M. levator anguli oris anterior pars rostri</i>
la	<i>M. labialis anterior</i>	PT	propterygium of the pectoral fin
laoa	<i>M. levator anguli oris anterior</i>	PTP	palatine tooth plates
laop	<i>M. levator anguli oris posterior</i>	PTY	pituitary gland
LB	lateral bulges of the yolk sac	PVG	pelvic girdle
LF	lateral flange	PXR	proximal radial elements of the paired fins
lh	<i>M. levator hyoideus</i>	rdp	<i>M. retractor dorsalis pectoralis</i>
LL	<i>ligamentum labialis</i>	REC	roof of the ethmoid canal
LLC	lateral line canal	RF	rostral foramen
LLP	lateral line canal pores	RL	<i>ligamentum rostralis</i>
LP	labial ampullary pore field	RLP	rostrolateral ampullary pore field
LRR	lateral rostral rod	rlvp	<i>M. retractor latero-ventralis pectoralis</i>
LW	lateral web of egg case	rmvp	<i>M. retractor mesio-ventralis pectoralis</i>
M	Meckel's cartilage	RP	retroarticular process
MES	mesencephalon	RPF	rostral ampullary pore field
MP	mandibular ampullary pore field	SAF	supraorbital ampullary field
MPT	metapterygium of pectoral fin	SCA	scapular process of pectoral girdle
MR	middle radial elements of the paired fins	SCL	supracaudal lobe of the tail
MRR	medial rostral rod	SD	symphyseal ridge of mandibular tooth plate
MS	mesopterygium of pectoral fin	SMX	superior maxillary cartilage
MTP	mandibular tooth plates	SN	snout
MW	margin of wear (the border between the attrition surface and unworn portion of the oral surface of the tooth plate)	SO	supraorbital lateral line canal
N	notochord	SOR	suborbital ridge
NA	nasal lateral line canal	SPD	spindle of egg case
NC	nasal capsule	SR	subrostral lateral line canal
NO	notochord	SRG	subrostral groove
NP	nasal ampullary pore field	SRP	suprarostral ampullary pore field
NV	superficial ophthalmic nerve	ST	supratemporal lateral line canal
NVII	cranial nerve VII	STP	supratemporal ampullary pore field
OC	occipital lateral line canal	SUB	subrostral ampullary pore field
OCC	occipital crest	SUL	subcaudal lobe of the tail
OF	oral ampullary pore field	sup	<i>M. superficialis</i>
		SYN	synarcual
		TD	trabecular dentine
		TEL	telencephalon
		TP	tooth plate
		TR	transverse ridges
		TS	tail sheath of egg case

TUD	tubular dentine
VA	vacuity in the anterior process of the pelvic girdle
VC	vascular canal
VTP	vomerine tooth plates
WS	oral surface (working surface) of the tooth plates

## MATERIALS AND METHODS

The taxa used in this study include all extant genera of chimaeroids belonging to the families Callorhynchidae, Rhinochimaeridae, and Chimaeridae. Six genera were studied: *Callorhinchus*, *Rhinochimaera*, *Harriotta*, *Neoharriotta*, *Chimaera*, and *Hydrolagus*. At least one species of each genus was chosen for detailed anatomical examination and whenever possible multiple species were studied to ensure that observed anatomical differences among genera were not interspecific. Outgroup comparisons were based on previously published studies, particularly Patterson (1965) and Maisey (1986).

*Hydrolagus colliei* (Pacific ratfish) were collected during May 1988 and June–September 1989 at Friday Harbor Laboratories, San Juan Island, Washington. Specimens were captured by the RV “Nugget” using a small otter trawl fishing on the bottom at depths ranging from 60 to 140 m (fig. 1A).

While in residence as a visiting scientist at the Portobello Marine Laboratory (October 1989–December 1990) I collected five species of chimaeroids from New Zealand. *Callorhinchus milii* (elephant fish) were collected by trawling at 57 m outside Tairoa Head, off the coast of Dunedin. Juvenile *Callorhinchus milii* were collected from coastal waters at 16–26 m just north and south of Dunedin (fig. 1B). *Hydrolagus novaezealandiae* (ghost shark) were caught by scallop fishermen at 240–288 m, 100 km off Cape Saunders, Dunedin, New Zealand (fig. 1B). *Harriotta raleighana* (no common name), *Hydrolagus* sp. B (pale ghost shark), and *Hydrolagus novaezealandiae* were trawled during a deep-sea fishing trip on the MAF Fisheries vessel, RV “James Cook,” May 21–27, 1990. Fishing was done over a range of 300–800 m in depth from Mernoo Bank and south to Dunedin, off the coasts of Canterbury and northern Otago (fig. 1B). Two specimens of *Rhinochi-*

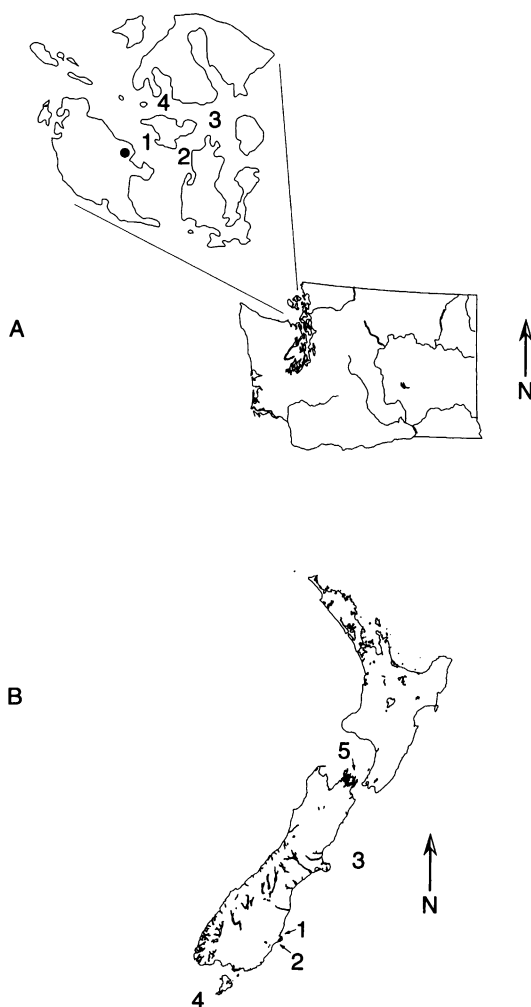


Fig. 1. Localities where chimaeroid fishes were collected for this study. A, Map of Washington state; inset, demarcated by dashed lines, shows the San Juan Islands. The location of Friday Harbor Laboratories is indicated by a dot. Primary collection sites for *Hydrolagus colliei* in Puget Sound are as follows: 1) San Juan Channel, 2) Lopez Channel, 3) Upright Head, and 4) West Sound. B, Map of the south island of New Zealand. Collection sites are numbered as follows: 1) Dunedin, Tairoa Head, Blueskin Bay, and Cape Saunders; 2) Green Island and Nugget Point; 3) Mernoo Bank; 4) Challenger Plateau; and 5) Marlborough Sounds.

*maera pacifica* were trawled from 1034 m on the Challenger Plateau (fig. 1B).

Eight egg cases were collected from captive females at Friday Harbor Laboratories in May 1988. Each egg case was tagged and held in

TABLE 2  
List of Specimens Dissected for Study of Muscles<sup>a</sup>

Callorhynchidae	
<u>Callorhinchus</u>	
<u>Callorhinchus milii</u>	CM34, CM35, CM36
Rhinochimaeridae	
<u>Rhinochimaera</u>	
<u>Rhinochimaera pacifica</u>	AMNH 96939, AMNH 96940
<u>Harriotta</u>	
<u>Harriotta raleighana</u>	AMNH 96931, AMNH 96935
<u>Neoharriotta</u>	
<u>Neoharriotta pinnata</u>	USNM 204778
Chimaeridae	
<u>Hydrolagus</u>	
<u>Hydrolagus colliei</u>	DAD36, HC18, HC5
<u>Hydrolagus novaezealandiae</u>	HNZ1, HNZ2
<u>Hydrolagus</u> sp. B	AMNH 96941, HspB1, HspB6
<u>Chimaera</u>	
<u>Chimaera</u> sp. C	NMNZ P19694
<u>Chimaera monstrosa</u>	USNM 222708

<sup>a</sup> Each number in the table refers to a single individual; data on these specimens available upon request and also on file at the AMNH.

a free-flowing seawater table. Two egg cases were opened each month and the embryos were removed and fixed in 4% glutaraldehyde in seawater. Of the eight egg cases, four embryos were collected. In June 1989, four additional egg cases were collected using similar procedures. Two of these egg cases contained embryos. An additional egg case containing an embryo was collected during July 1989 by the RV "Nugget" during a bottom trawl.

Egg cases of *Callorhinchus milii* were collected by SCUBA diving in the Marlborough Sounds, New Zealand, on June 5–6, 1990. A total of 44 egg cases was collected from 5 to 20 m at four sites (fig. 1B). Of the 44 egg cases collected, 38 were fertile and the remaining 6 were empty. Fourteen embryos, with their yolks intact, were fixed in the field in 10% formalin in seawater. The remaining 24 viable egg cases were transported in buckets of seawater to the Ministry of Agriculture and Fisheries laboratory in Wellington where they were held in two seawater tanks. All egg cases were opened within one week of collection and 20 embryos were fixed in 5–10% for-

malin and seawater. Four embryos were chosen randomly and fixed in 4% glutaraldehyde in seawater. Two additional embryos of *Callorhinchus milii* were collected from egg cases trawled off the coast of Dunedin and both were fixed in 10% formalin in elasmobranch Ringer's solution.

All material collected has been donated to the USNM, AMNH, FMNH, or UMA. Data for each specimen, including collection notes, locality, detailed measurements, and gut contents, are kept on file at the AMNH.

#### GROSS ANATOMICAL METHODS

At least one representative species of each genus was dissected for gross anatomical study of the musculature and skeleton (table 2). Species of the genus *Neoharriotta* are especially difficult to obtain for dissection, and I was unable to complete a detailed dissection of the musculature of any *Neoharriotta*; however, I was permitted to superficially dissect the musculature of *Neoharriotta pinnata*.

Adult specimens to be dissected were anes-

thetized in MS-222, fixed in 10% buffered formalin in seawater for a minimum of 2 weeks, and then transferred into 70% ethanol for long-term storage. Point-to-point measurements were taken on the left side of each specimen and gut contents were analyzed before any anatomical procedures were done. All dissections were done on the left side except for borrowed museum specimens, which were dissected on the right side. Separate individuals were dissected for study of lateral and ventral musculature to ensure that the lateral dissection did not affect ventral musculature. The heads of three *Hydrolagus coliei* and one *Callorhinchus milii* were also studied in sagittal section by cutting preserved specimens with a hacksaw.

Both wet and dry skeletons were prepared from fresh or fresh-frozen material. All skeletal material was prepared by immersing the specimen in hot water for 1–5 minutes, then handpicking the flesh from the cartilage. Wet skeletons were immersed and kept in 70% ethanol. Dry skeletal preparations were either left to air dry for several days or dried in a lyophilizer.

The procedure used for clearing and double-staining follows Hanken's method (slight modification from Hanken and Wassersug, 1981), with some modifications adopted from Potthoff (1984). Table 3 lists specimens that were cleared and stained for comparative study of the developing skeleton and calcified tissues. Small juveniles were prepared whole, without skinning, so that the dermal denticles would not be lost. In order to study the calcified rings of the lateral line canals, pieces of skin were peeled from the heads of *Callorhinchus milii* (CM35, 890 mm TL), *Rhinochimaera pacifica* (AMNH 96940, 950 mm TL), *Harriotta raleighana* (AMNH 96935, 800 mm TL), *Hydrolagus coliei* (AMNH 96933, 470 mm TL), *Hydrolagus novaezealandiae* (HNZ12, 660 mm TL) and *Chimaera* sp. C (NMNZ P12921, 990 mm TL). Sections of the vertebral column, 3–5 cm long, were dissected out of the trunk or caudal region to study the vertebral calcifications in the following taxa: *Rhinochimaera pacifica* (AMNH 96939, 1100 mm TL), *Harriotta raleighana* (AMNH 96935), *Hydrolagus coliei* (HC8, 500 mm TL), and *Chimaera* sp. C (NMNZ P12921).

TABLE 3  
Specimens Prepared by Clearing and Double Staining<sup>a</sup>

<i>Callorhinchus milii</i>
CM17 juvenile male, 175 mm TL
CM18 juvenile male, 215 mm TL
CM19 juvenile female, 205 mm TL
CM20 juvenile female, 208 mm TL
CM73 juvenile female, 205 mm TL
CM45 embryo, 72 mm TL
CM48 embryo, 75 mm TL
CM49 embryo, 80 mm TL
CM54 embryo, 87 mm TL
CM53 embryo, 89 mm TL (sagittal preparation)
<i>Rhinochimaera pacifica</i>
ex NMNZ P25812 juvenile female, 227 mm TL
<i>Neoharriotta pinnata</i>
USNM 217445 juvenile female, 167 mm TL
<i>Harriotta raleighana</i>
NMNZ P21442 juvenile male, 253 mm TL
<i>Hydrolagus coliei</i>
DAD26 (UMA) juvenile male, 113 mm TL
<i>Hydrolagus novaezealandiae</i>
HNZ11 juvenile male, 110 mm TL
<i>Hydrolagus mirabilis</i>
BM(NH) 1990.9.11:6 juvenile male, 232 mm TL
<i>Chimaera monstrosa</i>
BM(NH) 1990.9.11:1 juvenile male, 172 mm TL

<sup>a</sup>Data on these specimens are available upon request and are also on file at the AMNH.

## HISTOLOGICAL METHODS

To study the histology of chimaeroid tooth plates the right mandibular tooth plates of adult *Rhinochimaera pacifica* (AMNH 96940, 950 mm TL), *Harriotta raleighana* (AMNH 96931, 850 mm TL), *Chimaera* sp. C (NMNZ 19694, 944 mm TL), and a juvenile *Hydrolagus coliei* (AMNH 96933, 470 mm TL) were removed from formalin-fixed specimens. The tooth plates averaged a maximum labiolingual width of 2 cm, measured along the posterior edge, and a mesiodistal length of 2–3 cm along the symphyseal edge. Tooth plates were decalcified in formic acid A (10 ml formalin and 5 ml formic acid in 85 ml water; Humason, 1972) for up to 1 month. Dehydration, infiltration, and embedding in low viscosity nitrocellulose (LVN) followed the methods of Thomas (1980). The tooth plates were sectioned transversely at 30  $\mu$ m thickness on a Reichert sliding microtome (vintage 1920) and stained with Ehrlich's he-

TABLE 4  
Histological Preparations of Embryos of *Callorhinchus milii*

Embryo	mm TL	Section	Stain
CM68	23 <sup>a</sup>	transverse	hematoxylin and eosin
CM70	23	transverse	hematoxylin and eosin
CM72	24	transverse	hematoxylin and eosin
CM69	26	transverse	hematoxylin and eosin
CM47	57	transverse	hematoxylin and eosin
CM46	61	transverse	hematoxylin and eosin
CM43	62	frontal	hematoxylin and eosin
CM50	67	transverse	hematoxylin and eosin
CM44	70	frontal	hematoxylin and eosin
CM42	74	transverse	Mallory's trichrome
CM40	79	transverse	Mallory's trichrome
CM51	85	sagittal	Mallory's trichrome
CM52	89	transverse	Mallory's trichrome

<sup>a</sup> Estimated measurement for this specimen due to loss of the tail.

matoxylin and picro-ponceau (Humason, 1972). The tooth plates of one juvenile *Callorhinchus milii* (228 mm TL) were removed from a fixed specimen and prepared using standard paraffin techniques (prepared by Gerald Stokes, University of Otago, Dunedin, New Zealand).

To study the developmental morphology of the head, 13 embryos and 1 juvenile *Callorhinchus milii* (166 mm TL) were transected behind the pectoral girdle with a razor blade. The anterior half of each embryo was prepared using paraffin techniques and serial sectioned at 8–10  $\mu$ m thickness. Sections were stained with Lillie-Mayer haemalum and eosin or Mallory's trichrome collagen stain, Hughesdon's modification (Carleton and Leach, 1947; prepared by Gerald Stokes). Table 4 lists the data for each embryo of *Callorhinchus milii* that was prepared.

In addition, the entire head of one *Hydrolagus colliei* embryo (39 mm TL) was embedded in LVN and transversely sectioned at 30  $\mu$ m thickness. Sections were stained with Ehrlich's hematoxylin and picro-ponceau (Humason, 1972).

Scanning electron microscopy was used to examine hard tissues and whole embryos of *Hydrolagus colliei* and *Callorhinchus milii*. Material to be studied with SEM was fixed in either 4% glutaraldehyde or 10% formalin in Gomori's phosphate buffer or elasm-

branch Ringer's solution. Tooth plates were removed from the jaws of fixed adult specimens and smashed with a hammer into 5-mm<sup>2</sup> pieces. The tooth plates of one juvenile *Callorhinchus milii* (234 mm TL) were removed intact from the jaws and studied. The fin spine was also removed from this specimen and cut into three pieces, each approximately 4 mm long, for study of the internal anatomy in transverse and longitudinal view. To study the calcifications of the lateral line canals, fresh pieces of skin peeled from the heads of a juvenile *Callorhinchus milii* (190 mm TL), a juvenile *Harriotta raleighana* (AMNH 96944, 887 mm TL), and an adult *Hydrolagus* sp. B (AMNH 96945, 824 mm TL) were air-dried and sputter-coated before study under the SEM. The heads of two embryos were also studied using SEM (*Hydrolagus colliei*, 44 mm TL; *Callorhinchus milii*, 40 mm TL).

Two procedures for SEM preparation were followed. At Friday Harbor Laboratories specimens were postfixed in 1% OsO<sub>4</sub>, dehydrated and dried in a Samdri-790 critical point dryer, sputter-coated with gold palladium (300–400 Å thick), and examined under a JEOL JSM 35 scanning electron microscope.

At the University of Otago School of Dentistry in Dunedin, New Zealand, a Cambridge Stereoscan 360 scanning electron microscope

was used. Specimens were dried in a Polaron E3000 critical point dryer and coated using a Polaron E5100 sputter coater.

## REVIEW OF HOLOCEPHALAN SYSTEMATICS

As shown in figure 2, relationships among the extant taxa are an unresolved trichotomy. This cladogram (from Maisey, 1986) is my working hypothesis of holocephalan relationships, and this study focuses on the unresolved trichotomy of the extant families of chimaeroid fishes. In this work the chimaeroid fishes are "crown-group" holocephalans. These include all Recent holocephalans and their immediate fossil relatives, whose relationships I have not attempted to resolve in the diagram. The chimaeriform fishes include all chimaeroids plus certain stem-group holocephalans.

Several recent studies have examined holocephalan relationships with an emphasis on modern phylogenetic concepts (Zangerl and Case, 1973; Lund, 1977, 1986a, b; Zangerl, 1981; Maisey 1984, 1986). Some of these studies are problematic; nevertheless, the perspectives warrant discussion.

The recent discovery of a new order of Pennsylvanian Chondrichthyes, the Iniopterygia, which was interpreted to have an autostylic jaw suspension like that of Holocephali with the upper jaw fused to the neurocranium (Zangerl and Case, 1973), led to new interpretations of the origin of Holocephali. Based on comparative anatomical studies of iniopterygians and other chondrichthyan fishes, Zangerl and Case (1973: 64) determined that the iniopterygians represent structural intermediates between elasmobranchs and chimaeroids, and it was concluded that Holocephali and Iniopterygii are sister groups that evolved from a common chondrichthyan ancestor. The subclass Subterbranchialia (Zangerl, 1979) was erected to include all Chondrichthyes with an autostylic jaw suspension and gill arches concentrated underneath the neurocranium. It was later discovered that autostyly is not found in all Iniopterygii (Stahl, 1980). Although Subterbranchialia is not a monophyletic group because it is united by a symplesiomorphy (Zangerl, 1981: 39), it remains in the litera-

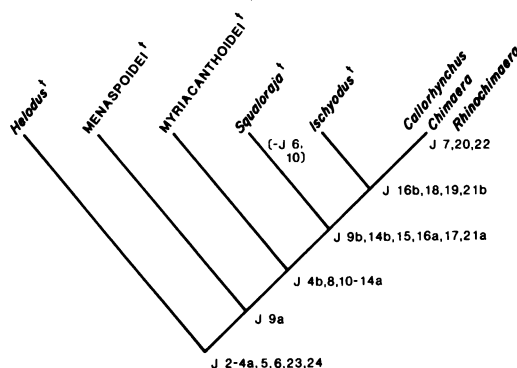


Fig. 2. Phylogenetic interpretation of Maisey (1986). In this first cladistic analysis of holocephalan relationships only the best known fossil forms are indicated and the living forms, represented by *Callorhynchus* (= *Callorhinchus*), *Chimaera*, and *Rhinochimaera*, are shown as the terminal branch of this cladogram united by characters J7, J20, and J22. Characters J1–J24 are renumbered in this study and listed in table 3 (reproduced from Maisey, 1986: 220).

ture today as a "wastebasket" group of chondrichthyan fishes that excludes elasmobranchs.

A second perspective (Lund, 1977) resurrected the subclass Bradyodonti to include Holocephali and was defined as the sister group to Elasmobranchii. Lund (1977) united the Bradyodonti on the basis of slow tooth replacement and an operculate gill chamber. With the discovery of new cochliodont fossils from the Mississippian, Lund (1986a, b) revised his previous (1977) interpretation of holocephalan relationships and dismissed Bradyodonti as an invalid taxonomic group. Instead, he suggested that holocephalans are probably closely related to the cochliodonts (Lund, 1986a, b).

In the most recent analysis of holocephalan relationships, Maisey (1986) completed a cladistic analysis of the following fossil and Recent taxa: *Helodus*, *Menaspoidei*, *Myriacanthoidei*, *Squaloraja*, *Ischyodus*, *Callorhynchus*, *Chimaera*, and *Rhinochimaera*. The resulting cladogram (fig. 2) was supported by 24 morphological characters of both the skeleton and soft tissues (Maisey, 1986: 220, table 5). Based on this cladistic analysis, *Ischyodus* was determined to be the immediate sister taxon to the living chima-

**TABLE 5**  
**Holocephalan Characters Summarized by Maisey (1986)**

- 
- 
- 24. (J2) Holostylic jaw suspension
  - 25. (J3) Branchial arches located below braincase
  - 26. (J4a) Synarcual articulates with dorsal basal
  - 27. (J5) Dibasal pectoral (propterygium and metapterygium)
  - 28. (J6) Erectile dorsal spine and associated cartilage
  - 29. (J23) Few intermediate segments between pelvic basipterygium and clasper
  - 30. (J24) Basipterygium spans entire pelvic fin
  - 31. (J9a) Tooth plates
  - 32. (J4b) Synarcual shorter than neurocranium
  - 33. (J8) Rostral cartilages
  - 34. (J10) Tritoral areas on tooth plates
  - 35. (J11) Polyspondylous notochordal rings
  - 36. (J12) Sensory canals in open grooves lined by crescent-shaped scales
  - 37. (J13a) Tenacula (prepelvic clasper) present only in males
  - 38. (J14a) Frontal clasper
  - 39. (J9b) Two upper pairs of tooth plates and one lower pair of tooth plates (more in some fossils)
  - 40. (J14b) Frontal clasper only in males
  - 41. (J15) Enlarged labial cartilages
  - 42. (J16a) Reduced squamation (nongrowing denticles)
  - 43. (J17) Characteristic sensory canal arrangement on head
  - 44. (J21a) Process on pelvic girdle for tenaculum
  - 45. (J21b) Process on pelvic girdle for tenaculum is jointed and movable
  - 46. (J16b) Denticles only at dorsal midline and along sensory canals
  - 47. (J1) Ethmoid region encloses superficial ophthalmic nerves in an ethmoid canal; no ethmoid keel
  - 48. (J19) Interorbital septum
  - 49. (J7) Lateral walls of fin-spine lack trabecular osteodentine (= trabecular dentine)
  - 50. (J20) Ventral fusion of scapulocoracoids
  - 51. (J22) Closure of adult hypophyseal foramen; isolation of ventral lobe of pituitary external to cranium in roof of oral cavity<sup>a</sup>
- 

<sup>a</sup> It is noted by Maisey (1986) that this feature may have evolved independently in Recent elasmobranchs and chimaeroids.

eroids, and *Helodus* was interpreted as representing the primitive holocephalan condition (Maisey, 1986: fig. 2).

Figure 3 is my summary diagram of the cladistic analysis of Maisey (1986). Although Maisey (1986) provided the most rigorous cladistic analysis of holocephalan relationships to date, he did not attempt to resolve the relationships of the extant chimaeroids. Nevertheless, I use Maisey's (1986) analysis for two reasons: first, this work is the most recent rigorous cladistic analysis of holocephalan relationships; and second, it is the only study with the specific goal of understanding the phylogeny of Recent taxa and therefore uses soft tissue characters and embryological evidence. This working hypothesis of holo-

cephalan relationships is my framework for phylogenetic study of the living forms.

I have renumbered the chondrichthyan and holocephalan characters of Schaeffer (1981) and Maisey (1984, 1986: tables 1, 5) according to my synapomorphy scheme (fig. 3; characters 1–23). It is accepted that Holocephali and Elasmobranchii are Chondrichthyes and that they are sister groups. Holocephali is a monophyletic group based on Maisey's (1986) characters: J2–4a, 5, 6, 23, 24 (24–30 in fig. 3). Characters at these levels will not be treated further in this study.

Because my goal is to understand the relationships of living forms, I have not attempted to resolve relationships among fossil taxa, whose relationships remain problem-



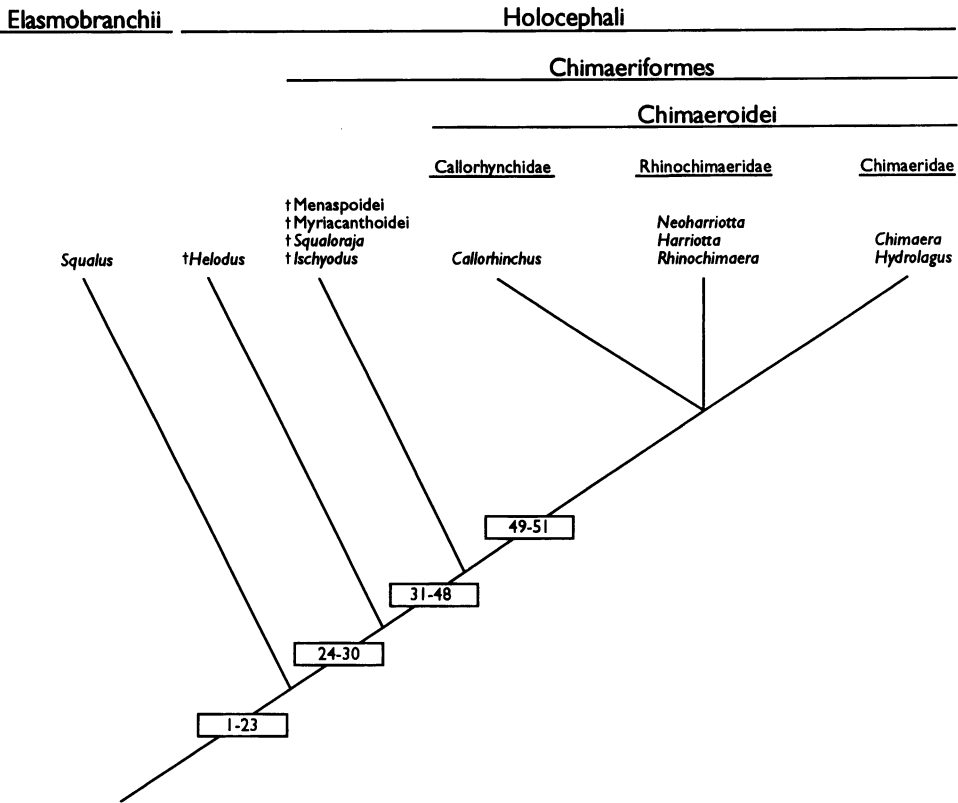


Fig. 3. Summary of phylogenetic interpretations. This summary diagram, based primarily on the cladistic interpretation of Maisey (1986), shows the three families of living chimaeroids as an unresolved trichotomy. Although some fossil taxa are here represented outside Chimaeroidei (e.g., *Ischyodus*), there is evidence to suggest that this is an oversimplification; however, the purpose of this analysis is to resolve relationships among the living forms and a thorough discussion of relationships among fossil taxa is beyond the scope of this study. Chondrichthyan characters (numbers 1–23) are taken from Schaeffer (1981) and Maisey (1986). The remaining characters (numbers 24–48) are from Maisey (1986). See text and table 1 for discussion of this interpretation and the characters.

atic. The fossil holocephalan taxa used by Maisey (1986) are grouped as a single lineage at the level of Chimaeriformes (fig. 3), all of which may or may not share characters 31–48. Because I do not deal with these characters individually in this analysis, I use them to artificially unite a diverse assemblage of fossil chimaeriforms; however, it should be understood that these taxa are not accepted as a single lineage (as indicated in fig. 3).

The relationships among Recent forms are still not well understood nor have the characters for defining monophyletic groups (e.g., at the familial level) among the extant forms been analyzed. This study focuses exclusively on relationships among Chimaeroidei.

TAXONOMIC REVIEW OF CHIMAEROID SPECIES

Species-level relationships of extant chimaeroids have yet to be examined and many species are still undescribed (Last, personal commun.; Stehmann, personal commun.; personal obs.). Table 6 lists all 34 known extant species of chimaeroids (Didier, 1993).

Three families of Recent chimaeroids are recognized (Nelson, 1984): Callorhynchidae, Rhinochimaeridae, and Chimaeridae. Gill (1898) published a classification in which the subfamily Harriottinae was erected, and Dean (1904b: 20) considered that *Harriotta* might more properly belong to its own family, Har-

**TABLE 6**  
**List of Recent Taxa and Synonymy**

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Family Callorhynchidae Garman, 1901

Callorhynchus Lacépède, 1798 (ex Gronovius, 1763)

Callorhynchus callorhynchus Linnaeus, 1758

= Callorhynchus antarcticus Lay and Bennett, 1839

= Callorhynchus peronii Duméril, 1865

= Callorhynchus argenteus Philippi, 1892

= Callorhynchus elephantinus Bory de St. Vincent, 1923

= Callorhynchus smythii Lay and Bennett, 1839

= Callorhynchus tritoris Garman, 1904

Callorhynchus milii Bory de St. Vincent, 1823

= Callorhynchus australis Owen, 1854

= Callorhynchus tasmanius Richardson, 1840

= Callorhynchus dasycaudatus Colenso, 1878

Callorhynchus capensis Duméril, 1865

Family Rhinochimaeridae Garman, 1901

Rhinochimaera Garman, 1901

Rhinochimaera pacifica (Mitsukurii, 1895)

Rhinochimaera atlantica Holt and Byrne, 1909

Rhinochimaera africana Compagno, Stehmann, and Ebert, 1990

Harriotta Goode and Bean, 1895

= Antelochimaera Tanaka, 1909

Harriotta raleighana Goode and Bean, 1895

= Antelochimaera chaetirhamphus Tanaka, 1909

= Harriotta curtis-jamesi Townsend and Nichols, 1925

= Harriotta opisthoptera Deng, Xiong, and Zhan, 1983

Harriotta haeckeli Karrer, 1972

Neoharriotta Bigelow and Schroeder, 1950

Neoharriotta pinnata (Schnakenbeck, 1929)

Neoharriotta carri Bullis and Carpenter, 1966

Family Chimaeridae Bonaparte, 1831

Chimaera Linnaeus, 1758

unavailable synonyms:

Callorhynchus americanus Gronovius, 1772<sup>a</sup>

Chimaera praecisa Walbaum, 1792<sup>a</sup>

Callorhynchus centrina Gronow in Gray, 1854<sup>a</sup>

Chimaera vaillanti Dean, 1906<sup>b</sup>

Chimaera monstrosa Linnaeus, 1758

= Chimaera argentea Ascanius, 1772

= Chimaera borealis Shaw, 1804

= Chimaera mediterranea Risso, 1826

= Chimaera cristata Faber, 1829

= Chimaera arctica Gistel, 1848

= Chimaera dubia Osorio, 1909

Chimaera cubana Howell-Rivero, 1936

Chimaera owstoni Tanaka, 1905

Chimaera jordani Tanaka, 1905

Chimaera phantasma Jordan and Snyder, 1900

Chimaera pseudomonstrosa Fang and Wang, 1932

Hydrolagus Gill, 1862

= Bathyalopex Collett, 1904

= psychichthys Fowler, 1902

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TABLE 6—(Continued)

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= <u>phasmichthyes</u> Jordan and Hubbs, 1925
<u>Hydrolagus mitsukurii</u> (Dean, 1904a)
= <u>Chimaera mitsukurii</u> Dean, 1904a
<u>Hydrolagus affinis</u> (Capello, 1868)
= <u>Chimaera plumbea</u> Gill, 1878
= <u>Chimaera abbreviata</u> Gill, 1883
<u>Hydrolagus africanus</u> (Gilchrist, 1922)
<u>Hydrolagus alberti</u> Bigelow and Schroeder, 1951
<u>Hydrolagus barbouri</u> (Garman, 1908)
= <u>Chimaera spilota</u> Tanaka, 1908
<u>Hydrolagus colliei</u> (Lay and Bennett, 1839)
= <u>Chimaera colliei</u> Lay and Bennett, 1839
= <u>Chimaera neglecta</u> Ogilby, 1888
<u>Hydrolagus deani</u> (Smith and Radcliffe, 1912)
<u>Hydrolagus eidolon</u> (Jordan and Hubbs, 1925)
= <u>Chimaera purpurescens</u> Jordan and Snyder, 1904
<u>Hydrolagus lemures</u> Whitley, 1939
<u>Hydrolagus macrophthalmus</u> Buen, 1959
<u>Hydrolagus media</u> (Garman, 1911)
<u>Hydrolagus mirabilis</u> (Collett, 1904)
<u>Hydrolagus novaezealandiae</u> (Fowler, 1910)
= <u>Chimaera australis</u> Hector, 1902
<u>Hydrolagus ogilbyi</u> (Waite, 1898)
= <u>Hydrolagus tsengi</u> (Fang and Wang, 1932)
<u>Hydrolagus purpurescens</u> (Gilbert, 1905)
= <u>Chimaera gilberti</u> (Garman, 1911)
<u>Hydrolagus waitei</u> Fowler, 1908
<u>Hydrolagus pallidus</u> (Hardy and Stehmann, 1990)

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<sup>a</sup> It is possible that these are synonyms of Chimaera monstrosa or perhaps Hydrolagus colliei because all lack an elongate rostrum and the respective localities are listed as "American Ocean" Gronovius (1772), Gronow in Gray (1854), and "American Pacific Ocean" Walbaum (1792); however, it is impossible to know exactly which species to refer these synonyms to and I have listed them as unavailable names under the genus. Dean (1906) suggested that the vague description of Callorhynchus centrina was a reference to Harriotta based on the locality, but the description does not fit that of a rhinochimaerid.

<sup>b</sup> This species exists as a name only, no description of a specimen or figure was ever published.

riottidae. Unfortunately Dean (1904b) did not provide a formal analysis of this familial distinction. Based on my analysis of the morphological features of rhinochimaerids, it seems that Harriotta and Neoharriotta might more properly be classified separately from Rhinochimaera.

Although the classification in table 6 is current, there are three notable taxonomic problems. First, note that the family name, Callorhynchidae, differs in spelling from the generic name, Callorhynchus. Although the generic name Callorhynchus is often found in the literature it was published in a work

that has been rejected by the International Commission on Zoological Nomenclature (Opinion 261, 1954; in Eschmeyer, 1990), and the emended generic name Callorhynchus is accepted in this work. Although correction in the generic name requires an emended family name (International Code of Zoological Nomenclature, 1985: art. 35d), the family name Callorhynchidae is maintained in this work for the sake of stability as being of "general acceptance" (ibid.: art. 40b, ii) until the International Commission on Zoological Nomenclature can address this problem.

The second taxonomic problem concerns

the suggestion that species of *Callorhinchus* may actually be variants of a single species (Norman, 1937; Bigelow and Schroeder, 1953: 562; Krefft, 1990: 117; Hardy, 1990: 88). The morphology of tritor pads on the tooth plates and the length of the pectoral fins are used to distinguish species of *Callorhinchus* (see Fowler [1941] for a key to species). Norman (1937) suggested that the pectoral fin and tooth plate characteristics used to distinguish species of *Callorhinchus* are highly variable and their usefulness as species-defining characteristics is questionable. This conclusion received support from Bigelow and Schroeder (1953: 562); nevertheless, until a revision of *Callorhinchus* is completed, all three species listed in table 6 will be accepted.

The third noteworthy point concerns the validity of *Chimaera* and *Hydrolagus* as distinct genera (Hardy and Stehmann, 1990). The only feature that distinguishes these two genera is the presence of an anal notch in the subcaudal fin of *Chimaera* that is absent in *Hydrolagus*. All known undescribed species of chimaeroids belong to the family Chimaeridae, but generic determination is difficult because the delicate fin webs are easily torn, making it impossible to determine if an anal notch is present. These undescribed species will likely remain so until the significance of the anal notch as a generic character is better understood and more reliable specific characters are defined.

#### COMPARATIVE ANATOMICAL STUDIES

In subsequent descriptions, general comments on anatomical features precede family-by-family treatments, with Callorhynchidae always first, Rhinochimaeridae second, and Chimaeridae third. This order reflects the systematic conclusions of this work. I first provide a brief discussion of some aspects of development including a description of the morphology of the egg capsules. All other anatomical descriptions focus on adult morphology with an analysis of external features, comparative anatomy of the lateral line canals, skeletal anatomy including descriptions of the neurocranium, gill arches, vertebral column, paired fins, and girdles, and gross

morphology and histology of the tooth plates. Lastly, the musculature is described for all six genera.

A list of all specimens studied in detail is provided in table 7. Adults are defined as sexually mature or maturing individuals. Relatively smaller individuals that do not exhibit any features of sexual maturity (such as eggs maturing in the ovaries of females or secondary sexual characteristics in males) are defined as juveniles. Embryos include all stages inside the egg case up to hatching. The number of skeletons is the total of wet and dry skeletal preparations of both adults and juveniles.

#### COMMENTS ON DEVELOPMENT

All chimaeroid fishes are oviparous. Because these fishes generally live at great depths, the only obstacle to collecting developmental material has been locating the eggs and spawning sites. Females have large yolky eggs that are fertilized inside the oviduct and enclosed within a keratinous egg case produced by the shell gland located at the anterior end of each oviduct. Two egg cases are deposited simultaneously, one from each oviduct. A single embryo will develop within the enlarged portion of the egg case. Inside the egg case the embryos always lie on their left side with the head facing anteriorly and the tail extending posteriorly into the tail sheath. Like elasmobranchs, these embryos beat their tails to facilitate circulation of water inside the egg case. Dean (1903) thought that constant movement of the tail is used to circulate water through the egg case for exchange of gases. This behavior has been observed for elasmobranchs, such as skates, that develop inside similar egg cases (Pelster and Bemis, 1992).

Although only two egg cases are deposited at a time, the ovaries of gravid females have developing eggs of all stages and a single female may deposit several pairs of eggs during the breeding season (Dean, 1906; Gorman, 1963; Stanley, 1963; Sathyanesan, 1966). It has been suggested that females may store sperm (as do other chondrichthyans) and this would facilitate multiple spawning events in chimaeroids (Stanley, 1963).

Due to the method of bulk collecting eggs

TABLE 7  
Summary of Specimens Examined in Comparative Morphological Analysis<sup>a</sup>

	adult	juvenile	embryo	TOTAL	skeletons
Family Callorhinchidae					
<u>Callorhinchus milii</u>	12	29	37	78	23
Family Rhinochimaeridae					
<u>Rhinochimaera pacifica</u>	2	3	-	5	1
<u>Harriotta raleighana</u>	3	5	-	8	5
<u>Neoharriotta pinnata</u>	1	1	-	2	-
Family Chimaeridae					
<u>Hydrolagus colliei</u>	33	53	7	95	32
<u>Hydrolagus novaezealandiae</u>	7	5	-	12	7
<u>Hydrolagus</u> sp. B	5	6	-	11	9
<u>Hydrolagus mirabilis</u>	-	1	-	1	-
<u>Chimaera monstrosa</u>	1	2	-	3	-
<u>Chimaera</u> sp. C	2	-	-	2	-

<sup>a</sup> For each specimen, collection data, locality, detailed measurements, and gut contents were recorded and are available from the author; data and collection numbers are also on file at the AMNH.

of *Callorhinchus* in the field, there was no reliable way to determine the age of embryos. Because there is no complete staging scheme for any chimaeroid embryos, the only way to determine relative stage of development was by comparing total lengths (TL). This is not a particularly good indicator of the actual state of development because temperature may have affected growth in subtle ways and allometric growth of the body relative to the length of the tail will lead one to mistakenly interpret total length measurements. Until a scheme for staging chimaeroid embryos is developed the total length measurement will serve as an indication of relative embryonic stage. A representative series of embryos of *Callorhinchus milii* is shown in figure 4.

In earliest embryonic stages the yolk sac (YS; fig. 4) is ovoid. As the embryo develops, the yolk sac changes shape, hardens, and forms characteristic bulges (LB). As the embryo grows, the head lies within the pocket formed by these bulges. This occurs in *Hydrolagus* as well as in *Callorhinchus*, and the shape of the yolk sac is the same in both species. The embryo is attached to its yolk sac by a yolk stalk just anterior to the pectoral girdle. Most of the yolk mass lies anterior to the embryo, and as it is resorbed the yolk sac becomes more ventral in position.

Early embryos have an anterior bulbous process, the rostral bulb (RB; fig. 4). This elongate rostral bulb is a hollow vesicle lined by a layer of columnar epithelium. It extends from the anterior end of the developing head and curves dorsally to lie directly in front of the head. The rostral bulb is at its maximum size in younger embryos 20–40 mm TL, and gradually becomes reduced in size until it is no longer evident. The fate of this structure is unknown; however, Allis (1917, 1926) suggested that the rostral bulb plays a role in shaping the neurocranium in its early stages of development.

External gill filaments (GF; fig. 4) first begin to develop when embryos are about 50 mm TL. Tiny, developing gill filaments can be seen as small loops from the external edges of the gill arches in even the very smallest embryos. As the embryo grows the external gill filaments lengthen and appear bright red as they are infused with blood. Each gill filament consists of a single, looped blood vessel, an outgrowth of the aortic arch, which extends from the back of the developing gill arch. These blood vessels are looped by folding back on themselves and a thin membrane of tissue holds the loop to itself. The external gill filaments reach their maximum length of 20–30 mm in embryos of 75–80 mm TL. As

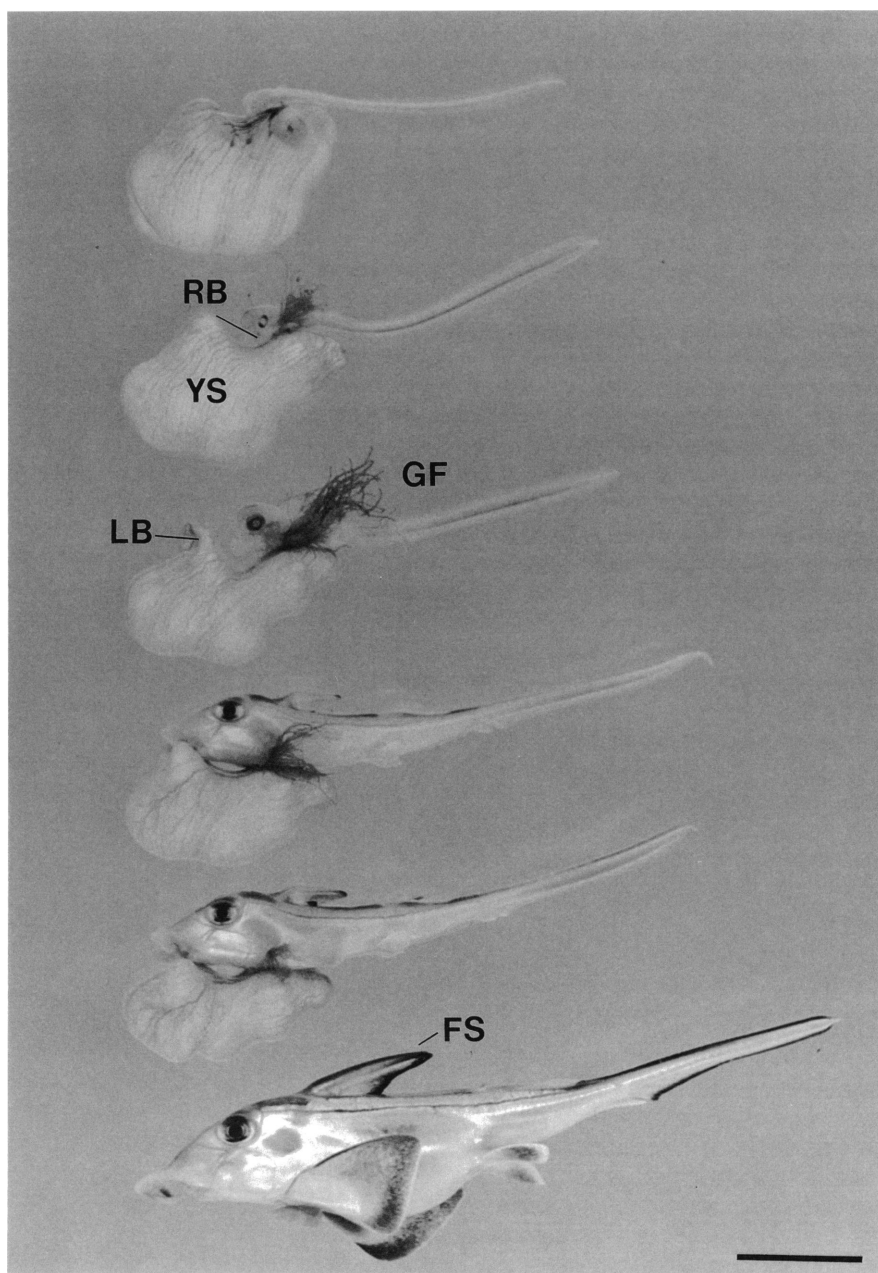


Fig. 4. Series of embryos of *Callorhinchus milii*. These six embryos of *Callorhinchus milii* range in size from 53 mm TL (at top) to 122 mm TL (bottom). In all chimaeroid embryos studied the yolk sac (YS) develops a unique bulged shape (LB). Embryos develop long external gill filaments (GF) that are gradually resorbed as the functional gills and operculum develop. The tail, which in this species is heterocercal, does not develop its characteristic morphology until the embryo is near hatching. Based on the relatively straight tail in this embryo, it appears that some posthatching development and modification of the tail occurs before it is fully heterocercal. The fin spine (FS) remains relatively soft until after hatching, when it soon becomes mineralized. Scale bar = 2 cm.

the gill arches and opercular flap become fully developed the external gill filaments are gradually resorbed by the embryo until they are no longer visible externally.

The eyes (E) are extremely large and well developed in early embryonic stages and the pigment of the retina is evident in embryos that are 50 mm TL. The large eyes play a key role in shaping the neurocranium, as is evident when examining the neurocranial structure of adults, especially species with extremely large orbits. It has been hypothesized (Dean, 1906; Allis, 1917, 1926; de Beer and Moy-Thomas, 1935; Holmgren, 1942) that the formation of a connective tissue interorbital septum as well as the unique brain formation in which the brain lies behind the eye and the olfactory tracts run ventral to the eye are the result of development of such large eyes.

Pigmentation is first visible as a series of dark patches on the dorsal surface of *Callorhynchus* embryos that are 75 mm TL. The dorsal surface of the head becomes darkly pigmented shortly thereafter. Older embryos (100 mm TL) are fully pigmented, showing the adult color patterns with black saddle-like bands on the dorsal surface and black patches along the trunk. The paired and median fins become darkly pigmented at their distal ends.

The dorsal fin spine (FS; fig. 4) begins to form in association with the first dorsal fin in embryos of about 50 mm TL. In these early stages the fin spine is soft and is bent to fit inside the egg case.

Embryos and newly hatched juveniles possess denticles on top of the head and along the dorsal surface of the body. The early development of these denticles was first described by Schauinsland (1903). The head denticles lie medial to the supraorbital lateral line canal and form a U-shaped pattern atop the head. Occasionally a few denticles may develop lateral to the supraorbital lateral line canal. Along the dorsal surface there are two rows of denticles in the interspaces between the first and second dorsal fins and between the second dorsal and caudal fins. These denticles are absent in adults.

The palatoquadrate becomes indistinguishably fused to the trabecular cartilages at a very early stage in development. In the *Cal-*

*lorhynchus* embryos that I studied, the palatoquadrate had already fused to the neurocranium in embryos of about 75 mm TL. Procartilaginous rudiments are evident in embryos of 60–70 mm TL. At this stage the trabecular, polar, and parachordal cartilages are beginning to form the base of the neurocranium. The roof of the neurocranium has not yet begun to form and the ethmoid and otic regions are in early stages of formation. Extending from the lateral edges of the trabecular cartilages in the anterior region of the developing neurocranium are two small triangular cartilages. In a cleared and stained embryo (72 mm TL) there is a small space between these triangular cartilages and the trabeculae. In all other stages these small cartilages are attached to the lateral edge of the trabecular cartilage and extend ventrally. It appears that these cartilages may be involved in the formation of the quadrate process of the upper jaw. The fusion of these cartilages to the base of the neurocranium can be seen in a histological section (PQ; fig. 5). I am unable to determine the exact boundaries of the palatoquadrate cartilage, but I interpret it to be, at least in part, the tiny triangular cartilage that fuses to the trabeculae very early in development (Didier, 1990). Further study of earlier stages should confirm the exact formation of the autostylic palatoquadrate. Schauinsland (1903: fig. 130) illustrated this tiny cartilage in his reconstruction of the neurocranium of an embryonic *Callorhynchus* (60 mm TL), and this beautiful figure has been cited and refigured many times in the literature (e.g., de Beer and Moy-Thomas, 1935: fig. 16). Unfortunately, Schauinsland (1903: fig. 130, md) has misinterpreted or mislabelled this cartilage as Meckel's cartilage and in his text states that Meckel's cartilage is not yet developed. In my study of *Callorhynchus* embryos a well-developed Meckel's cartilage is evident below the developing neurocranium in early stages, so I must disagree with Schauinsland's (1903) interpretation.

A spiracle is present in early developmental stages of *Callorhynchus* and becomes obliterated as the opercular flap develops. The spiracle has also been reported in embryonic *Hydrolagus* (Dean, 1906). Before skeletal elements are beginning to form (in embryos of

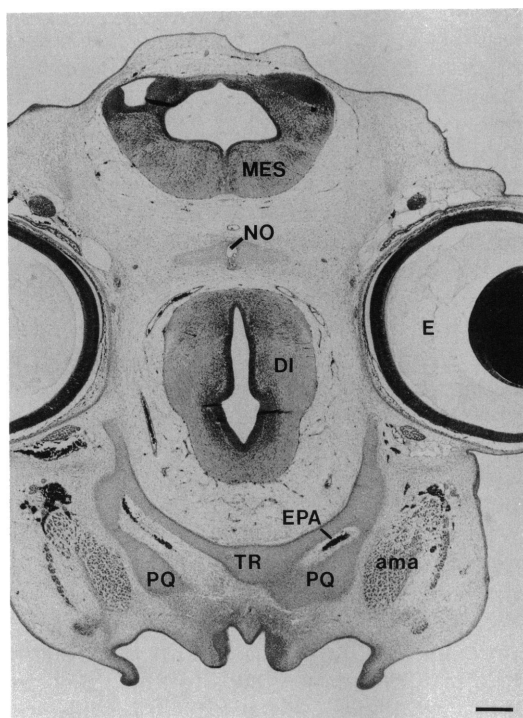


Fig. 5. Development of the autostylic jaw in *Callorhynchus milii*. In this cross section of the head of an embryo of *Callorhynchus milii* (CM42, 74 mm TL), the fusion of the palatoquadrate to the lateral edges of the trabeculae (TR) is evident. The efferent pseudobranchial artery (EPA) is enclosed in a short canal formed by the connection of the palatoquadrate to the neurocranium. The EPA is visible in more posterior sections dorsal to the trabeculae for a very short distance before entering the orbit. The dorsal surface of the embryo is at the top of the figure where the tip of the notochord (NO), surrounded by developing parachordal cartilages, lies dorsal to the diencephalon (DI) and ventral to the mesencephalon (MES). Scale bar = 0.5 mm.

20–30 mm TL), the hyoid arch is displaced anteriorly and lies in close proximity to the developing jaws. Anterior to the hyoid arch the spiracle can be seen as a small, dorsally located opening (SP; fig. 6). Posterior to the hyoid arch is an enlarged first gill opening. The opercular flap develops as a sheet of tissue extending from the posterior edge of the hyoid arch and grows caudally to cover the developing gill arches. It is almost completely formed in embryos of 100 mm TL.

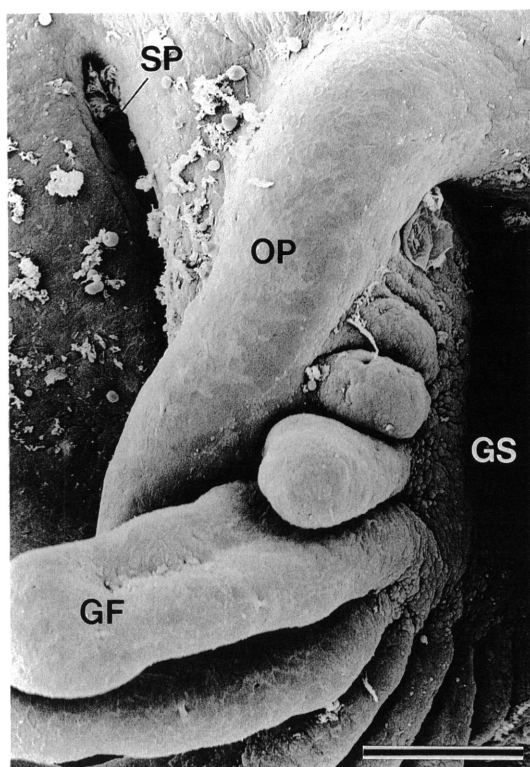


Fig. 6. Development and closure of the spiracle. A close-up of the spiracle is shown in this scanning electron micrograph of an early embryo of *Callorhynchus milii* (CM74, 40 mm TL). Dorsally, near the top of the figure, the spiracle is evident as a tiny opening anterior to the hyoid arch. From the posterior edge of the hyoid arch the opercular flap (OP) and external gill filaments (GF) are beginning to develop. As the hyoid arch and opercular flap develop, the spiracle closes and is not present in adults. Scale bar = 1 mm.

#### EGG CASES

Chimaeroid egg cases are composed of a flexible keratinous material that hardens as it ages in water. The egg cases are of three distinct types, each characteristic of one of the three families. It is difficult to associate chimaeroid egg cases with a particular genus or species unless an embryo is found within the egg case itself or only one species is known from the locality; therefore, most egg cases should be attributed to a family and not to a genus or species.

Callorhynchids have extremely large ovoid egg cases. A representative egg case of *Cal-*



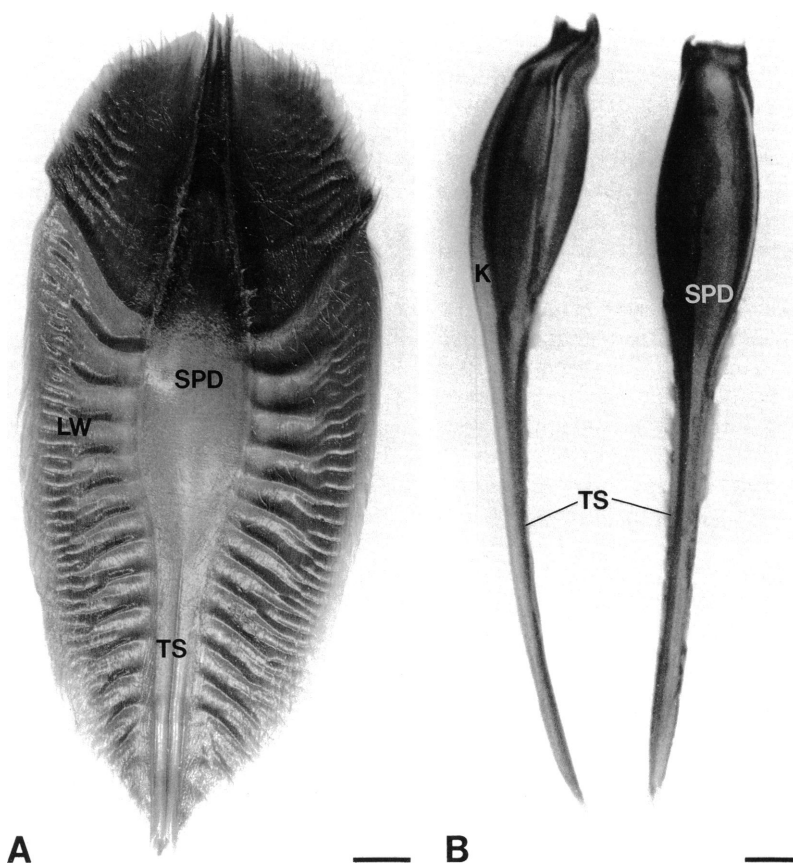


Fig. 7. Egg cases of two chimaeroid fishes. **A**, An egg case of *Callorhynchus milii*. The dorsal surface is shown with the anterior end of the egg case at the top. The embryo will develop within the central spindle (SPD), with its long tail extending into the tail sheath (TS). The egg cases of callorhynchids have well-developed, ridged lateral webs (LW). Scale bar = 1 cm. **B**, The egg cases of an undetermined species of *Hydrolagus* shown in lateral (left) and ventral (right) view. The flattened anterior end of the spindle (SPD; top of the page) is equipped with perforated lateral edges to allow easy separation of the egg case during hatching. On the dorsal surface of the spindle is a raised keel (K). Scale bar = 1 cm.

*lorhinchus milii* is 270 mm long and 130 mm wide (fig. 7A). The central spindle (SPD) consists of an enlarged oval capsule that tapers to a point at each end; the elongate posterior end forms the tail sheath (TS), which houses the tail of the developing embryo. The thick walls of the central spindle form a sturdy protective shell for the developing embryo. A wide-ribbed lateral web (LW) extends around the edges of the central spindle. The web is quite thin and nearly transparent when held to the light; it is easily ripped and often tattered in older egg cases. The dorsal surface of the egg case is convex and is covered by

fine filamentous hairs that trap sediment and camouflage the egg case on the bottom. The smooth ventral side of the egg case is concave. At the anterior end of the egg case are two slits at the edge of the central spindle. These slits will gradually open to allow flow of water through the egg case and provide an opening from which the embryo hatches.

The egg cases of rhinochimaerids (not figured) are similar to those of callorhynchids in that they have a ribbed lateral web, but the central spindle is constricted giving the egg case a pearlike shape. The dorsal surface is convex and the ventral side is concave. The

egg cases of rhinochimaerids are smaller than callorhynchid egg cases. A typical egg case is about 145 mm long and 60 mm wide. Along the posterior edges of the central spindle is a series of small pores. These pores are tightly closed in newly laid egg cases and will gradually open to allow flow of water through the egg cases. The anterior end of the spindle has slits that open for release of the embryo at hatching.

Egg cases of *Hydrolagus* and *Chimaera* have a relatively smooth teardrop shape with a small lateral web (fig. 7B). The dorsal surface of the egg case is identified by the presence of a raised keel (K) along the midline. A representative egg case is 170 mm long and 25 mm at its maximum width. The anterior end of the spindle is bulbous and tapers posteriorly to an elongate tail sheath (TS). Along each side of the tail sheath is a series of small pores that open during later stages of embryonic development (Dean, 1906). A raised lip extends around the anterior edge of the egg capsule. This lip demarcates the opening through which the embryo is hatched from the egg case. The lip is tightly sealed during the early stages of development and gradually loosens along its edge during development.

#### EXTERNAL FEATURES OF ADULTS

All chimaeroid fishes have large heads and long, tapering bodies. They rarely exceed 1 m in length, but will grow to massive sizes by increasing their overall bulk. Each of the three families of chimaeroids is distinguished by a unique snout, which is specialized to house numerous electroreceptive ampullary sense organs (Fields and Lange, 1980; Fields et al., 1993). Internally, the snout is supported by three rostral rods, a dense jelly like material, and connective tissue. Externally, the snout is characterized by groups of ampullary sense organs that appear as clusters of open pores on the surface. The pores vary in number and size but are located in a consistent pattern next to the cranial lateral line canals in all species examined.

The notochord extends to the tip of the tail which often terminates in an extremely long, thin whiplike extension. In callorhynchids, all of which have a heterocercal tail, the no-

tochord is bent upward and a small hypocercal lobe supported by a few small cartilaginous elements is present ventral to the notochord. All other chimaeroids have a leptocercal tail in which the notochord is straight. The leptocercal tail is characterized by dorsal and ventral fin webs (the supracaudal and subcaudal lobes of the tail, respectively), which lie opposite each other on the dorsal and ventral side of the notochord and are almost the same size and shape. The fin webs of the supracaudal and subcaudal lobes of the tail are supported solely by ceratotrichia.

Pigmentation of these fishes ranges from pale white, gray, or brown to a deep purple-black. Some species (e.g., *Hydrolagus colliei*, *Hydrolagus novaezealandiae*, and *Chimaera monstrosa*) are patterned with spots and lines. The scaleless skin is smooth with an almost rubbery texture. Small denticles are present on the head and dorsal surface of embryonic and juvenile chimaeroids but are lacking in adults.

One of the most distinctive external features of chimaeroids is the unusual lateral line canal system that forms a pattern of grooves or tubes on the surface of the skin. In all chimaeroids the canals are supported by C-shaped calcified rings that are open to the surface. These have been regarded as modified scales (Schauinsland, 1903: 13; Patterson, 1965: 198). The primitive condition is undoubtedly to have tubular canals, as in elasmobranchs and primitive osteichthyans. This condition is retained in callorhynchids; however, in rhinochimaerids and chimaerids the canals are modified as open grooves.

Although many workers have examined the lateral line canals, there have been few attempts to compare them among chimaeroids. The first comparative study (Garman, 1888) examined the pattern of lateral line canals in *Chimaera monstrosa* and *Callorhynchus antarcticus*. An extensive study of the lateral lines of *Chimaera colliei* was done by Reese (1910). The lateral line canals of rhinochimaerids were described and figured by Garman (1904), Bullis and Carpenter (1966), Karrer (1972), and Compagno, Stehmann, and Ebert (1990). Bigelow and Schroeder (1953) provided detailed descriptions of the pattern of lateral line canals in a variety of chimaeroid species, including *Chimaera cu-*

*bana*, *Hydrolagus affinis*, *Hydrolagus alberti*, *Harriotta raleighana*, and *Callorhinchus milii*.

The overall pattern of lateral line canals in chimaeroids is unique and difficult to homologize among vertebrates (Patterson, 1965; Northcutt, 1989). The pattern of lateral line canals is poorly understood in chimaeroid fishes and further study of their development is essential for determining their exact homologies and evolution. Until these issues are worked out, any scheme of nomenclature will be incomplete. For my descriptive purposes, I use a simplified nomenclature based on morphological landmarks rather than nervous innervation (although Fields et al., [1993] provide new information which should result in changes to the interpretation presented here). The terminology I use is based on the system first devised by Garman (1888); with modern terminological modifications from Northcutt (1989), Compagno et al. (1990), and Fields et al. (1993). Occasionally the pattern of lateral line canals differs slightly between the right and left sides of the animal (Bigelow and Schroeder, 1954; personal obs.). Significant variations are noted in the text.

The pattern of cranial lateral line canals is similar for all chimaeroids, and this description begins at the otic region and follows the canals anteriorly and ventrally. Figure 8 illustrates the general lateral line canal pattern in chimaerids, although there are some significant differences that are noted in the individual family descriptions. The supratemporal canal (ST) forms a commissure across the top of the head just anterior to the fin spine. At the dorsal midline there may be a tiny caudally directed extension of this canal toward the fin spine. This short extension varies among individuals from a straight line to a tiny curl (Bigelow and Schroeder, 1954). From the supratemporal canal the supraorbital canal (SO) passes anteriorly above the eye. At this junction the occipital canal (OC) continues ventrally and intersects the lateral line canal of the trunk (LLC), which extends posteriorly along the lateral surface of the body to the tip of the tail. In all specimens studied the lateral line canal runs along the lateral body wall and makes a dramatic ventral dip at the origin of the supracaudal fin

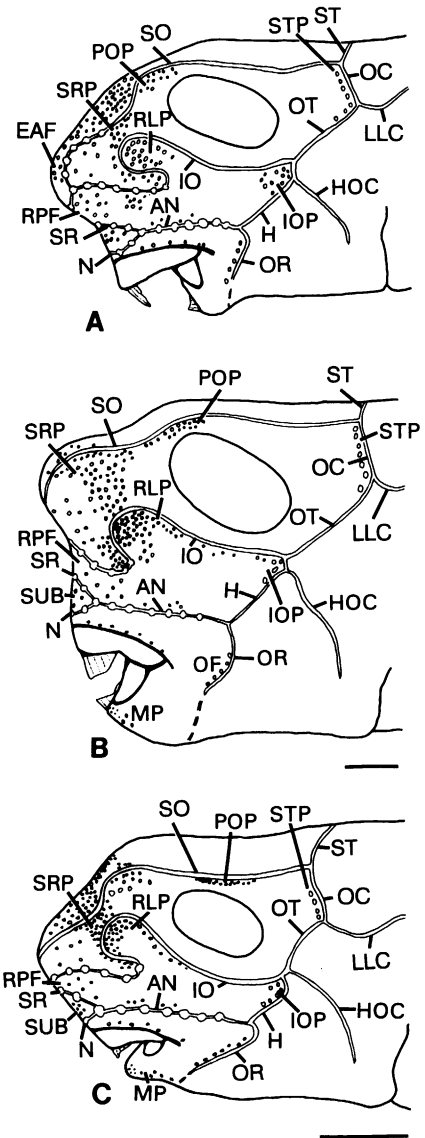


Fig. 8. Comparative cranial lateral line canals and ampullary pore fields of chimaerids. A comparison of the lateral view of the head is shown for A, *Hydrolagus* sp. B; B, *Chimaera* sp. C (NMNZ P19694); and C, *Chimaera monstrosa* (USNM 222708). Varying branching patterns of the preopercular (HOC) and oral (OR) canals are shown, and this feature may be species specific. The ampullary pore fields are also shown for comparison, although the labial and mandibular ampullary fields were not observed in all specimens. See text for a more detailed description of the lateral line canals and ampullary fields of chimaerids. Scale bars = 2 cm.

to run along the ventral edge of the caudal fin to its tip (fig. 8B).

The otic canal (OT) runs posterior to the eye and ventral to the branch point of the lateral line canal. Just below the eye the preopercular canal (=hyomandibular canal [HOC], Fields et al., 1993) extends ventrally over the opercular flap. This canal ends abruptly and continues around to the ventral midline as a series of short canals. Anterior to the preopercular canal a short canal runs horizontally, and in many species extends ventrally from the infraorbital canal. This horizontal canal (H) soon branches into the angular canal (AN) and the oral canal (OR). The angular canal runs above the mouth and the oral canal extends ventrally below the lower jaw where it breaks up into a series of short canals. The infraorbital canal (IO) runs underneath the orbit and extends rostrally onto the snout.

Associated with the lateral line canals of the head and snout are groups of pores that open to canals housing the ampullary sense organs. These clusters of pores, here termed ampullary fields, were first figured for *Hydrolagus coliei* by Allis (1916) and are homologous to the ampullae of Lorenzini of elasmobranchs (Fields et al., 1993). In Allis' unpublished drawings, three rostral ampullary fields and four cranial ampullary fields were identified on the basis of internal anatomy and innervation. Allis (1916, unpubl.; 1917) also identified a group of tiny, closely packed pores on the snout lying just above the nares in *Hydrolagus coliei* that he described as the openings of tiny epidermal gland cells. In keeping with the nomenclature for ampullary fields already established, I adopt the terminology of Fields et al. (1993).

Thirteen ampullary pore fields have been identified for *Hydrolagus coliei* on the basis of their innervation and pore location (Fields et al., 1993). These ampullary pore fields can be easily identified externally in all chimaeroids, although the relative location of the pore fields and the size and number of pores may vary between species. For a general illustration of the ampullary pore fields see figure 8; significant differences are noted in the text.

Eight discrete ampullary pore fields are evident on the lateral surface of the head. The

supratemporal ampullary pore field (STP) lies just posterior to the orbit along the anterior edge of the otic canal. Just above and slightly anterior to the eye is the preorbital ampullary pore field (POP). Ventral to the supraorbital canal, lying anterior to the preorbital ampullary pore field and bounded anteriorly by the junction of the supraorbital and infraorbital canals, is the suprarostal ampullary pore field (SRP). The rostralateral ampullary pore field (RLP) lies below the infraorbital canal anterior to the eye. In chimaeroids this field lies within the anterior loop of the infraorbital canal. At the junction of the infraorbital and oral canals is the infraorbital ampullary pore field (IOP), which is bounded caudally by the horizontal lateral line canal. Along the anterior edge of the oral lateral line canal is the oral ampullary pore field (OF), which usually can be seen continuing anteriorly along the dorsal edge of the lip. Along the dorsal edge of the angular canal is the angular ampullary pore field (APF). These pores sometimes appear to be part of the more anterior rostral ampullary pore field (RPF), which is located ventral to the infraorbital canal and dorsal to the subrostral canal near their junction on the snout. A ninth, spiracular ampullary pore field shown as a small cluster of pores posterior to the preopercular canal was described by Fields et al. (1993). I have not found such a group of ampullary pores; however, I have observed a few individual ampullary pores (not shown) posterior to the preopercular canal in some chimaerid species only. These may be part of the spiracular ampullary pore field described by Fields et al. (1993).

There are four ampullary pore fields visible on the ventral surface of the snout and around the mouth. The nasal ampullary field (NP) lies below the nasal canal and above the nares. Dorsal to the nasal canal, in the region bounded by the subrostral canal, is the subrostral ampullary pore field (SUB). Surrounding the mouth are two ampullary fields consisting of small groups of tiny ampullary pores. The mandibular ampullary pore field (MP) consists of groups of tiny pores at the oral edge of the lower lip, near the corners of the mouth, with some larger pores located near the short, ventral portions of the oral canal. The labial ampullary pore field (LP) is located

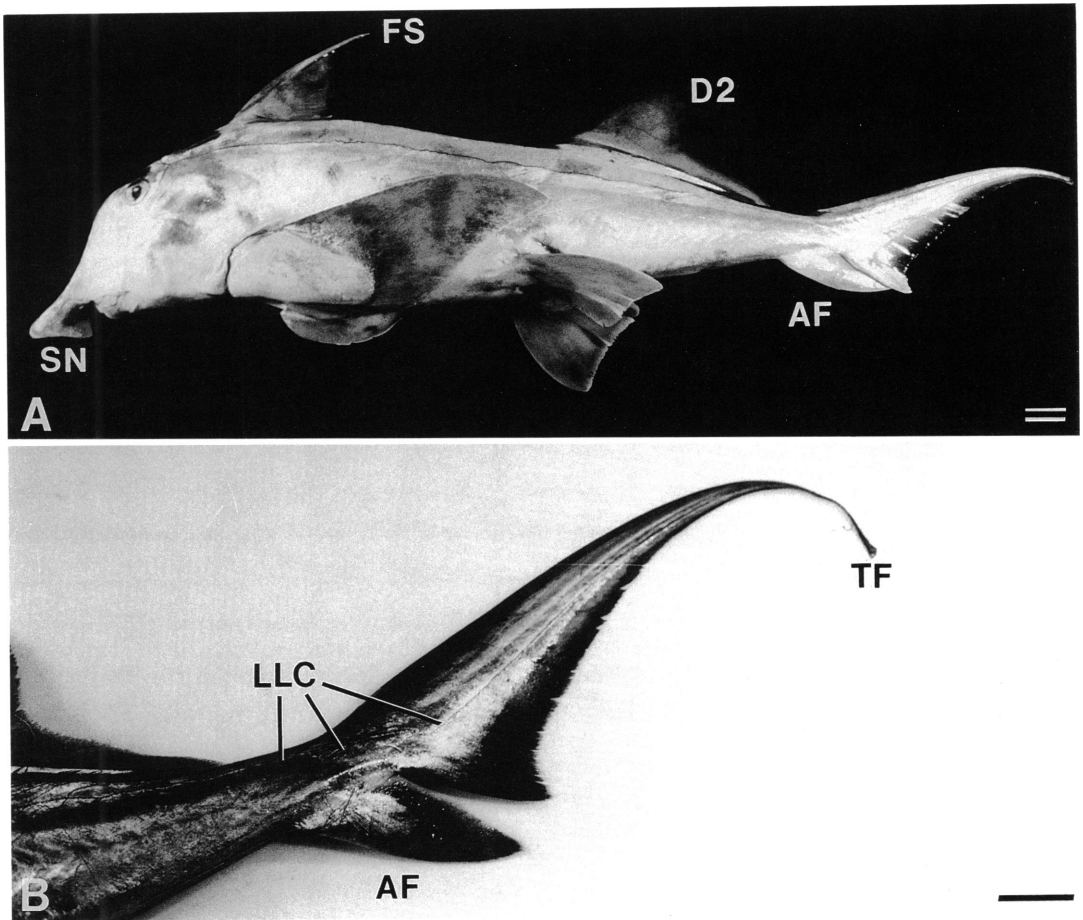


Fig. 9. External morphology of *Callorhynchus milii*. A, This specimen is an adult female showing the distinctive external features of callorhynchids, including a plowlike snout (SN), stout fin spine (FS), prominent second dorsal fin (D2), and anal fin (AF). Scale bar = 1 cm. (photograph courtesy of Clive Roberts, NMNZ) B, Heterocercal tail of *Callorhynchus milii*. The tail figured here shows the posterior dip of the trunk lateral line canal (LLC) and a short distal tail filament (TF). In all chimaeroids the trunk lateral line canal lies dorsal to the horizontal septum until it reaches the caudal fin. At the origin of the supracaudal lobe the trunk lateral line canal turns downward and runs along the ventral edge of the tail. Scale bar = 2 cm.

on the skin surrounding the labial cartilages at the corners of the mouth. The mandibular and ampullary pore fields could not be positively identified in all specimens. This may indicate their absence in some species or may be due to the small size of the pores and the shrinkage that occurs in preserved specimens.

Along the dorsal surface of the snout is what I term the ethmoid ampullary pore field (EAF), which lies between the supraorbital canals. This includes ampullary pores dorsal

to the supraorbital canal and above the junction of the supraorbital and infraorbital canals. This ampullary pore field is described from external observations only, and a detailed internal examination of these ampullary organs has not been completed. There is no reference to this group of ampullary pores in Fields et al. (1993) and it may be that these ampullary organs are not consistently present in all species or are unrelated to the ampullary organs described in their work.

CALLORHYNCHIDAE: Callorhynchids are

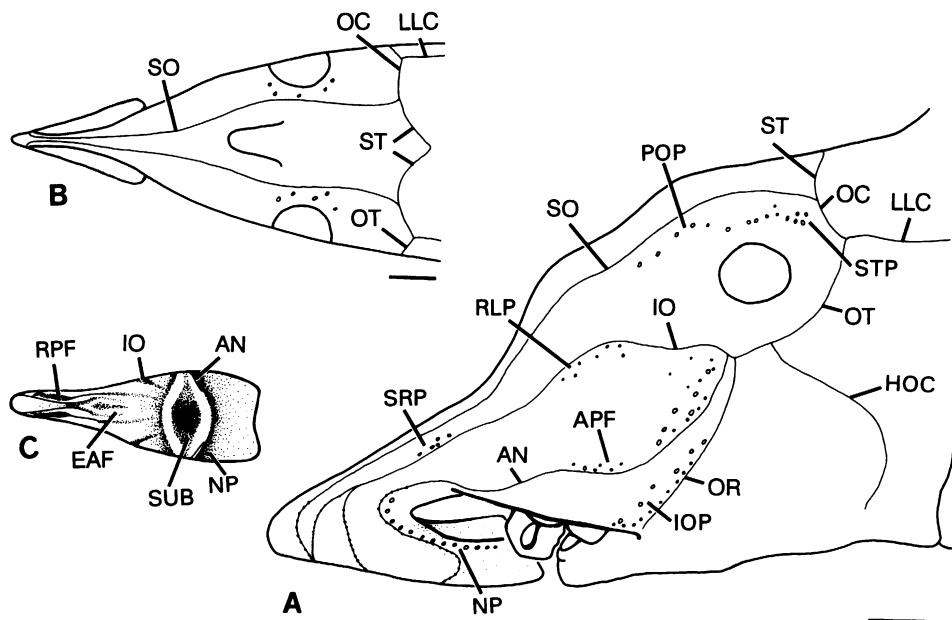


Fig. 10. Cranial lateral line canals and ampullary pore fields of *Callorhynchus milii*. Lateral line canals and ampullary fields are shown in A, lateral and B, dorsal view; C, ventral surface of the fleshy rostral flap. See text for detailed description of lateral line canals and ampullary pore fields. Scale bar = 2 cm.

characterized by an elongate snout with a fleshy plow-shaped flap that has no cartilaginous support (fig. 9A). The ventral surface of the fleshy flap is covered with dense concentrations of tiny pores that house electroreceptive organs (fig. 10). Although the canal pattern on the ventral surface of the snout flap differs from that of other chimaeroids in that the canals are not continuous across the midline, a nasal, subrostral, and ethmoid ampullary pore field can be recognized. The remaining ampullary fields in *Callorhynchus* are not as extensive as those found in other chimaeroids. The pores are much smaller and fewer in number. This difference in the ampullary fields may be related to the presence of a closed lateral line canal in callorhynchids.

All callorhynchid species have a heterocercal tail (fig. 9B) with a hypocercal lobe in which the ceratotrichia are supported by a series of small cartilaginous basal elements (usually five in number). The tail remains straight throughout development and only after hatching from the egg case does it achieve its heterocercal shape. A short tail filament

extends from the distal end of the epicercal lobe of the tail. Callorhynchids also have a distinct anal fin (AF) that is supported by a single basal element embedded in the ventral musculature of the tail.

The basic pattern of cranial lateral line canals in *Callorhynchus milii* is shown in figure 10. *Callorhynchus* is the only chimaeroid in which the oral (OR) and angular (AN) canals branch separately from the infraorbital canal. The oral canal ends at the margin of the mouth and continues around the lower jaw as a series of short canals. The angular canal runs above the mouth and ends abruptly on the ventral surface of the snout. Both the supraorbital and infraorbital canals extend onto the flap of the snout where they end. The supraorbital and infraorbital canals are joined near the tip of the rostrum by a short canal.

The lateral line canals are tubular, as opposed to the open grooves found in other chimaeroid families (fig. 11A). Although the canals appear as enclosed tubes in callorhynchids, they are supported by the calcified rings characteristic of all other chimaeroids. These calcified rings are relatively tiny and closely

spaced with about 53 per centimeter. The canal is almost entirely enclosed within these calcified rings and the tissue covering the lateral line canal is invested with numerous tiny calcifications.

**RHINOCHIMAERIDAE:** All members of this family are characterized by a fleshy, elongate snout that tapers to a point anteriorly (fig. 12A, B). Sexually mature males of the genus *Harriotta* are interesting in that they develop a series of rounded tubercles on the tip of the snout. The caudal fin is leptocercal, and basal cartilages are lacking in both the supracaudal and subcaudal fins in all rhinochimaerids. The tail ends in a long whiplike extension that extends posteriorly beyond the supracaudal and subcaudal lobes of the tail. This tail filament may be extremely long, almost equal to body length in some species. In *Rhinochimaera* and *Neoharriotta* the subcaudal lobe has long ceratotrichia, whereas the ceratotrichia of the supracaudal lobe are short, giving the tail an externally heterocercal shape. In *Rhinochimaera* the supracaudal lobe of males develops a series of paired tubercles along the distal margin of the fin web. *Neoharriotta* is distinguished among rhinochimaerids by the presence of an anal fin. The anal fin in *Neoharriotta* consists of a web of ceratotrichia that is supported by three tiny cartilages that form the fin base. Callorhynchids are the only other chimaeroids known to have an anal fin.

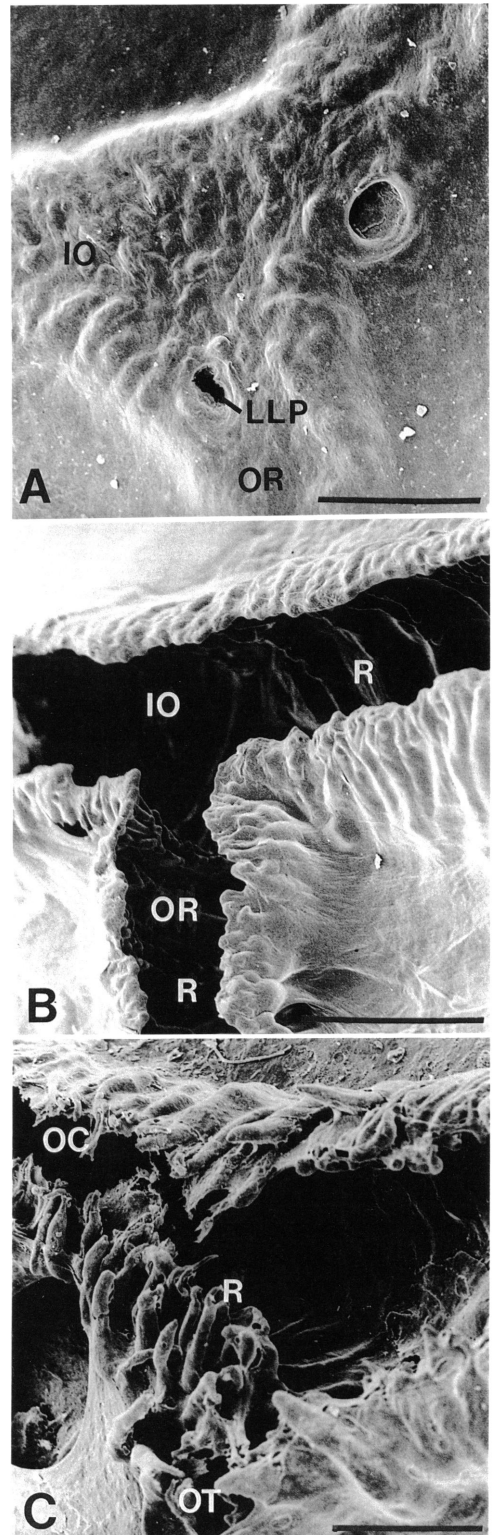


Fig. 11. Comparison of the lateral line canals among the three families of chimaeroids. A, Scanning electron micrograph of the closed lateral line canals of *Callorhinchus milii* at the junction of the infraorbital (IO) and oral (OR) canals. Lateral line openings (LLP) occur along the length of the canal. Scale bar = 0.5 mm. B, Scanning electron micrograph of the open lateral line canals of *Harriotta raleighana* (AMNH 96944) at the junction of the infraorbital (IO) and oral (OR) canals. The canals are open grooves supported by C-shaped calcified rings (R). Scale bar = 1 mm. C, Scanning electron micrograph of the open lateral line canals of *Hydrolagus* sp. B at the junction of the occipital (OC) and otic (OT) canals. A large ampullary pore lies lateral to the grooved canal, which is supported by calcified rings (R). The open, C-shaped rings are branched at their dorsal ends (often seen in chimaeroids), giving the edge of the canal a fringed appearance. Scale bar = 0.5 mm.



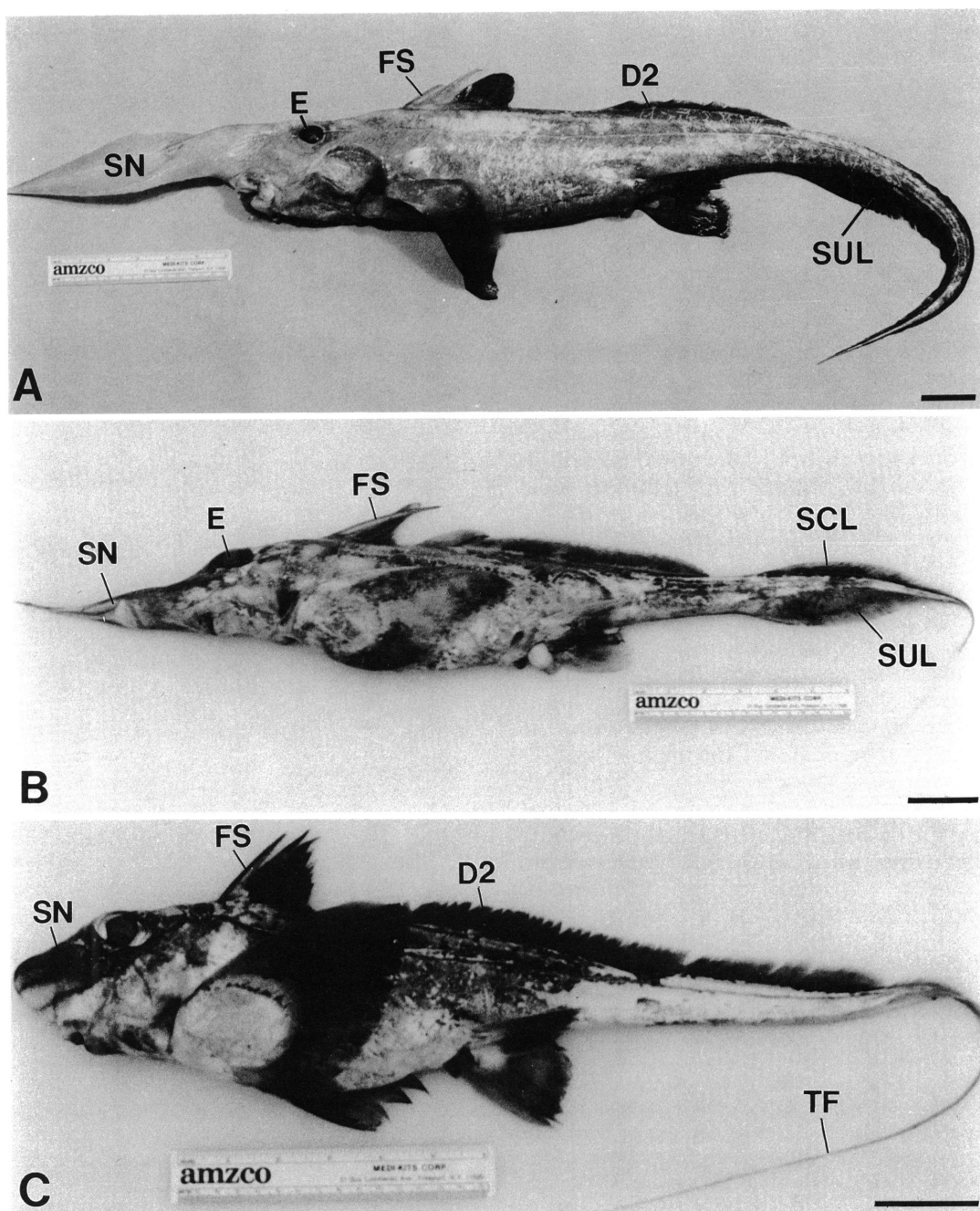


Fig. 12. External morphology of rhinochimaerid and chimaerid fishes. **A**, Photograph of *Rhinochimaera pacifica* (AMNH 96940). This immature male specimen, from the Challenger Plateau (fig. 1B, #4), measures 950 mm TL with a snout length of almost 250 mm. Characteristic of this genus is the wide, fleshy snout (SN), small eyes (E), and whiplike tail with elongate supracaudal (SCL) and subcaudal (SUL) lobes, the subcaudal lobe being much deeper. The fin spine (FS) in this specimen is broken. **B**, Photograph of *Harriotta raleighana* from Mernoo Bank (fig. 1B, #3). The snout (SN) of this genus is more firm than fleshy and tapers to a fine point anteriorly. Unlike *Rhinochimaera*, the eye is relatively



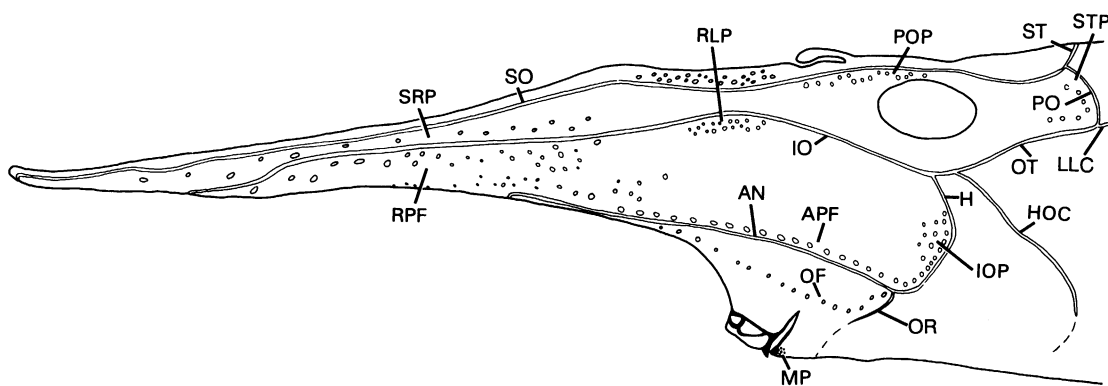


Fig. 13. Cranial lateral line canals and ampullary pore fields of *Rhinochimaera pacifica* (NMNZ P24198). Both the hyomandibular and oral lateral line canals terminate in a ventral series of short "broken" canals, illustrated dashed lines. The ampullary pore fields are shown in their approximate locations as groups of open circles. The size and number of pores shown are indicative of their actual size and density. See text for a detailed description and terminology. Scale bar = 2 cm.

All rhinochimaerids have open lateral line canals supported by calcified rings (fig. 11B). The canals of *Rhinochimaera pacifica* are supported by 39 calcified rings per centimeter. In *Harriotta raleighana* there are 18 rings per centimeter.

In rhinochimaerids the angular (AN) and oral (OR) canals share a common trunk, the horizontal canal (H), which curves antero-ventrally from the infraorbital canal (figs. 13–15). Although the rostrum is elongate, the general pattern of lateral line canals is conserved (fig. 16). The supraorbital canal runs along the dorsal surface of the snout, turning under at the anteriormost tip, where it continues on the ventral side of the snout to join the infraorbital canal. Posterior to this junction this canal continues along the lateral edge of the snout as the subrostral canal (SR), which joins the angular canal in *Harriotta* and *Neoharriotta*. *Rhinochimaera* lacks a connection

between the angular and subrostral canal (Garman, 1904; Compagno, Stehmann and Ebert, 1990). This connection between the angular and subrostral canals is not a synapomorphy of *Harriotta* and *Neoharriotta* because a connection is lacking in *Neoharriotta carri* (observed but not figured; Bullis and Carpenter, 1966).

The angular canal runs above the mouth and dips down onto the ventral surface of the snout where it loops above the nostrils. The nasal canal (N) is distinguished as that portion of the angular canal anterior to the junction of the subrostral canal. In *Rhinochimaera*, which lacks such a connection, the nasal canal is distinguished as that portion of the angular canal looped above the nostrils.

**CHIMAERIDAE:** Members of this family are characterized by a blunt fleshy snout (fig. 12C). The cartilaginous rostral rods that support the snout are greatly reduced. The snout is

←

large and the supracaudal and subcaudal lobes of the leptocercal tail are not elongate and are almost equal in size. C, Photograph of *Hydrolagus* sp. B. This species of *Hydrolagus* is common from Mernoo Bank, New Zealand, at 500–800 m depth. Evident in this photograph is the filamentous whip of the tail (TF) found in many chimaeroid species, an elongate second dorsal fin (D2), and snub-nosed snout (SN) characteristic of chimaerids. Scale bar = 5 cm; a 15-cm ruler is shown for scale in all three photographs.

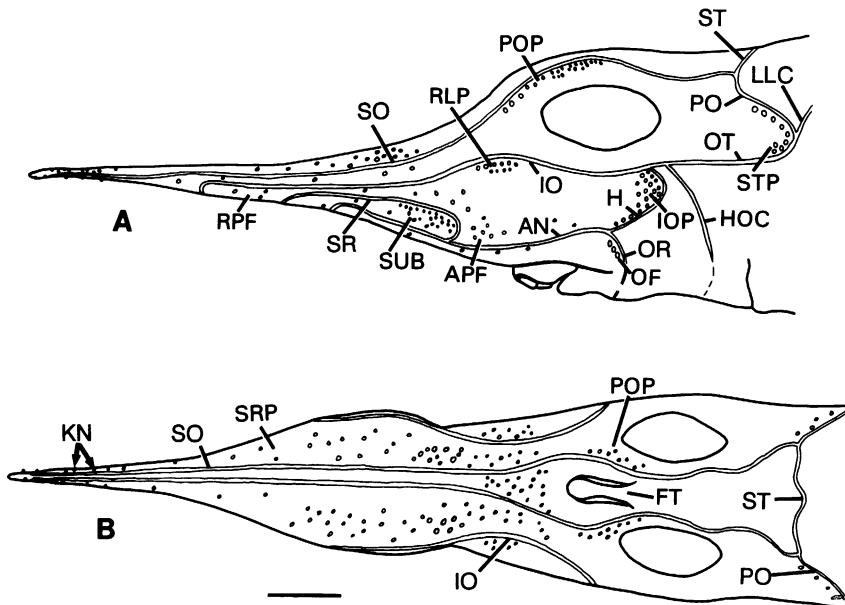


Fig. 14. Cranial lateral line canals and ampullary pore fields of *Harriotta raleighana*. The pattern of lateral line canals and location of ampullary pore fields is shown in A, lateral and B, dorsal view. The tubercles on the tip of the rostrum (KN) are shown as solid black dots, and in dorsal view the frontal tenaculum (FT) is shown atop the head. The oral (OR) and hyomandibular (HOC) canals end in a series of short "broken" canals, illustrated as dashed lines. The size and density of open pores reflect their actual size and density; the labial and mandibular ampullary pore fields are often small and were not observed in this specimen. See text for more detailed description and terminology. Scale bar = 2 cm.

supported by dense connective tissue and is almost entirely filled with a firm jellylike matrix.

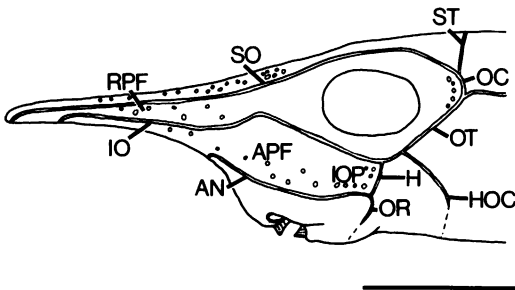


Fig. 15. Cranial lateral line canals and ampullary pore fields of *Neoharriotta pinnata* (UF 23839). Only the more prominent ampullary pore fields are shown. The general pattern of lateral line canals in *Harriotta* and *Neoharriotta* is similar, although in this figure the subrostral canal is not evident in lateral view. See text for more detailed description and terminology. Scale bar = 2 cm.

The tail is leptocercal with small supra-caudal and subcaudal lobes. Distally, the tail extends to a long, whiplike tail filament (TF). There is no anal fin present; however, the genus *Chimaera* is defined by the presence of a notch in the subcaudal fin that separates the anal fin web from the subcaudal fin web.

The lateral line canals are open grooves supported by calcified rings (fig. 11C). In all species of chimaeroids with open lateral line canals the calcified rings tend to split at the ends, giving the edge of the canal a fringed appearance. The narrow portions of the canals are supported by numerous calcified rings ranging from 28 per centimeter in *Chimaera* sp. C to 53 per centimeter in *Hydrolagus novaezealandiae*. The enlarged snout canals are supported by more widely spaced rings (e.g., five rings between each dilation in *Hydrolagus novaezealandiae* and five to seven rings between each large dilation in *Hydrolagus collieri*).

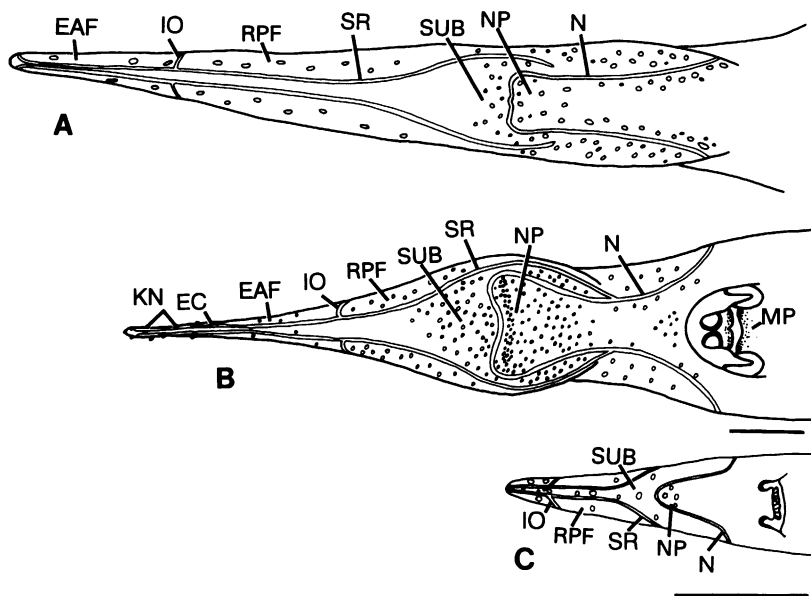


Fig. 16. Ventral view of snouts of rhinochimaerids. The snouts of A, *Rhinochimaera pacifica* (NMNZ P24198), B, *Harriotta raleighana*, and C, *Neoharriotta pinnata* (UF 23839) are shown in ventral view to illustrate the different branching patterns of the subrostral (SR) and nasal (NA) canals. Also shown are the ampullary pore fields to allow comparison of the relative size and abundance of ampullary pores among these species. See text for a detailed discussion of the different canal patterns. Scale bars = 2 cm.

The basic pattern of cranial lateral line canals in chimaerids follows that described above for callorhynchids and rhinochimaerids. The supratemporal, occipital, otic, hyomandibular, supraorbital, and infraorbital canals share the same branching pattern in all taxa of chimaerids studied (fig. 17). The horizontal canal in most chimaerids branches off the infraorbital canal separate from the preopercular canal; however, in some species the preopercular canal may also share a common trunk with the horizontal canal (fig. 8). On the basis of the comparisons made in this study this feature appears to be species-specific within Chimaeridae.

In the snout region the supraorbital, angular, subrostral, nasal, and infraorbital canals of chimaerids become enlarged and are interrupted by dilations at regular intervals along their length. The supraorbital and infraorbital canals, which are narrow along most of their length, begin to widen and open into large pores as they extend into the snout region, where they join at the anterior tip of

the snout. From this junction a short canal forms a Y-shaped commissure across the snout. At its ventral end the right and left subrostral canals split and join the angular canals on the ventral surface of the snout. The nasal canal extends from the junction of the subrostral and angular canals and forms an inverted "V" on the ventral surface of the snout above the nostrils.

#### SKELETAL ANATOMY

Skeletal features have long been held to have special phylogenetic importance because these characters can be studied in fossils as well as in living forms. Many workers have described aspects of the skeletal anatomy of chimaeroid fishes (e.g., Hubrecht, 1876; Schauinsland, 1903; Dean, 1906; Allis, 1917, 1926; Rabinerson, 1925; de Beer and Moy-Thomas, 1935; de Beer, 1937; Patterson, 1965; Stahl, 1967; Ribbink, 1971; Raitkow and Swierczewski, 1975; Jarvik, 1980). This description is the first comprehensive

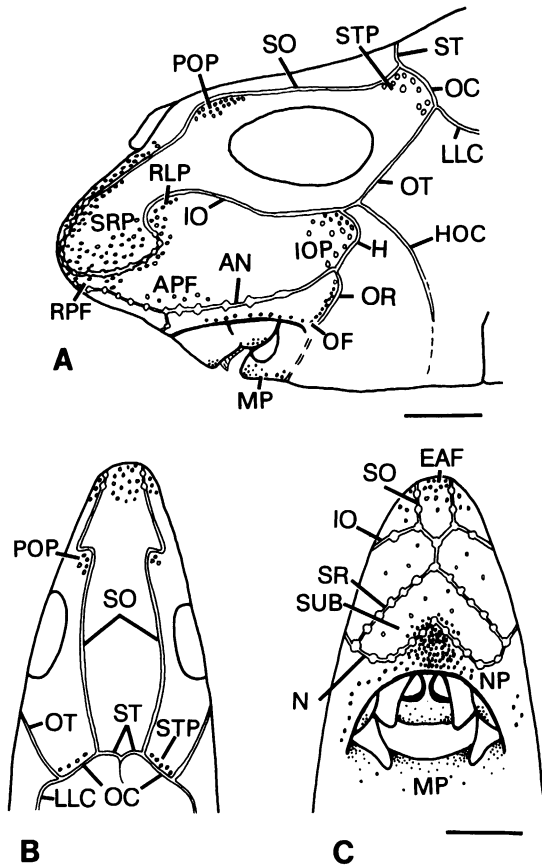


Fig. 17. Cranial lateral line canals and ampullary pore fields of *Hydrolagus novaezealandiae*. The lateral line canals and ampullary fields are shown in A, lateral, B, dorsal and C, ventral view. All of the ampullary pore fields described in the text are shown in this figure, including the labial ampullary pore field (shown in C, not labelled), which appears as a group of small pores on the fleshy lips surrounding the mouth. The relative abundance and size of pores are to scale. See text for more detailed description and terminology. Scale bar = 2 cm.

study of the skeleton of all three families of chimaeroid fishes and is based on detailed examination of six species in five different genera (table 7).

#### NEUROCRANIUM, JAWS, AND LABIAL CARTILAGES

The neurocranium is characterized by several specializations, particularly the autos-

tylic jaw. As in other autostylic gnathostomes, the hyoid arch does not participate in supporting or suspending the lower jaw. The class name, *Holocephali* (Müller, 1834), derives from the fact that there is complete fusion of the palatoquadrate to the neurocranium.

Some features of the neurocranium can be generalized among all chimaeroids (refer to fig. 18A). The orbit is anterior to the brain and dorsal to the paired olfactory tracts, which pass ventral to the orbit into the ethmoid region of the skull. Anteriorly, the orbit is bounded by a sheet of dense connective tissue from which the adductor mandibulae muscles originate. Dorsally, at the anterior edge of the orbit, the antorbital crest (ANC) forms a small lateral projection from which originates a caudally directed sheet of connective tissue that forms the top of the orbit. This connective tissue sheet inserts onto the post-orbital ridge (POR), which forms the posterior boundary of the orbit. The orbit is bounded ventrally by the suborbital ridge (SOR). This shelf of cartilage originates just posterior to the jaw joint and ends at the otic process (OP). The orbits are separated by a thin wall of connective tissue, which forms the interorbital septum.

The ethmoid region of the neurocranium is a broad area anterior to the orbit. The nasal capsules (NC) bulge laterally from the anteroventral portion of the ethmoid region. They are open posteriorly for the passage of the olfactory tracts into the olfactory bulbs. At the external opening of each nasal capsule is a scroll of cartilage that divides the nostril into incurrent and excurrent openings. The nasal openings lie within the fleshy tissue of the lips and are continuous with the mouth. This connection between the mouth and nostrils was described by Jarvik (1980) as a pseudochoana. Extending anteriorly from the ethmoid region are paired lateral rostral rods (LRR) that lie medial to the nasal capsules. Dorsal to the lateral rostral rods is a single median rostral rod (MRR).

The ethmoid canal and olfactory tracts extend into the ethmoid region. The ethmoid canal is an enclosed tube dorsal to the nasal capsules. The ophthalmic foramen (OPF) at the anterior edge of the orbit forms the en-

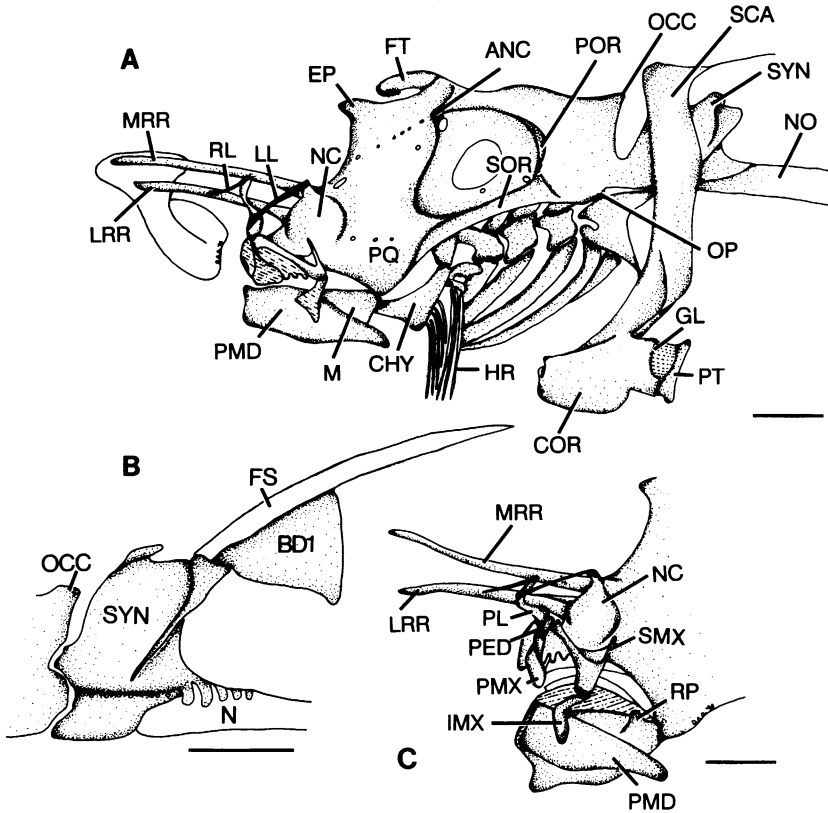


Fig. 18. Neurocranium of *Callorhynchus milii*. A, In this illustration of the neurocranium the gill arches and pectoral girdle are shown in their natural position in relation to the neurocranium. The labial cartilages are partially concealed by connective tissue (dashed lines). B, Detail of the synarcual and articulation of the dorsal fin spine (FS) and basal cartilage of the first dorsal fin (BD1). C, Lateral view of the six labial cartilages of *Callorhynchus milii* illustrated as they articulate within the connective tissue surrounding the mouth. See text for a detailed description of neurocranial anatomy and terminology. Scale bar = 2 cm.

trance to this canal, which exits from the rostral foramen (RF) at the base of the median rostral rod. The canal contains arteries passing to the snout, a mass of lymphoid tissue, and nerves for the skin and special sense organs of the snout. The nerves that traverse the ethmoid canal are the superficial ophthalmic branch of the anterior lateral line nerve and the profundal nerve (Cole, 1896a; Holmgren, 1942; Northcutt, 1989; Song and Northcutt, 1991). The anterior cerebral vein also runs within the ethmoid canal along part of its length (Holmgren, 1942: 200). Based on the study of a single embryo it was suggested that this canal forms as a secondarily roofed-over passage (de Beer and Moy-Tho-

mas, 1935). Holmgren (1942) disagreed with this interpretation and suggested that this canal is a remnant of the cranial cavity. My study of the skeleton of *Rhinochimaera* shows that the ethmoid canal is entirely enclosed within the ethmoid region and studies of the embryonic development of the ethmoid canal in *Callorhynchus* show it to be formed as an extracranial space, which is roofed over relatively late in development (fig. 19).

Posterior to the orbit in all chimaeroids is the otic region. The semicircular canals are visible as external bulges on the dorsal surface of the neurocranium. An important derived feature of chimaeroids is that the otic capsule has no internal wall. Posteriorly, the

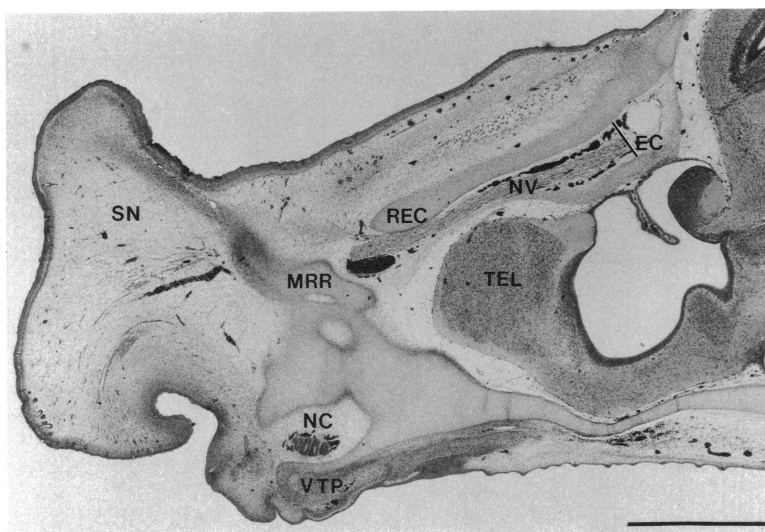


Fig. 19. Development of the ethmoid region in *Callorhinchus milii*. In this sagittal section of the head of an embryo (CM51, 85 mm TL) the developing ethmoid canal (EC) lies above the telencephalon (TEL) and is separated from the brain by a cartilaginous floor. Within the ethmoid canal is a branch of the Vth cranial nerve (NV). The roof of the canal develops later and is almost fully formed in this embryo. The median rostral rod (MRR) extends into the snout (SN) and develops dorsal to the nasal capsule (NC). The vomerine tooth plate (VTP) is evident directly below the nasal capsule. Scale bar = 1 mm.

otic region extends to a prominent dorsal process, the occipital crest (OCC). From this crest a sheet of dense connective tissue inserts onto the anterior edge of the synarcual (SYN) and tightly binds the neurocranium to the synarcual. The synarcual is a cartilaginous plate formed by the fusion of the first 10 vertebral segments. On the dorsal edge of the synarcual is an articulation surface for the basal cartilage of the first dorsal fin and the fin spine (fig. 18B). At the back of the neurocranium are two condyles that articulate with the base of the synarcual. There is only a loose connection between the neurocranium and synarcual at this joint. The otic process (OP) is the posterior edge of the suborbital shelf ventral to the otic capsule. I use the term otic process for convenience only, with no reference to its embryological origin.

The ventrally directed jaws are located anterior to the orbit. The jaw articulation of all Recent chimaeroids is anterior to the eye, and all the jaw closing muscles originate anterior to the eye. Meckel's cartilage (M) forms the lower jaw and is fused at the symphysis forming a U-shaped element that is suspended

below the neurocranium. This lower jaw cartilage is short and deep with the line of the symphysis extending to a prominent chin process (CP) at the posteroventral edge of the lower jaw. All chimaeroids have a double-articulating jaw joint in which the quadrate process is equipped with a lateral process and medial fossa that interlock with the lateral fossa and medial process of Meckel's cartilage (Didier, 1988). This type of jaw joint was interpreted to be primitive for gnathostomes by Hotton (1952) and Miles (1964). Along the posterior edge of the lower jaw is the retroarticular process (RP).

Labial cartilages are found in selachians and batoids as well as chimaeroids; however, in no other extant chondrichthyans are the labial cartilages as complex as among the living chimaeroids. Large, complex labial cartilages, similar to those found in chimaeroids, are described for *Hybodus basanus* (Maisey, 1983). However, the homology of these labial cartilages is difficult to determine and will require further study, including comparative examination of the embryonic development of labial cartilages in chimaeroids and mod-

ern sharks. With the exception of *Callorhinchus*, which has five pairs of upper labial cartilages, chimaeroids have four pairs of upper labial cartilages and one pair of lower labial cartilages. The terminology used to describe the labial cartilages is based primarily on Holmgren (1942: 242–243).

**CALLORHYNCHIDAE:** In *Callorhinchus milii* the neurocranium is dorsoventrally compressed, with an elongate antorbital and otic regions giving the neurocranium a long, low profile when compared with other chimaeroids (fig. 18A). The prominent ethmoid process (EP) extends from the dorsal midline of the ethmoid region. Likewise, the occipital crest (OCC) is a prominent posterior process extending from the dorsal midline of the otic region. In *Callorhinchus* the orbit and interorbital septum are small.

The plow-shaped snout of *Callorhinchus* is supported by two lateral rostral rods and a single median rostral rod, all three being of approximately equal length. A posteriorly directed flap of tissue is suspended from the distal ends of these rods. In *Callorhinchus* the median rostral rod is located just dorsal to the nasal capsules, in close proximity to the origin of the lateral rostral rods.

There are five paired labial cartilages in *Callorhinchus* (fig. 18C). The prelabial cartilage (PL) is a dorsally directed S-shaped cartilage that lies anterior to the nasal capsule and lateral to the rostral rods. A ligament extends from the dorsal tip of the prelabial cartilage and inserts onto the lateral rostral rod. Another ligament originates from a tiny dorsal process of the nasal capsule and inserts onto the prelabial cartilage. At its ventral end, the prelabial cartilage articulates with the pedicular cartilage (PED). The pedicular cartilage is directed medially and lies at the anteroventral edge of the nasal opening. Articulating with the pedicular cartilage is the premaxillary cartilage (PMX), which is ensheathed in dense connective tissue and hangs ventrally to support the upper lip. The elongate superior maxillary cartilage (SMX) also articulates with the pedicular cartilage and lies ventral to the nasal capsule. The superior maxillary cartilage is deeply curved along its dorsal edge and has a dorsal extension at its posterior end. Articulating at the ventral edge of the superior maxillary cartilage is the in-

ferior maxillary cartilage (IMX). This cartilage lies lateral to the mouth and is enveloped in a fold of connective tissue that forms the side of the mouth. The premandibular cartilage (PMD) is the only labial cartilage associated with the lower jaw. These large paired elements lie lateral to Meckel's cartilage within the thick tissue of the lower lip.

**RHINOCHIMAERIDAE:** *Rhinochimaera* has a robust neurocranium with an elongate, tapering ethmoid region (fig. 20A). There is no prominent ethmoid process. The elongate median rostral rod articulates with the neurocranium dorsal to the nasal capsules and extends to the tip of the snout, becoming deeper and laterally flattened midway along its length (MRR). The lateral rostral rods are angled upward and support only the base of the rostrum. The otic region is long with a rounded occipital crest. The neurocranium of *Rhinochimaera* is less angular and box-shaped than is that of *Callorhinchus* and instead appears as though it is stretched in a cranio-caudal direction. As in *Callorhinchus*, the orbit and interorbital septum are small.

In *Harriotta* and *Neoharriotta* the neurocranium is deep dorsoventrally with short ethmoid and otic regions (fig. 21A). The orbits are large with an extensive interorbital septum composed of connective tissue. The ethmoid and otic regions are almost equal in size, and in lateral view the neurocranium appears to be very short and tall.

The labial cartilages of *Rhinochimaera* are large (fig. 20B). The prelabial cartilage (PL) is a nearly straight rod and does not have a ligamentous connection either to the rostral rods or to the nasal capsule. This prelabial cartilage curves below the nasal capsule and extends medially to articulate with the neurocranium. There is no pedicular cartilage. The long, thin premaxillary cartilage (PMX) articulates with the ventral edge of the prelabial cartilage and hangs ventrally within the skin of the upper lip. The blocklike superior maxillary cartilage (SMX) articulates at the posterior edge of the prelabial cartilage. Articulating with the superior maxillary cartilage is a large, ventrally directed cartilage, the inferior maxillary (IMX), that lies lateral to the mouth opening and supports the edge of the lip. Associated with the lower jaw are the paired premandibular cartilages (PMD).

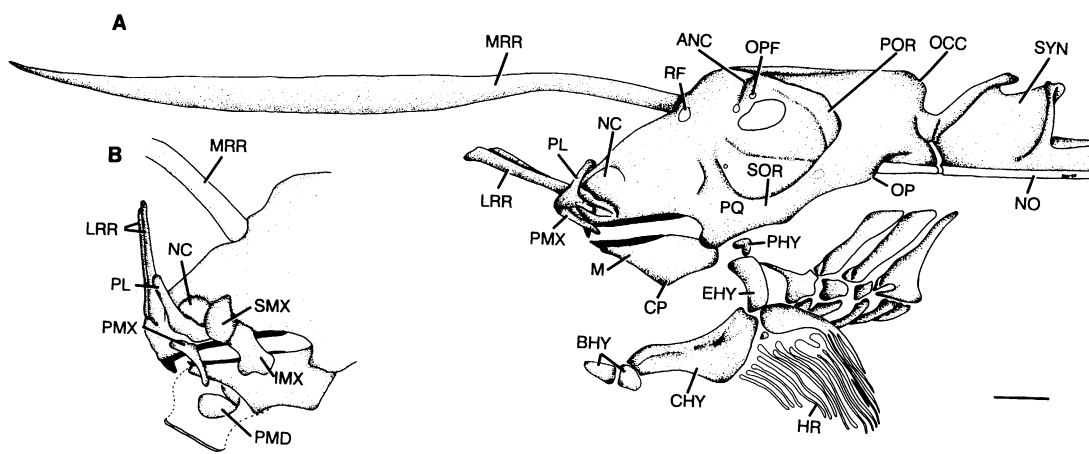


Fig. 20. Neurocranium of *Rhinochimaera pacifica* (AMNH 96939). A, The pectoral girdle has been removed to reveal the gill arches which have been displaced ventrally from their normal position to illustrate their structure in lateral view. All of the labial cartilages except the prelabial (PL) and premaxillary (PMX) have been removed. B, Detail of the labial cartilages of *Rhinochimaera pacifica* showing all five labial cartilages in approximate relationship to each other. The premandibular cartilages (PMD) lie within connective tissue ventral to the lower jaw and are illustrated as though the connective tissue were cut and peeled away from Meckel's cartilage. Scale bar = 2 cm.

These thin, flat cartilages are joined by connective tissue at the symphysis and lie within the connective tissue of the lower lip.

The labial cartilages of *Harriotta* and *Neo-*

*harriotta* are similar in their arrangement and articulations to those of *Rhinochimaera* (fig. 21B). The premaxillary cartilage (PMX) is tiny and located entirely within the upper lip;

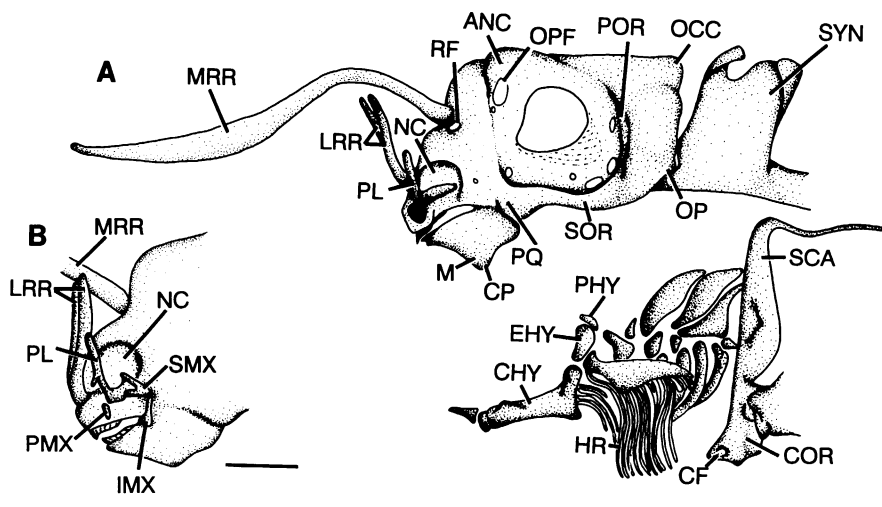


Fig. 21. Neurocranium of *Harriotta raleighana*. A, The gill arches and pectoral girdle have been ventrally displaced in this illustration to expose details of their anatomy in lateral view. Of the labial cartilages only the prelabial cartilage (PL) is illustrated. B, Detail of the four upper labial cartilages of *Harriotta raleighana* (AMNH 96935). The mandibular cartilages are small elements buried in connective tissue ventral to the lower jaw and are not shown here. Scale bar = 2 cm.



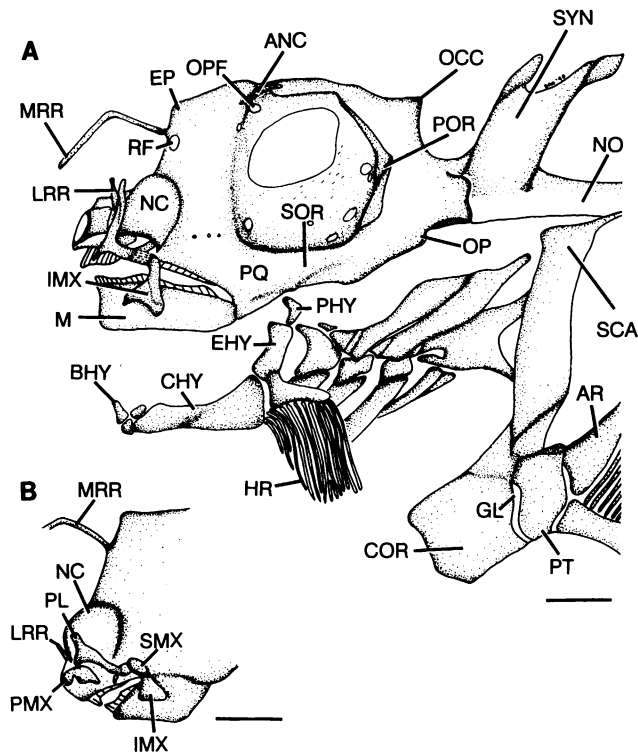


Fig. 22. Neurocranium of *Hydrolagus novaezealandiae*. A, In this lateral view the pectoral girdle and gill arches have been displaced ventrally. Only the prelabial (PL) and inferior maxillary (IMX) labial cartilages are shown. B, Detail of the four upper labial cartilages of *Hydrolagus novaezealandiae*. The mandibular labial cartilages, not shown, are reduced to two very tiny bits of cartilage ventral to the lower jaw. Scale bar = 2 cm.

it may or may not articulate with the prelabial cartilage. The superior maxillary and inferior maxillary cartilages are similar to those described for *Callorhynchus* and *Rhinochimaera*, but are much smaller. There is a single flat premandibular cartilage embedded in dense connective tissue at the symphysis of the lower jaw.

**CHIMAERIDAE:** The chimaerids *Hydrolagus* and *Chimaera* have tall neurocrania with large orbits (fig. 22A). The ethmoid and otic regions are short and almost equal in length. In these respects, the neurocrania of *Chimaera*, *Hydrolagus*, *Neoharriotta*, and *Harriotta* are similar; however, this is probably a correlated set of characters. Anteriorly, there is a slightly rounded ethmoid process (EP). The prominent occipital crest extends from the dorsal midline of the otic region and differs morphologically from the rounded occipital crest (OCC) of rhinochimaerids.

The small lateral rostral rods lie along the medial edge of the nasal capsule and are directed upward. A strand of connective tissue extends from the tips of the lateral rostral rods to a sheet of connective tissue that supports the rostrum and its associated ampullary organs. The small median rostral rod articulates just ventral to the ethmoid process and is embedded in the connective tissue of the fleshy snout.

The labial cartilages are small in all chimaerids (fig. 22B). The prelabial cartilage (PL) of *Hydrolagus* has a short dorsally directed process and is elongate posteriorly. The premaxillary cartilage (PMX) articulates with the anterior edge of the prelabial cartilage and this flat, crescent-shaped cartilage lies within the upper lip. The superior maxillary (SMX) and inferior maxillary cartilages (IMX) retain the same positional relationships as described above for rhinochimaerids. In some

specimens a tiny cartilage or fibrocartilaginous mass lies between the prelabial and superior maxillary cartilage. The paired premandibular cartilages are minute fibrocartilage masses embedded in connective tissue at the symphysis of the lower jaw (not shown).

#### GILL ARCHES

All holocephalans have a morphologically complete hyoid arch plus five typical gill arches. The branchial skeletal elements are concentrated underneath the neurocranium and covered laterally by a fleshy opercular flap. There is a single gill opening on each side that opens ventrally just anterior to the pectoral fin. There is a single demibranch on the hyoid arch and four holobranchs, one associated with each subsequent gill arch. The fifth gill arch is reduced and lacks respiratory specializations.

Holocephalans are the only gnathostomes that have a hyoid arch in which a pharyngohyal element is present. This has been interpreted as a retention of the plesiomorphic condition for gnathostomes (de Beer and Moy-Thomas, 1935) on the basis of a study of a single embryo of *Callorhinchus milii*. However, Maisey (1984) argued that the hyoid arch of Recent chimaeroids is not an unmodified primitive hyoid arch on the basis of five anatomical features that do not support the hypothesis of de Beer and Moy-Thomas (1935): (1) the pharyngohyal of chimaeroid fishes lies lateral to the efferent hyoidean artery; (2) the embryonic spiracle is small and does not represent a complete gill slit; (3) the epihyal does not bear endoskeletal rays; (4) the hyoid arch of Recent chimaeroids does not have branchial adductor muscles; and (5) the interpharyngobranchial muscles do not insert on the pharyngohyal. Furthermore, Maisey (1989) suggests that there is no evidence that the hyoid arch of gnathostomes was ever unmodified in the sense that it exhibited the characteristic morphology of a typical branchial gill arch.

In my observations of some earlier developmental stages a discrete cartilage anlage for each hyoid arch element is present. Each anlage appears to develop into a single element with no contribution to or from any nearby

elements, suggesting that this hyoid arch does develop in an unmodified form; however, based on this developmental evidence alone, it is not clear that this hyoid arch represents the primitive state. Instead, the development of a complete hyoid arch may be a secondarily derived feature associated with the evolution of autostyly in this lineage. This seems a reasonable hypothesis based on the conclusion of Maisey (1980) that an amphistylic jaw suspension (Maisey's hyostyly) is the primitive condition for gnathostomes. Outgroup comparison would then dictate that autostyly is derived in Holocephali, and it is therefore more parsimonious to accept the complete hyoid arch as a secondary derivation.

The hyoid arch in chimaeroids consists of pharyngohyal, epihyal, ceratohyal, and basihyal elements (fig. 23A, B). The epihyal articulates at the dorsal end of the ceratohyal. At its posterior edge is a facet for the opercular cartilage that articulates at the junction of the epihyal and ceratohyal. This cartilage extends posteriorly to a thin filament. Continuous with the opercular cartilage are numerous filamentous processes, the hyoid rays, which support the opercular flap. Several hyoid rays also articulate independently with the posterior edge of the ceratohyal. The ceratohyal is the largest of the hyoid arch elements. It is angled with a short dorsally directed caudal portion and a cranial portion that extends anteriorly to articulate with the basihyal. A single basihyal supports the tongue pad and in many species there are additional paired cartilages or fibrocartilaginous masses just posterior to the basihyal element.

The remaining gill arches are almost identical among all chimaeroid genera, and the condition in *Callorhinchus* serves to illustrate the general pattern (fig. 23A, B). Ventrally, there are four unpaired basibranchial elements, the anterior three of which exist as fibrocartilage lumps embedded within the connective tissue of the branchial basket (BBR). In chimaerids there are accessory paired fibrocartilages associated with the first three basibranchials. These are figured by Garman (1904). The fourth basibranchial is a flat, posteriorly directed cartilage that inserts into a connective tissue sheet attached to the medial surface of the coracoid. Basibranchial 1 articulates directly with hypo-

branchial 1; basibranchial 2 lies between but does not articulate with hypobranchials 2 and 3; and basibranchial 3 lies between but does not articulate with hypobranchials 3 and 4. These basibranchial elements are interconnected to the hypobranchials and to each other by a surrounding loose connective tissue fascia.

There are four separate hypobranchial elements (HBR). Each articulates with one ceratobranchial except for the most caudal one, which articulates with both ceratobranchials 4 and 5. I consider that this hypobranchial element may have arisen by fusion of originally separate hypobranchials 4 and 5 and therefore term it HBR 4-5. Each of the three anterior hypobranchial elements articulates with its corresponding ceratobranchial element.

The five ceratobranchials are long dorsoventrally curved elements (CTB). Ceratobranchials 1-3 have posteriorly directed processes at their ventral articulation surfaces that articulate with the hypobranchial elements. This ceratobranchial process is most evident in the first ceratobranchial and becomes smaller in ceratobranchials 2 and 3.

Dorsal to the ceratobranchials are three epibranchial elements (EBR) that articulate with ceratobranchials 1, 2, and 3. The first epibranchial is concave along its anterior edge with a dorsal anterior process that articulates at the junction of the pharyngohyal and epihyal. There are no epibranchial elements associated with ceratobranchials 4 and 5.

There are two elongate, bladelike pharyngobranchial elements (PBR) that are angled dorsoventrally and medially. The first pharyngobranchial articulates at the junction of epibranchials 1 and 2, and the second pharyngobranchial articulates at the junction of epibranchials 2 and 3. The third pharyngobranchial is a large element and is probably formed by the fusion of several cartilages, including epibranchials 4 and 5; thus, I label this element PBR 3-5. This element lies directly behind pharyngobranchial 2 and articulates with epibranchial 3 anteriorly. Its anterodorsal edge continues as an elongate dorsal process that is bound to the ventral side of the notochord by dense connective tissue. Ceratobranchials 4 and 5 articulate at the ventral edge of the body of this element. The

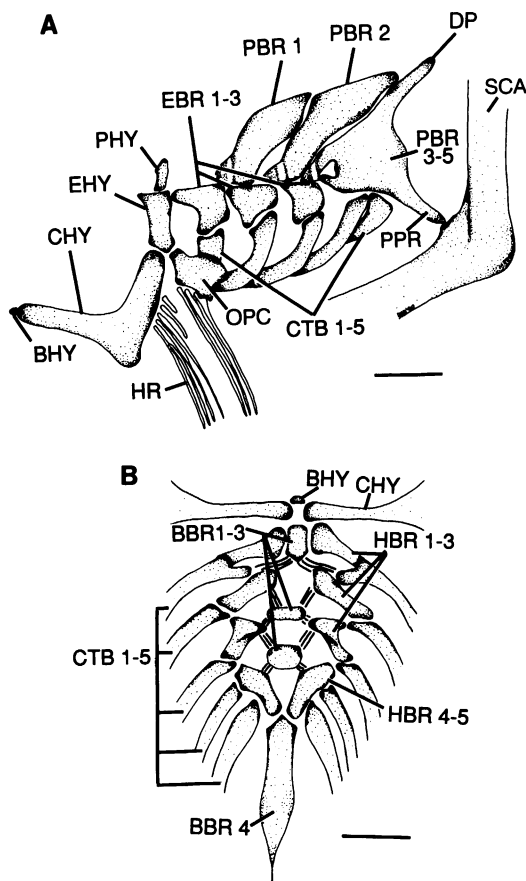


Fig. 23. Gill arches of *Callorhynchus milii* (AMNH 96954). A, Lateral view of the gill arches shown in this figure as representative of the gill arch morphology for all chimaeroids. B, Gill arches shown in ventral view. The solid lines represent loose connective tissue that binds the basibranchial elements (BBR) to the hypobranchial elements (HBR). The ceratobranchial elements (CTB) are shown in cutaway view. See text for specific details of gill arch morphology. Scale bar = 2 cm.

element extends caudally as a posterior process that is tightly bound to the medial side of the scapular process.

**CALLORHYNCHIDAE:** The very tiny pharyngohyal articulates at the dorsal surface of the epihyal and is roughly rectangular in *Callorhynchus* (PHY; fig. 23A). The basihyal in *Callorhynchus* is quite small and is the only cartilage observed in the tongue pad (BHY).

The opercular cartilage (OPC) is a roughly square blocklike cartilage that supports about

five hyoid rays. An additional five or six hyoid rays are attached to the posterior edge of the ceratohyal. It is unlikely that the number of rays is constant among individuals, because the hyoid rays often split and fuse.

**RHINOCHIMAERIDAE:** The pharyngohyal is a tiny boomerang-shaped element in *Rhinochimaera* (PHY; fig. 20A). The basihyal is composed of two elements; the anteriormost is roughly triangular in shape and extends to a point at its tip. This cartilage is followed by a second smaller element. In *Rhinochimaera* the basihyal element is robust, whereas in *Harriotta* and *Neoharriotta* the basihyal is more slender and pointed. The epibranchial cartilages figured for *Harriotta* (unlabeled; fig. 21A) are small; however, this is a young individual and my observations of other taxa indicate that larger adults have better developed branchial cartilages and this may be the case for *Harriotta* as well. In *Harriotta* a tiny cartilage element has been observed dorsal to epibranchial 1 and just anterior to the first pharyngobranchial (unlabeled; fig. 21A). This element has also been observed in species of *Hydrolagus* and may be a transient element.

The elongate opercular cartilage in species of Rhinochimaeridae is largest at its articulation with the hyoid arch and curves to a thin filament posteriorly (figs. 20A, 21A). *Rhinochimaera* has roughly 7 hyoid rays articulating with the opercular cartilage and 12 hyoid rays that articulate at the posterior edge of the ceratohyal. There are about 13 hyoid rays that originate from the opercular cartilage in *Harriotta* and only 5 hyoid rays associated with the ceratohyal. *Neoharriotta* has a total of 15 hyoid rays, 6 of which articulate at the posterior edge of the ceratohyal.

**CHIMAERIDAE:** The pharyngohyal in *Hydrolagus* resembles that of rhinochimaerids (PHY; fig. 22A). The basihyal (BHY) is a large, squared element that does not extend to a prominent point anteriorly.

The opercular cartilage in species of *Hydrolagus* and *Chimaera* is a thin, lunate cartilage that supports numerous hyoid rays. It is difficult to distinguish hyoid rays that articulate along the ceratohyal from those that extend from the opercular cartilage. The number of hyoid rays is variable. For example, *Hydrolagus coliei* has a total of 25–

27 hyoid rays, *Hydrolagus mirabilis* has 21, and there are 27 in *Chimaera monstrosa*. This increase in number of hyoid rays may be characteristic of the family Chimaeridae; however, a more thorough survey of this character is needed.

#### VERTEBRAL COLUMN AND UNPAIRED FINS

The vertebral column of all chimaeroids lacks true centra. The sheath of the notochord in chimaeroids is invested with numerous calcified rings, although *Callorhinchus* is an important exception to this. These notochordal rings are not segmentally organized and there are typically many rings per segment. External to the calcified rings, along the dorsal and ventral surfaces of the notochord, is a series of small cartilages that are unrelated to the pattern of calcified rings. In all species examined these cartilages are well developed anteriorly with triangular-shaped dorsal cartilages, minute interdorsal cartilages, and small ventral cartilages. In the anterior half of the body, anterior to the pelvic girdle, these cartilages seem to reflect a segmental pattern, although the dorsal and ventral series do not necessarily exhibit a one-to-one correspondence. In the posterior half of the body, and into the tail, the cartilages are formed into irregular rectangular shapes and no longer exhibit any recognizable pattern. These cartilages are probably homologous to the basidorsal and basiventral series in the vertebral column of elasmobranchs and other fishes.

All chimaeroids have a vertical bladelike synarcual (SYN; fig. 18B) that supports the first dorsal fin and fin spine. The synarcual forms the anterior portion of the vertebral column and encloses the notochord. The base of the synarcual is penetrated by 10 foramina through which emerge the anterior spinal nerves.

The first dorsal fin is supported by a single basal element and is preceded by a stout fin spine that is attached to the basal of the first dorsal fin and together they articulate on the dorsal process of the synarcual (fig. 18B). The fin spine and first dorsal fin can collapse into a fleshy groove along the dorsal midline.

The fin spine is roughly triangular in external shape and is thickest at the base and

tapers to a needle-sharp point. The anterior edge of the spine may be smooth or deeply keeled. The posterior face is concave with a series of recurved hooks along the lateral edges. The fin spine is considered to be venomous and the tissue within the posterior concavity of the fin spine of *Hydrolagus collieri* contains venom glands (Halstead and Bunker, 1952).

The second dorsal fin is supported by numerous small radial cartilages embedded in connective tissue along the dorsal midline. These radial elements support the ceratotrichia, which form the fin web. The number of radials varies depending on the length of the fin.

**CALLORHYNCHIDAE:** Species of *Callorhynchus* do not have calcified rings in the sheath of the notochord, but they do possess a series of small basidorsal and basiventral cartilages external to the notochordal sheath.

The fin spine is smooth along its anterior edge and extends well beyond the distal edge of the first dorsal fin (FS; fig. 9). The second dorsal fin (D2) is roughly triangular in shape, tall anteriorly, and tapers posteriorly. The tail is heterocercal with an anal fin that is supported by cartilage.

**RHINOCHIMAERIDAE:** In all rhinochimaerids the notochord is surrounded by numerous calcified rings that are closely packed together. In an adult *Rhinochimaera* there are approximately 11 rings per centimeter. In adults these calcified rings completely ensheath the notochord, which extends to the tip of the tail. Juveniles usually lack these calcified rings and the number of rings seems to increase with age.

The fin spine in *Rhinochimaera* is shorter than the first dorsal fin (FS; fig. 12A). *Harriotta* and *Neoharriotta* have a fin spine that is slightly longer than the first dorsal fin (FS; fig. 12B). The elongate second dorsal fin in rhinochimaerids has an even height along its length (D2). Rhinochimaerids all possess a leptocercal tail. *Neoharriotta* is the only neo-chimaeroid to possess an anal fin that is supported by cartilage.

**CHIMAERIDAE:** Calcified rings are present in the notochordal sheath of all adult chimaerids. I have counted 12 calcified rings per centimeter in the notochordal sheath of an adult *Hydrolagus collieri*.

The fin spine in chimaerids may be smooth anteriorly or with a prominent keel along the anterior edge (FS; fig. 12C). The fin spine may be slightly longer or shorter than the first dorsal fin. The second dorsal fin has an even height along its length. A leptocercal tail is present in all chimaerids. The anal fin web is separated from the subcaudal fin in *Chimaera* by a notch, but there is no cartilaginous support for this anal fin, and by definition I do not consider it a true anal fin.

#### PAIRED FINS AND GIRDLES

The pectoral girdle lies just posterior to the neurocranium (e.g., figs. 18A, 21A, 22A). This large element is fused at the symphysis and can be divided into two regions based on the location of the pectoral fin articulation at the glenoid fossa (GL). Ventral to the glenoid fossa is the coracoid region, which forms the ventralmost portion of the pectoral girdle (COR). The anterior surface has two large depressions where the *m. coracobrachialis* complex originates. Passing through the coracoid is a canal for the passage of blood vessels and nerves to the pectoral fin. This canal originates on the medial face of the scapular process, just above the pectoral fin, and exits ventrally at the anterior end of the coracoid (CF). Spanning the pectoral girdle is a dense sheet of connective tissue that runs transversely along the dorsal edge of the coracoid region to form the posterior pericardial wall.

The elongate scapular process (SCA) is angled anteriorly at the pectoral fin articulation where it joins the coracoid and extends dorsally to lie lateral to the base of the synarcual. At its dorsal end the scapular process becomes thin and flat with an elongate cartilaginous filament extending posteriorly from the tip. It is embedded in a complex musculature except at its dorsal end, which is exposed above the epaxial muscles.

The pectoral fins of *Callorhynchus milii* and *Harriotta raleighana* are shown in figure 24. They articulate at the glenoid fossa on the posterior edge of the coracoid by a small propterygial element. This articulation demarcates the coracoid from the scapular process. Articulating at the anterior edge of the propterygial element is a single cartilaginous element, which I interpret to be formed by

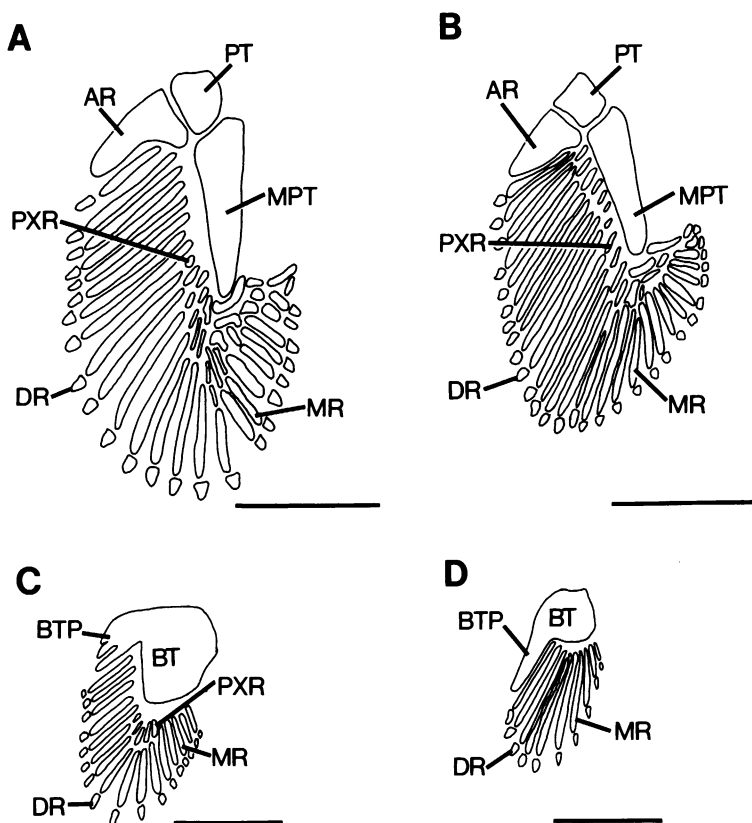


Fig. 24. Skeletal anatomy of the paired fins of *Callorhinchus milii* and *Harriotta raleighana*. A, Left pectoral fin of *Callorhinchus milii* (CM77). B, Left pectoral fin of *Harriotta raleighana* (AMNH 96946). The pectoral fins are dibasal, possessing only a propterygial (PT) and metapterygial (MPT) element. A single anterior radial element (AR) articulates with the propterygium, and the remaining radials, which are usually segmented into proximal (PXR) and middle (MR) radials, articulate with the metapterygium. The tiny distal radials (DR) support the ceratotrichia (not shown) of the fin web. C, Left pelvic fin of *Callorhinchus milii*. D) Left pelvic fin of *Harriotta raleighana*. The single large basipterygial element (BT) is characterized by a lateral extension, the basipterygial process (BTP). All of the radials articulate with the basipterygium and may be segmented into proximal and middle radials or remain unsegmented. The distal radials support the ceratotrichia (not shown) of the pelvic fin. Scale bars = 2 cm.

the fusion of the anterior radials of the pectoral fin (AR). Future developmental studies will confirm the precise formation and homology of this anterior radial element in the pectoral fin. The remaining radials articulate with the metapterygial element.

The propterygium and metapterygium support the radials of the pectoral fin; thus it is defined as dibasal. A tribasal fin in which there are three basal elements (propterygium, mesopterygium, and metapterygium) that bear radials is a derived feature among elasmobranchs (Rosen et al., 1981). In juveniles

all of the radials are singly jointed, but in adults there is a tendency for the proximal elements (PXR) to fuse to the longer middle radials (MR). The long middle radials develop central regions of prismatic calcification. At the medial edge of the pectoral fin there are several small uncalcified cartilages that are not in parallel with the middle radials. The number of radials varies; for example, in three juveniles there were 22 middle radials, whereas adults had 21–27. Articulating at the distal ends of the middle radials is a series of small triangular carti-

lages. These small distal radial cartilages are variable in number, but there are roughly two per radial element. One lies ventral and the other lies dorsal to each radial, forming a ridge of small distal radials that support the ceratotrichia of the large, winglike pectoral fins.

The pelvic girdle lies embedded within the ventral body musculature and forms no articulation with any other skeletal elements. In *Callorhinchus* the pelvic girdle is separated at the symphysis and the two halves are connected by a broad ligament. In all other chimaeroids the two halves of the pectoral girdle are tightly joined at the symphysis. Laterally, the pelvic girdle tapers to an elongate process, which extends dorsally and posteriorly into the muscle of the body wall. On either side of the symphysis the pelvic girdle is gently rounded anteriorly and is penetrated by one or two foramina for the passage of nerves and blood vessels to the pelvic fin. In *Callorhinchus* these rounded anterior edges of the pelvic girdle are greatly enlarged and each has a central vacuity that is closed off by a connective tissue membrane. This enlarged anterior process of the pelvic girdle in callo-rhynchids supports the large prepelvic tenacula in males.

The pelvic fins lie along the ventral surface of the body and are almost identical in all taxa studied (fig. 24). The single basipterygium (BT) of the pelvic fin articulates at a raised acetabulum located on the posterior edge of the pelvic girdle. The basipterygium of the pelvic fin is a flat ovoid cartilage. The first few radials fuse to the basipterygium and form an elongate basipterygial process, which extends along the anterior margin of the fin (BTP). Articulating with the basal cartilage is a series of long radial elements (MR), which lie parallel to the basipterygial process, and like the pectoral fin radials, these radials have a region of calcification in the center. Pelvic radials were counted in at least one member of each genus and usually 12–15 radials were found in all chimaeroids examined. In some specimens as few as 8 or 10 have been counted, but it is possible that some of the radial elements were lost in preparation. Like the pectoral fins, the pelvic fins possess a distal series of small triangular cartilages that support the ceratotrichia.

## SECONDARY SEXUAL CHARACTERS

Pelvic claspers specialized for internal fertilization are characteristic of all Chondrichthyes, but prepelvic and frontal tenacula are unique to Chimaeriformes. Only in males are these secondary sexual characteristics fully developed at the onset of sexual maturity; however, cartilage rudiments of frontal tenacula have been observed in females of all taxa examined and some even possess tiny cartilage rudiments of pelvic claspers, particularly *Callorhinchus*. The claspers and their musculature in *Callorhinchus* and *Chimaera* were described by Jungersen (1899). Leigh-Sharpe (1922, 1926) described the morphology of these secondary sexual structures in detail for *Callorhinchus*, *Rhinochimaera*, *Chimaera*, and *Hydrolagus*. The morphology of the urogenital system has been described for *Chimaera monstrosa* (Burlend, 1910) and more recently for *Hydrolagus coliei* (Stanley, 1963) and will not be discussed here.

In addition to the pelvic claspers, all male chimaeroids have paired organs extending anteriorly from the pelvic girdle known as prepelvic tenacula. The term tenaculum means "a holder," and the prepelvic tenacula derive their name from the interpretation that they are specialized organs to hold females during copulation, although this has never been observed. The prepelvic tenacula are formed by a single cartilaginous element that articulates at the anterior edge of the pelvic girdle. These tenacula bear denticles in all chimaeroids and are housed within fleshy prepelvic pouches that are found on the ventral side of the trunk just anterior to the pelvic girdle in all males.

In sexually mature males a single median frontal tenaculum is found atop the head. The tenaculum is composed of dense fibrocartilage with a cluster of sharp denticles at its tip (Patterson, 1965; Raikow and Swierczewski, 1975). The anterior end of the frontal tenaculum rests in a fleshy pouch that may be lined with placoid denticles (e.g., *Hydrolagus novaezealandiae*). The morphology of the frontal tenaculum is variable and examples of the frontal tenacula of chimaeroids are illustrated in figure 25. The frontal tenaculum is attached to the neurocranium by two ligaments that run from the supraorbital crest to the

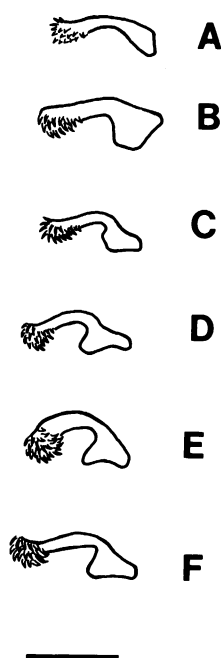


Fig. 25. Comparative anatomy of the frontal tenacula. The frontal tenaculum is shown for A, *Callorhinchus milii*, B, *Rhinochimaera pacifica*, C, *Harriotta raleighana*, D, *Chimaera* sp. C, E, *Hydrolagus colliei*, and F, *Hydrolagus* sp. B. The tenacula exhibit a diverse morphology across taxa. Although the exact number of tenacular denticles is not shown, the figures are intended to represent the approximate size and shape of the denticles for each species. Scale bar = 2 cm.

concave tenacular base (not illustrated). The frontal tenaculum can be raised and lowered and it shares a complex musculature with the labial cartilages (Raikow and Swierczewski, 1975).

The development of this structure has never been described in detail, but it is interesting to note that the frontal tenaculum is not fully developed until late in life, during the transition from juveniles to sexually mature adults. In juvenile males a small white streak along the dorsal midline of the head, anterior to the orbits, marks the location where the frontal tenaculum will develop. Females do not have this structure externally; however, mature females possess a tiny fibrocartilage rudiment underneath the skin at the site where the frontal tenaculum develops in males.

The exact function of the frontal tenaculum

is unknown; however, because it is sexually dimorphic, it has been assumed to be important for courtship or copulation. Dean (1906: 24) examined the pattern of scratches on the dorsal surface of females and concluded that the frontal tenaculum was used to grasp the female during copulation.

**CALLORHYNCHIDAE:** In *Callorhinchus* the pelvic claspers are in the form of smooth hollow tubes formed by a thin sheet of cartilage wrapped around itself in scroll-like fashion (fig. 26A). The pelvic clasper is composed of two cartilages: the anterior clasper cartilage (ACC) articulates with the basal cartilage of the pelvic fin at its posteromedial edge, and the posterior clasper cartilage (PCC) forms the more distal tubular portion of the clasper. At its articulation with the posterior clasper cartilage the anterior clasper cartilage has a small fold of cartilage that forms an opening to the interior of the posterior clasper cartilage. The clasper tapers distally to a rounded tip with an external opening that is partially covered by a fleshy tissue flap.

The prepelvic tenacula of *Callorhinchus* are extremely complex, unlike those found in any other chimaeroids (fig. 26A). The prepelvic tenacula articulate at the anterior edge of the pelvic girdle, which is greatly enlarged in *Callorhinchus*. The cartilaginous skeleton of the prepelvic tenaculum (PPT) has two distinct parts. The larger part is a flat, wide cartilage blade covered by tiny denticles with scalloped edges. Lying deep to this flat cartilage is a rolled tube of cartilage, open at its posterior end. Attached to the flat cartilaginous blade is a ruffled flap of dense tissue. Within the prepelvic pouch is an elongate sac and associated gland (not shown). This glandular component is only found in callorhinchids.

At rest, this entire complex is housed within the prepelvic pouch. It can be extended anteriorly out of the pouch to lie flat along the ventral body surface. It does not seem possible that the prepelvic tenacula in *Callorhinchus* could be used for grasping because the denticles are extremely tiny. The presence of a glandular component suggests that the prepelvic tenacula of *Callorhinchus* play an accessory role in fertilization (Leigh-Sharpe, 1922, 1926).

In female *Callorhinchus* there are small prepelvic slits that house tiny cartilaginous



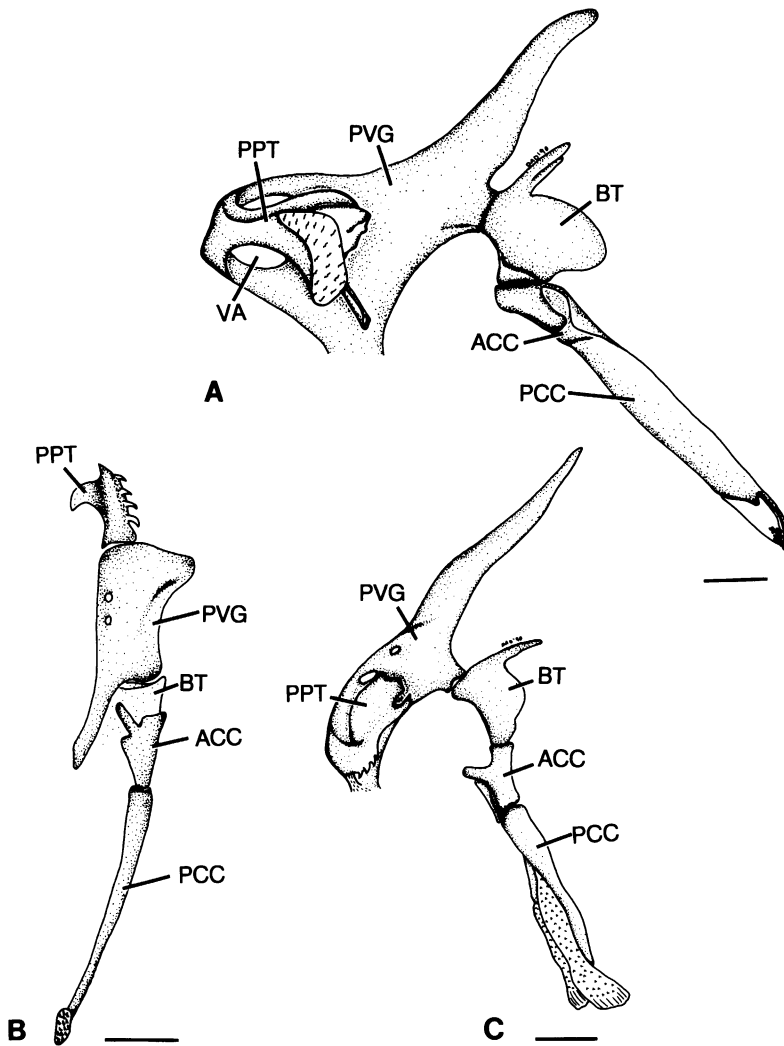


Fig. 26. Skeletal anatomy of the pelvic claspers and prepelvic tenacula of *Callorhinchus milii*, *Rhinochimaera pacifica*, and *Hydrolagus novaezealandiae*. **A**, Ventral view of the left side of the pelvic girdle (PVG) of *Callorhinchus milii* showing the pelvic clasper and prepelvic tenaculum in their normal anatomical relationship as they would appear at rest. The pelvic clasper, consisting of an anterior clasper cartilage (ACC) and posterior clasper cartilage (PCC), articulates with the medial side of the basipterygium (BT) of the pelvic fin. At the anterior edge of the pelvic girdle the prepelvic tenaculum (PPT) overlies a large vacuity (VA) within which lies a sheet of connective tissue (not shown). **B**, Left half of the pelvic girdle of *Rhinochimaera pacifica* shown in dorsal view. The pelvic clasper, consisting of an anterior clasper cartilage and posterior clasper cartilage, is shown as it would appear externally, extending posteriorly from the basipterygium of the pelvic fin. The prepelvic tenaculum is armed with denticles and is shown extended anteriorly as it would be when extended from the prepelvic pouch. **C**, Ventral view of the left side of the pelvic girdle of *Hydrolagus novaezealandiae*. The pelvic clasper, with anterior clasper cartilage and posterior clasper cartilage, and the prepelvic tenaculum are shown in their normal anatomical relationships as they would appear at rest. Scale bars = 2 cm.

rudiments of prepelvic tenacula. This is the only occurrence of this secondary sexual character among female chimaeroids.

The frontal tenaculum, present only in males, is flat with a broad denticulate tip in *Callorhinchus*. The denticles are small.

**RHINOCHIMAERIDAE:** The pelvic claspers and prepelvic tenacula of *Harriotta raleighana* are shown in figure 26B as representative of Rhinochimaeridae. All rhinochimaerids possess simple, rodlike pelvic claspers consisting of two elements. The anterior clasper cartilage articulates with the pelvic fin at the medial edge of the basal cartilage and the posterior clasper cartilage is a slender, almost solid rod. At its tip is a fleshy bulb, composed of a loose tissue with cavernous vascular spaces, which is covered with placoid denticles.

The prepelvic tenacula of rhinochimaerids are simple blades of cartilage, narrow at the proximal end and expanded distally (fig. 26B). At the distal end is a notch that may be a deep groove or a shallow depression. Along the medial edge is a single row of placoid denticles. The prepelvic tenacula vary among the genera and species of Rhinochimaeridae in the shape of the distal end and the number of denticles, but the range of variation has not been thoroughly examined.

The frontal tenaculum in *Rhinochimaera* is robust with a broad base and flat dorsal surface, whereas *Harriotta* has a more slender frontal tenaculum with a distinct dorsal curve (fig. 25). In all species the bulbous tip has numerous recurved denticles on its ventral surface.

**CHIMAERIDAE:** The greatest variation and complexity of pelvic claspers among chimaeroids is found within the family Chimaeridae. The anterior clasper cartilage (ACC; fig. 26C) articulates with the basal cartilage of the pelvic fin at its posteromedial edge. This cartilage is forked at its anterior end and a thin flap of cartilage forms a channel along the medial edge. Articulating with the anterior clasper cartilage is the posterior clasper cartilage (PCC), which divides into two or three distal rods. The distribution of this character does not seem to be of systematic relevance at the generic level. All species of *Chimaera* have trifold pelvic claspers, as do

some species of *Hydrolagus* (e.g., *Hydrolagus affinis* and *Hydrolagus pallidus*).

In species with bifurcate claspers (e.g., *Hydrolagus collieri*) the two arms of the posterior clasper cartilage are enveloped by fleshy tissue along most of their length. Externally this fleshy tissue is covered with a shagreen of tiny denticles and internally it consists of cavernous vascular spaces. Each arm of the clasper has a central canal that is a continuation of the channel formed by the anterior clasper cartilage. In species that possess trifold pelvic claspers, the medial arm is a smooth straight rod with only a small patch of denticulate tissue at the tip (e.g., *Chimaera* sp. C). This third arm is equal in length to or sometimes slightly longer than the two lateral fleshy rods.

There are large paired swellings on the ventral midline posterior to the pelvic fins. This postanal pad may be found only in females (e.g., *Hydrolagus collieri* Dean, 1906, and *Hydrolagus* sp. B) or in both males and females (e.g., *Hydrolagus novaezealandiae*). The postanal pads are composed primarily of dense connective tissue and their function is unknown (McCutcheon, 1980).

The prepelvic tenacula of chimaerids are simple, bladelike cartilages with a distinct notch at the expanded distal end (fig. 26C). The lateral edge is armed with a single row of four to six recurved denticles. The frontal tenaculum is slender and deeply curved dorsally with numerous recurved denticles at the tip. The frontal tenaculum varies in shape among species of chimaerids (fig. 25).

#### TOOTH PLATES

Hypermineralized tooth plates are one of the most important synapomorphies of Holocephali, and the presence of one pair of tooth plates in the lower jaw and two pairs in the upper jaw is a synapomorphy of Chimaeriformes. The tooth plates are assumed to be related to durophagy, yet gut content analysis shows that living chimaeroids include a variety of soft- and hard-bodied prey in their diet (Graham, 1939; Gorman, 1963; Didier, personal obs.; Stehmann, personal communication.).

Because tooth plates are one of the few mineralized tissues in holocephalans, they

also fossilize well and most fossil holocephalans are known only from tooth plates. As a result, a large effort has been dedicated solely to their description and analysis (Egerton, 1843; Newberry and Worthen, 1870; Saint John and Worthen, 1883; Zittel, 1887, 1932; Woodward, 1892, 1921; Schauinsland, 1903; Dean, 1906; Hussakof, 1912; Chapman, 1918; Nielsen, 1932; Bargmann, 1933, 1941; Moy-Thomas, 1936a, b, 1939; Berman, 1967; Peyer, 1968; Ward, 1973; Ward and McNamara, 1977; Lund, 1977, 1986a, b; Ørvig, 1980, 1985; Zangerl, 1981; Kemp, 1984; Duffin, 1984; Ward and Duffin, 1989; Ward and Grande, 1991).

All chimaeroids have six tooth plates: two pairs of tooth plates in the upper jaw and one pair in the lower jaw (refer to fig. 27). In the upper jaw is an anterior pair of small vomerine tooth plates (VTP) followed by a pair of palatine tooth plates (PTP). In the lower jaw are the two large mandibular tooth plates (MTP). The oral surfaces (or working surfaces, WS) of the tooth plates are easily identified by their rough texture, which appears to be riddled with tiny pores. The oral surface of the tooth plates is characterized by regions of hypermineralized tissue commonly called tritons. Distal to the working surface a covering of oral epithelium prevents the surface tissue from wearing away and the tooth plate is smooth and shiny. The margin of wear (MW) demarcates the worn and unworn portions of the oral surface of the tooth plate. The aboral surface is characterized by the presence of a distinct ridge, the descending lamina (DL; Patterson, 1992). This descending lamina is well developed in all the tooth plates of *Callorhinchus*, but has been observed to be variously developed in only the mandibular and palatine tooth plates of other chimaeroids and may be absent or extremely reduced in *Rhinochimaera* (personal obs.).

Recent lungfishes also possess six hypermineralized tooth plates as well as an autostylic jaw suspension and have often been compared to holocephalans (see Jarvik [1980] for a recent review); however, on the basis of characters other than the jaws and tooth plates the lungfishes are clearly sarcopterygians, a well-established monophyletic lineage that does not include holocephalans (e.g., Rosen

et al., 1981; Lauder and Liem, 1983). Although the tooth plates of lungfishes and holocephalans possess the same tissues by definition (Kemp, 1984), they develop differently. The tooth plates in lungfishes develop by fusion of several individual tooth primordia (Kemp, 1977, 1984, *Neoceratodus*; Bemis, 1984, *Protopterus*), whereas each of the six tooth plates of chimaeroids has been observed to develop from an individual tooth plate primordium (Schauinsland, 1903; Kemp, 1984).

Recently, the tooth plates of adult *Callorhinchus milii* and *Chimaera monstrosa* have been observed to have a compound structure; therefore, their development may be more complex than reported previously (R. Zangerl, personal commun.). A new analysis of tooth plate development in *Callorhinchus milii*, with a comparative microanatomical study of tooth plates in all other genera, indicates that living chimaeroids possess tooth plates of a compound structure that represents the fusion of adjacent tooth-forming territories. This type of tooth plate development is reminiscent of what would be expected by the fusion and reduction of two elements of a typical chondrichthyan tooth family (Didier et al., 1994).

I have confirmed these basic points in a preliminary histological study of embryos of *Callorhinchus milii*. The primordia of the tooth plates are first evident as an infolding of the dental epithelium, which forms a cap over the entire tooth plate field in *Callorhinchus milii* embryos of 70–80 mm TL (DE; fig. 28A). In later stages this DE extends ventrally and a second, aboral tooth-forming territory begins to form. This aboral territory is related to the DL, which demarcates the region of aboral tooth plate territory growth (Didier, 1993; Didier et al., 1994, in press). The development of the tooth plates occurs rapidly and in embryos of 80–85 mm TL mineralized tissues are beginning to form and the tooth plates are already developing their characteristic structure (fig. 28B). Hypermineralized tissue begins to form in distinct patches after the initial framework of trabecular dentine has been established (Kemp, 1984). I have confirmed this early formation of hypermineralized tissue in embryos of 103–

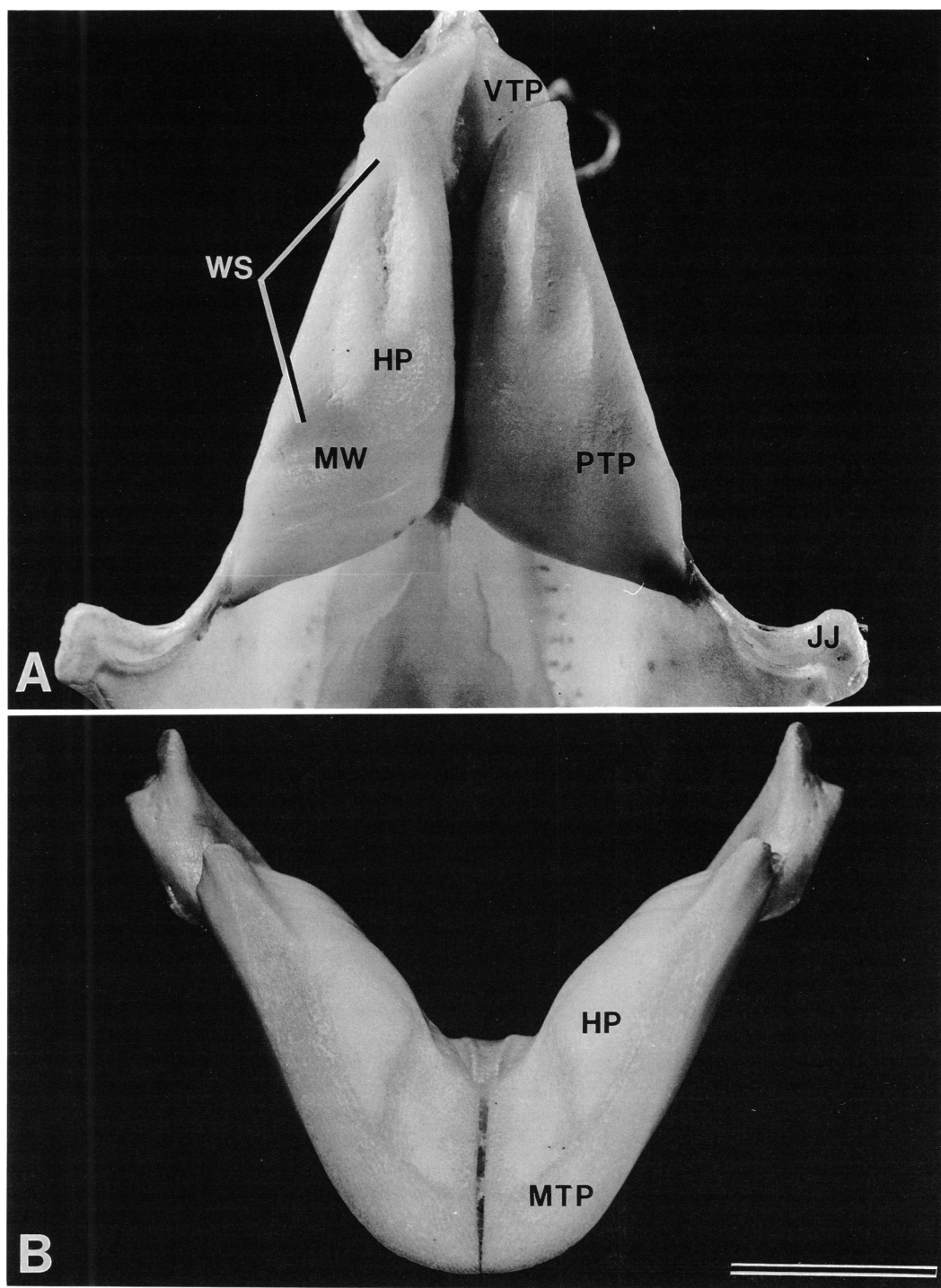


Fig. 27. Tooth plates of *Callorhinchus milii* (AMNH 96954). A, Ventral view of a dried neurocranium showing the palatine (PTP) and vomerine (VTP) tooth plates in the upper jaw of *Callorhinchus milii*. The large hypermineralized pad (HP) is evident in the center of the oral surface (WS) of the palatine

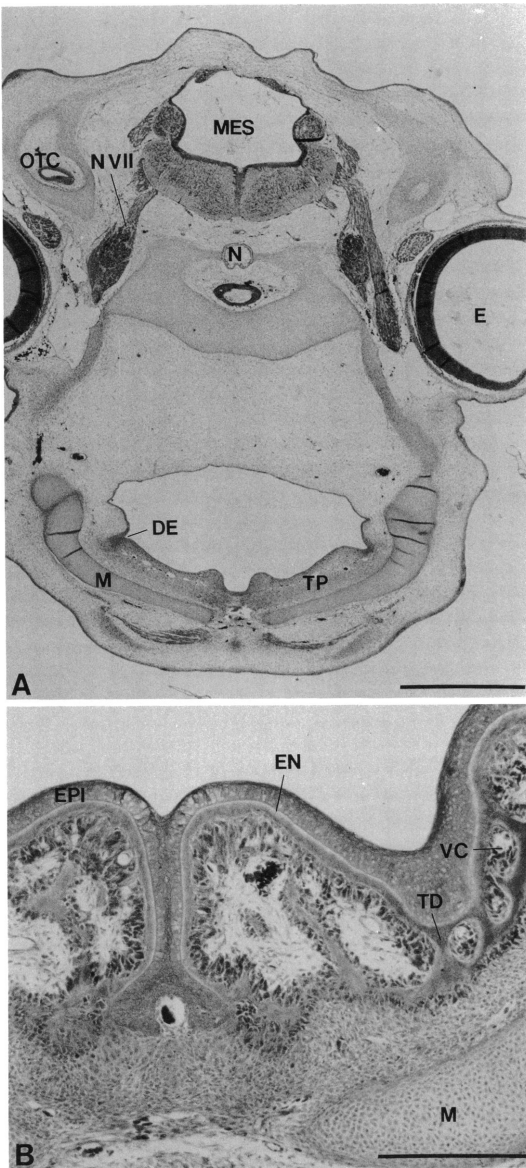


Fig. 28. Development of tooth plates of *Callorhinchus milii*. **A**, Transverse section through the head of an embryo (CM40, 79 mm TL) showing the early development of the mandibular tooth plates (TP), which begin to form as mesenchyme cells, aggregate below the infolded dental epithelium (DE). The lower jaw (M), mesencephalon (MES), notochord (N), and otic capsule (OTC) are shown as morphological landmarks. Scale bar = 1 mm. **B**, Transverse section of the head of an older embryo (CM52, 89 mm TL) showing the later development of the mandibular tooth plates. Underneath the oral epithelium (EPI) lies a layer of mineralized tissue that has been variously (and perhaps incorrectly) named "enameloid" (EN) or "vitrodentine." Internally, the tooth plate consists of trabecular dentine (TD) and vascular canals (VC). There are no hypermineralized tissues at this early stage. Scale bar = 0.5 mm.

109 mm TL. The trabecular dentine matrix continues to develop around the areas of hypermineralization until these two tissue types appear in direct continuity (fig. 29). Future research on the ontogeny of tooth plates of chimaeroids should focus on the development of hypermineralized tissues in order to clarify the morphological and histological distinctions.

In all chimaeroids trabecular dentine comprises the bulk of the tooth plate and forms a mineralized network of tissue penetrated by blood vessels (TD; fig. 29). At the oral surface of the tooth plate the trabecular dentine forms a solid layer and the vascular canals become aligned in a parallel arrangement. This surface layer of trabecular dentine in which the vascular canals are parallel to each other is also known in the literature as tubular dentine (Denison, 1974), a misleading identification that is no longer accepted. The trabecular dentine matrix is less dense near the base of the tooth plate where large vascular spaces form the pulp cavity (PC).

In direct contact with the trabecular dentine is the hypermineralized tissue (HT; = tritons), which is penetrated by dentine tubules. The hypermineralized tissue occurs in two forms that appear on the oral surface of the tooth plates as either a single large triton or a series of small beadlike tritons, the

lium (DE). The lower jaw (M), mesencephalon (MES), notochord (N), and otic capsule (OTC) are shown as morphological landmarks. Scale bar = 1 mm. **B**, Transverse section of the head of an older embryo (CM52, 89 mm TL) showing the later development of the mandibular tooth plates. Underneath the oral epithelium (EPI) lies a layer of mineralized tissue that has been variously (and perhaps incorrectly) named "enameloid" (EN) or "vitrodentine." Internally, the tooth plate consists of trabecular dentine (TD) and vascular canals (VC). There are no hypermineralized tissues at this early stage. Scale bar = 0.5 mm.

tooth plate. The margin of wear (MW) demarcates the worn, oral surface of the tooth plate from the more distal, unworn portion. **B**, Lower jaw of *Callorhinchus milii* showing the mandibular tooth plates (MTP) with a large hypermineralized pad (HP). Scale bar = 1 cm.

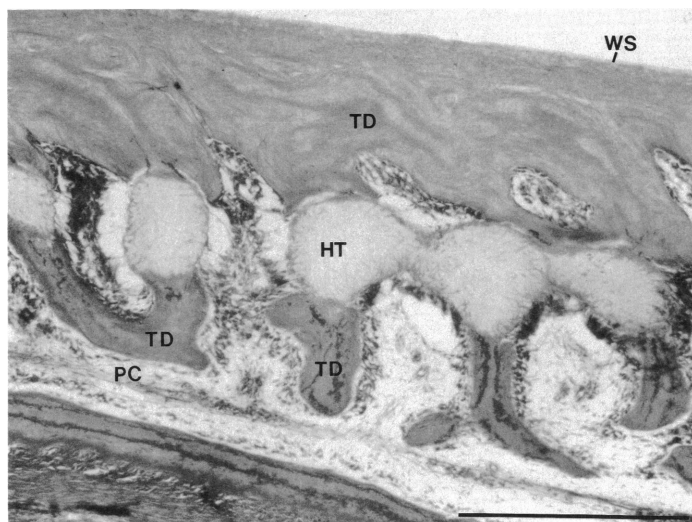


Fig. 29. Microscopic anatomy of the tooth plates of *Callorhinchus milii*. A sagittal section of the mandibular tooth plate illustrates the tissues of the tooth plate and their relationship to each other. Trabecular dentine (TD) is a dark-staining tissue forming a thick layer at the oral surface (WS). The hypermineralized tissue (HT) stains lightly and is in direct contact with, and surrounded by, trabecular dentine. Discrete regions of hypermineralized tissue appear to be fusing to form a large, hypermineralized pad. Scale bar = 0.5 mm.

“pearlstrings” of Bargmann (1933). Ørvig has defined these two types of tritons as vascular pleromin and compact pleromin, respectively. Vascular pleromin is distinguished by the enclosure of nearly parallel vascular canals whereas compact pleromin lacks vascular canals and is formed into columns (Ørvig, 1985). The term pleromin has sparked controversy because by definition it implies a developmental mechanism whereby the tissue develops to fill in spaces and is deposited by a population of cells that Ørvig has identified as pleromoblasts. In an effort to clarify the nature of the hypermineralized tissue itself, the term orthotrabeculine has recently been proposed by Zangerl et al. (1993). I refer to Ørvig’s compact pleromin as hypermineralized rods (HD) and vascular pleromin as hypermineralized pads (HP), respectively. I have defined these as hypermineralized rods and hypermineralized pads in order to make the morphological distinction clear while making no assumptions about the histology of these tissues.

There are potential problems with some tooth plate characters. It appears that there is a developmental continuity between the

two forms of hypermineralized tissue. This continuity of hypermineralized tissues was first suggested by Garman (1904). Comparative microscopic anatomical study of the mandibular tooth plates of *Callorhinchus*, *Harriotta*, *Chimaera*, and *Hydrolagus* shows that the distinction between hypermineralized rods and hypermineralized pads is blurred and developmentally they seem to be continuous (Didier, 1991). These results are only preliminary, but the implication may be of systematic importance because the pattern of hypermineralized tissue on the surface of the tooth plates is used to identify species, particularly fossil taxa (e.g., Ward, 1973, Ward and McNamara, 1977; Duffin, 1984).

Unlike the teeth in other chondrichthyan fishes, which are regularly shed and replaced, the tooth plates of holocephalans are never replaced. The tooth plates have an active growing region at the base (GB) and underneath the descending lamina. As the tooth plate is abraded, the trabecular dentine wears away, leaving a relief of hypermineralized tissue. The pattern of hypermineralized tissue on the oral surface of the tooth plates may not be a good character because there is no

way to assess the affect of wear on shaping the hypermineralized tissues.

**CALLORHYNCHIDAE:** The tooth plates of *Callorhynchus* are robust, crushing plates (fig. 27A,B). On the oral surface of the tooth plates the hypermineralized tissue is in the form of large tritoral pads. A well-developed descending lamina is present on the aboral surface of all tooth plates. The vomerine tooth plates are firmly attached to the ethmoid region of the neurocranium and, except for the tips, are obscured by the palatine tooth plates. There is no obvious hypermineralized tissue exposed on the surface, but histological sections show evidence of a tiny hypermineralized pad in the center of the tooth plate.

The triangular palatine tooth plates cover the roof of the mouth. In the center of each tooth plate is a bifurcate hypermineralized pad (HP).

In the lower jaw the mandibular tooth plates are tightly bound to Meckel's cartilage by a dense connective tissue pad. The labial edge of these tooth plates gently curves medially, with the curve continuing around to the anterior tip of the tooth plate to a nearly straight symphyseal edge where left and right tooth plates meet. In the center of each mandibular tooth plate is a large hypermineralized pad.

**RHINOCHIMAERIDAE:** All six tooth plates of *Rhinochimaera* are triangular, very thin, and bladelikey with smooth surfaces (fig. 30). The lateral edges of these tooth plates are darkly pigmented, fading to a light gray-brown near the center. Externally the tooth plates appear as a sharp beak where the anterior tips of the vomerine and mandibular tooth plates meet. The only visible sign of wear on these tooth plates is at the edges. There is no hypermineralized tissue exposed at the surface of the tooth plates of *Rhinochimaera*, and in transverse sections through a mandibular tooth plate of an adult *Rhinochimaera pacifica* there is no evidence of hypermineralized tissue (fig. 31). At the surface is a layer of dentine and the interior of the tooth plate consists of a very loose trabecular dentine with numerous large vascular spaces (PC). A descending lamina has not been observed on the aboral surface of any of the tooth plates.

The tooth plates of *Harriotta* and *Neoharriotta* have hypermineralized tritors in the form of pads and rods (fig. 32). Although these

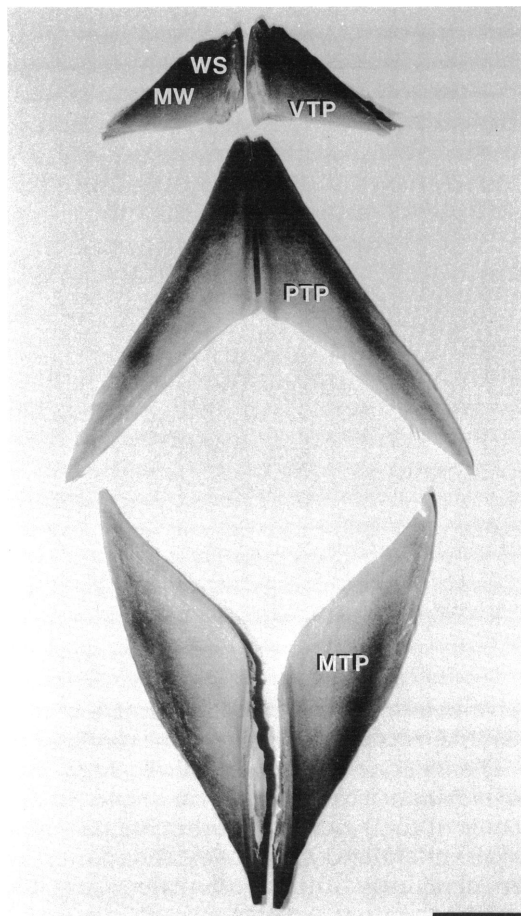


Fig. 30. Tooth plates of *Rhinochimaera pacifica*. The three pairs of tooth plates are oriented as they would be in a wide-open mouth with vomerine (VTP) and palatine (PTP) tooth plates at the top of the figure and mandibular tooth plates (MTP) facing downward. The margin of wear (MW), demarcating the worn oral surface (WS) from the unworn portions of the tooth plate, is difficult to distinguish because of the dark pigmentation of these tooth plates. Scale bar = 1 cm.

tooth plates are robust, the edges are blade-like, forming a sharp cutting edge. On the aboral surface of the palatine and mandibular tooth plates, at the symphyseal edge, is a descending lamina. The descending lamina is reduced in these species and is especially small in the mandibular tooth plates.

In both *Harriotta* and *Neoharriotta* the vomerine tooth plates are ventrally directed, incisiform blades. There are five to seven hy-



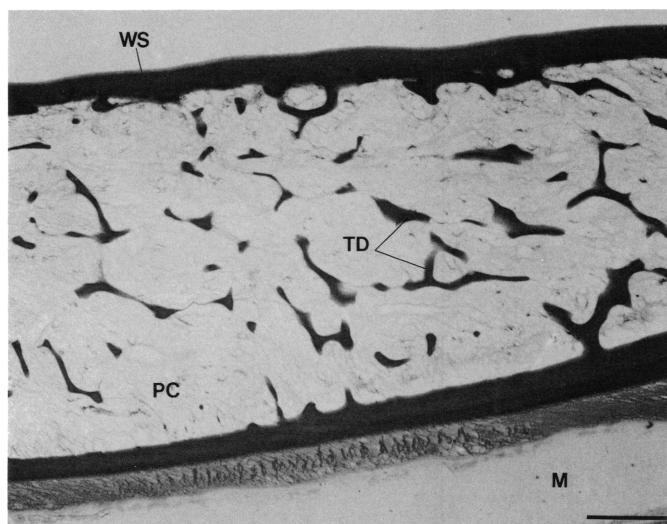


Fig. 31. Microscopic anatomy of the tooth plates of *Rhinochimaera pacifica* (AMNH 96940). This transverse section of the mandibular tooth plate of an adult shows the loose network of trabecular dentine (TD) and pulp (PC) in the interior of the tooth plates. No hypermineralized tissue has been observed in the tooth plates of *Rhinochimaera*. Scale bar = 0.5 mm.

permineralized rods that appear as a row of beadlike dots on the surface of the tooth plate.

The palatine tooth plates of *Harriotta* and *Neoharriotta* are triangular in shape. In the center of each palatine tooth plate is a large hypermineralized pad that extends almost to the labial edge of the tooth plate. Along the labial edge of the palatine tooth plate is a series of hypermineralized rods.

The mandibular tooth plates of *Harriotta* and *Neoharriotta* have a raised hypermineralized pad located just lateral of the center. A series of hypermineralized rods is visible along the labial edge of the tooth plate (HR).

**CHIMAERIDAE:** The tooth plates of chimaerids are relatively thin and the sharp anterior edges form nipping blades (fig. 33). A small descending lamina is present along the symphyseal edge of the palatine and mandibular tooth plates, but no descending lamina has been observed in the vomerine tooth plates. The pigmentation of these tooth plates is species specific and ranges from a dark brown or black in *Hydrolagus* sp. B to white in *Hydrolagus colliei* and *Hydrolagus novae-zealandiae*.

The vomerine tooth plates of *Hydrolagus* are similar to those of *Harriotta* and *Neoharriotta*. These incisorlike blades are di-

rected ventrally and meet the mesial edge of the mandibular tooth plates near the symphysis. There are five hypermineralized rods visible at the cutting edge of the vomerine tooth plates. On the posterior face of the oral surface of the vomerine tooth plates is a series of transverse ridges (TR). Although the vomerine tooth plates of chimaerids are similar in external morphology to those of *Harriotta* and *Neoharriotta*, these transverse ridges are found only in the vomerine tooth plates of chimaerids.

The palatine tooth plates of *Hydrolagus* are roughly triangular with a prominent lateral flange (LF). As in all other chimaeroids these tooth plates lie flat on the roof of the mouth directly behind the vomerine tooth plates. At the mesial edge is a prominent hypermineralized rod and extending along the cutting edge of the tooth plate are numerous smaller hypermineralized rods, usually about 10.

The mandibular tooth plates of *Hydrolagus* and *Chimaera* have a series of hypermineralized rods along the cutting edge of the tooth plate. There is no obvious hypermineralized tritor pad although some species, especially *Chimaera monstrosa*, appear to have a small, centrally located pad at the margin of wear, and microanatomical obser-



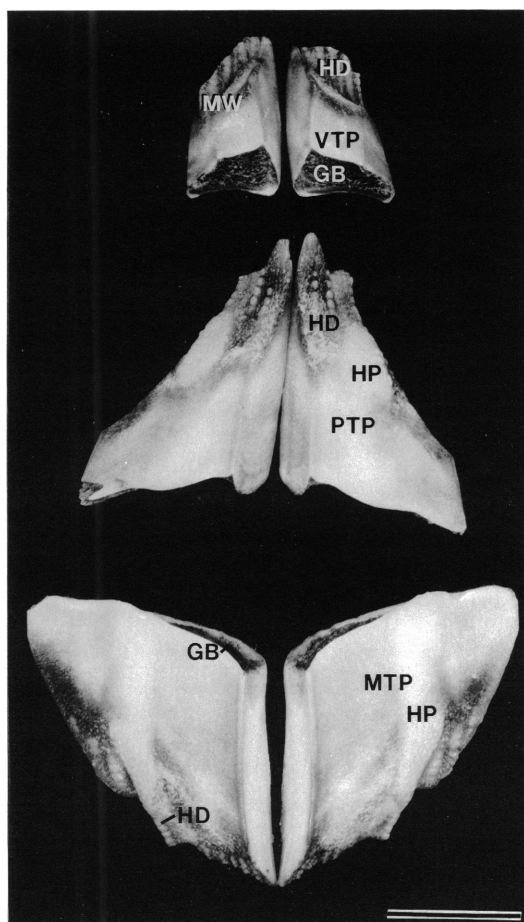


Fig. 32. Tooth plates of *Harriotta raleighana*. The tooth plates are oriented as they would be in the mouth if it were open wide. Exposed on the oral surfaces of these tooth plates are tritons in the form of hypermineralized pads (HP) and rods (HD). At the distal ends of the mandibular (MTP) and vomerine (VTP) tooth plates a region of growth (GB) is visible. Scale bar = 1 cm.

ventions confirm the presence of a small hypermineralized tritor pad in the mandibular tooth plates of both *Hydrolagus* and *Chimaera*.

#### MUSCULATURE

The comparative musculature of all extant genera of chimaeroid fishes is described below, including descriptions of the musculature of the head, gill arches, pectoral girdle, and trunk. Although soft characters cannot

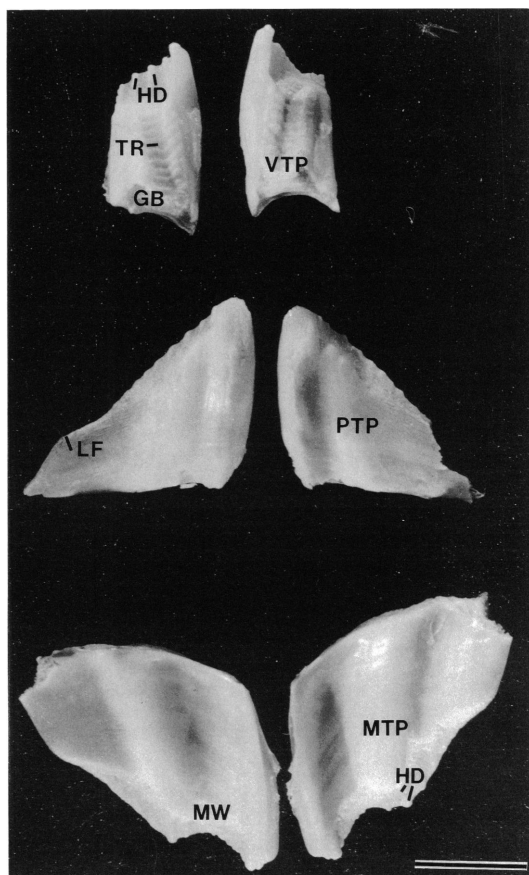


Fig. 33. Tooth plates of *Hydrolagus novaezealandiae*. The tooth plates are oriented as they would be in the mouth if it were open wide. The hypermineralized rods (HD) are difficult to distinguish in these white tooth plates, but can be seen at the edges as prominent knobs. The palatine tooth plates (PTP) have a prominent lateral flange (LF; broken in the right tooth plate). Transverse ridges (TR) are characteristic of the vomerine tooth plates (VTP) of chimaerids. Scale bar = 1 cm.

help resolve relationships between fossil and Recent taxa, muscle characters can be used in outgroup comparison with Recent elasmobranchs.

Nomenclature for the muscles follows Vetter (1878) on the basis of primacy. In cases where developmental evidence refutes Vetter's (1878) work, the nomenclature of Edgeworth (1935) takes precedence. Shann (1919) provided the most complete description of the muscles of the pectoral girdle for chimaeroids. I confirm his descriptions for *Chi-*

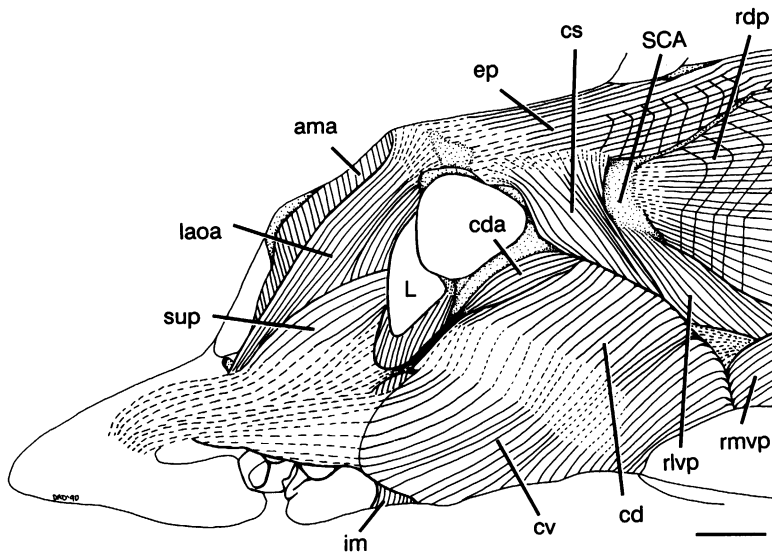


Fig. 34. Superficial muscles of the head and pectoral region of *Callorhynchus milii*. The skin, connective tissue, and ampullary canals have been removed to reveal the underlying muscles. See text for a detailed description of the musculature. Scale bar = 2 cm.

*maera* and *Callorhynchus* and find them appropriate; therefore, I follow his terminology.

Table 8 is a complete list of all the muscles described in this study with a list of the synonymous names and remarks regarding identification or description of the muscle. The descriptions of the musculature are based on detailed study of *Callorhynchus milii* and representatives of the remaining five extant genera of chimaeroids that were dissected (see table 2). Significant differences among genera are noted in the remarks and where no remarks are made, it is understood that I have found the muscles to be identical in all genera examined.

#### MANDIBULAR GROUP

The following description is of muscles derived from the mandibular arch with Vth cranial nerve innervation.

*M. superficialis*, sup (fig. 34).

Origin: From connective tissue of the pre-orbital fascia.

Insertion (not shown): Into connective tissue of the rostral flap.

Remarks: Among chimaeroids this muscle is only found in *Callorhynchus*. It is a very

thin, almost indistinguishable sheet of muscle superficial to the *M. adductor mandibulae anterior*. Many of its fibers insert into the connective tissue sheet covering the antorbital portion of the head while a tiny bundle of muscle extends into the rostrum and inserts into the connective tissue of the flap of the rostrum. This muscle is probably derived from the *M. adductor mandibulae anterior* and is innervated by the Vth cranial nerve.

*M. levator anguli oris anterior*, laoa (figs. 34, 35, 38, 41, 43)

Origin: Via a connective tissue band from the antorbital crest; in males at the articulation of the frontal tenaculum.

Insertion: After passing under the labial ligament this muscle inserts on the ventromedial face of the superior maxillary cartilage with some fibers to the posterior end of this cartilage.

Remarks: In *Callorhynchus* a small bundle of anterior fibers inserts on the lateral rostral rod, and in *Rhinochimaera* and *Harriotta* a small anterior muscle bundle inserts on the inner angle of the prelabial cartilage. Both Luther (1909) and Kesteven (1933) distinguished this as a separate muscle in *Callorhynchus*. Raikow and Swierczewski (1975) in-

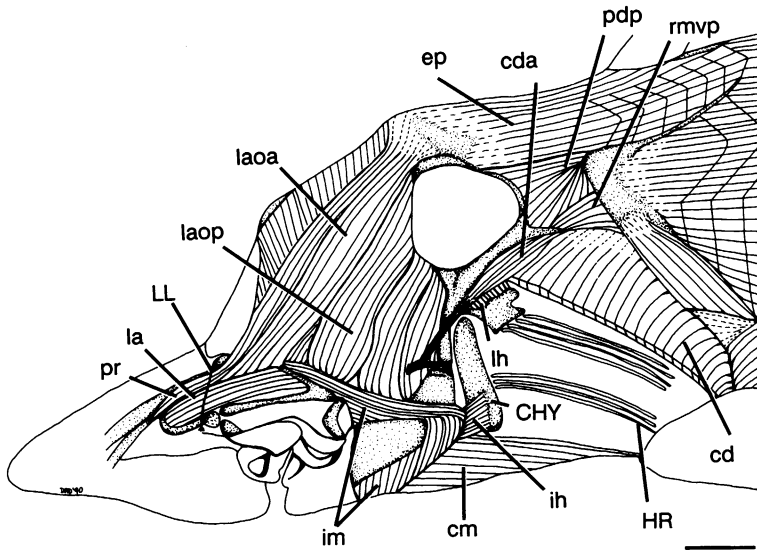


Fig. 35. Deep muscles of the head and pectoral region of *Callorhynchus milii*. Superficial muscles and opercular flap have been removed to reveal deep muscles of the jaws and labial cartilages. See text for a detailed description of the musculature. Scale bar = 2 cm.

indicated some anterior fibers to the upper lip in female *Chimaera* and I follow Kesteven (1933) and Raikow and Swierczewski (1975) in calling this portion of the *M. levator anguli oris anterior* the *M. levator anguli oris anterior pars rostralis* because of its rostral inser-

tion in *Callorhynchus* and its proximity to the rostrum in rhinochimaerids. In males this portion of the *M. levator anguli oris anterior* runs to the base of the frontal tenaculum with some fibers inserting onto the tenaculum by dense connective tissue fibers.

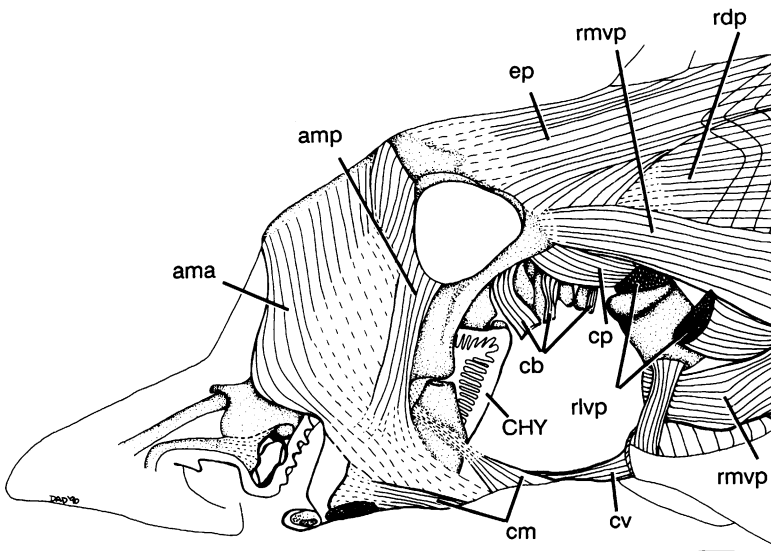


Fig. 36. Deep muscles of the head and pectoral region of *Callorhynchus milii*. Labial cartilages and gill arches have been removed to expose deep muscles of the snout and branchial region. See text for a detailed description of the musculature. Scale bar = 2 cm.

**TABLE 8**  
**Synonymy of Muscles of Chimaeroids**

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M. superficialis, sup

This muscle is possibly part of Kesteven's (1933) M. depressor rostri et veli, but I can find no description of this thin muscle sheet in any previous works. Kesteven (1933: 465) indicated that the many layers he described for the deep ventral constrictors may be portions of the same muscle. I believe this to be true as I cannot easily separate out the layers he described.

M. levator anguli oris anterior pars rostralis, pr

M. levator cartilagenous prelabialis, Luther (1909)

M. levator rostri, Kesteven (1933)

M. levator anguli oris pars rostralis, Raikow and Swierczewski (1975)

According to Edgeworth (1935), all of the superficial muscles that insert on the labial cartilages and lips share a common origin and are distinguished as separate muscles only at their insertions. Only Luther (1909) and Kesteven (1933) distinguished the anterior part of the M. levator anguli oris (below) as a separate muscle.

M. levator anguli oris anterior, laoa

M. levator anguli oris 1, Vetter (1878)

M. levator anguli oris anterior, Luther (1909)

M. levator labii superioris, Kesteven (1933)

M. levator anguli oris posterior, Edgeworth (1935)

M. levator anguli oris pars rostralis, Raikow and Swierczewski (1975)

M. levator anguli oris posterior, laop

M. levator anguli oris 2, Vetter (1878)

M. levator anguli oris posterior, Luther (1909)

M. levator labii inferioris, Kesteven (1933)

M. levator anguli oris posterior, Edgeworth (1935)

M. labialis anterior, la

M. labialis anterior, Vetter (1878)

M. labialis anterior, Luther (1909)

M. protractor labii superioris, Kesteven (1933)

M. labialis, Edgeworth (1935)

M. intermandibularis I, im

M. labialis posterior, Vetter (1878)

M. labialis inferioris, Luther (1909)

M. protractor superior labii inferioris, Kesteven (1933)

M. intermandibularis anterior, Edgeworth (1935)

M. intermandibularis II, im

M. labialis posterior, Luther (1909)

M. protractor inferior labii inferioris, Kesteven (1933)

M. intermandibularis posterior, Edgeworth (1935)

This two-part muscle is well developed in Callorhinchus where it runs from the posterior edge of the superior maxillary cartilage to the posterior two-thirds of the premandibular cartilage along its dorsal edge. Descriptions by Luther (1909) and Edgeworth (1935) as well as Vetter's (1878) illustrations indicate that in Chimaera a muscle runs ventrally along the lower jaw and inserts on the minute premandibular cartilage. Vetter (1878) also illustrated a second tiny muscle from the premandibular

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TABLE 8—(Continued)

cartilage to the lower jaw, but did not indicate that it is a separate muscle and I assume that he interpreted this as a continuation of his M. labialis posterior. Edgeworth (1935: 40) claimed to follow Luther in his description of the muscles but in the text he reversed the names and muscles as they are shown by Luther (1909: 39). I agree with Vetter's (1878) interpretation and believe these two muscles to be parts of the M. intermandibularis on the basis of a common innervation.

M. adductor mandibulae anterior, ama

M. adductor mandibulae, Vetter (1878)

M. preorbitalis, Luther (1909)

M. adductor mandibulae anterior head, Kesteven (1933)

M. levator mandibulae anterior, Edgeworth (1935)

Vetter (1878: 463) did not distinguish anterior and posterior portions of this muscle in his illustrations, but he described two portions of this muscle for Callorhinchus in his text.

Edgeworth (1935: 255) synonymized this anterior portion with Vetter's (1878) M. levator labii superior, but I find no mention of this muscle in Vetter's work.

M. adductor mandibulae posterior, amp

M. adductor mandibulae, Vetter (1878)

M. adductor mandibulae, Luther (1909)

M. adductor mandibulae posterior head, Kesteven (1933)

M. levator mandibulae posterior, Edgeworth (1935)

M. constrictor operculi dorsalis, cd

M. constrictor superficialis, Vetter (1878)

M. levator operculi, Kesteven (1933)

M. constrictor hyoideus, Edgeworth (1935)

Vetter (1878) illustrated this muscle as several parts in an attempt to homologize this muscle sheet with the dorsal and ventral constrictors of sharks. Vetter's (1878) Cs5 appears to be the part of the constrictor muscle sheet that is continuous with the M. coracomandibularis and extends into the connective tissue sheet of the rostrum. Kesteven (1933) indicated that this muscle is innervated by both the Vth and VIIth cranial nerves. Edgeworth (1935: 97-98) described the development of the muscles extending into the connective tissue of the rostrum from the hyoid constrictor muscle sheet; therefore, it seems reasonable to accept a VIIth nerve innervation of these muscles.

M. constrictor operculi ventralis, cv

M. constrictor superficialis, Vetter (1878)

M. superficial ventral constrictor, Kesteven (1933)

M. constrictor hyoideus, Edgeworth (1935)

According to Kesteven (1933), this muscle is innervated by only the Vth nerve.

M. constrictor operculi dorsalis anterior, cda

M. depressor mandibulae superior, Kesteven (1933)

This muscle is unique to Callorhinchus.

M. levator hyoideus, lh

M. hyoideus superior, Vetter (1878)

M. levator hyomandibulae, Edgeworth (1935)

TABLE 8—(Continued)

M. interhyoideus, ihM. hyoideus inferior, Vetter (1878)M. geniohyoideus, Kesteven (1933)M. interhyoideus, Edgeworth (1935)

Kesteven (1933) suggested that this muscle is a homologue to the M. intermandibularis or M. retractor hyoideus of elasmobranchs, and also indicated, as does Vetter (1878), that it is innervated by the VIIth nerve. According to Edgeworth (1935), both this muscle and the M. levator hyoideus originate from the hyoid constrictor muscle sheet.

Mm. constrictores branchiales, cbMm. interbranchiales, Vetter (1878)Mm. constrictores branchiales, Edgeworth (1935)

I interpret Kesteven (1933) to have described these muscles as part of the Mm. transversi ventrales series. Edgeworth (1935) indicated that elasmobranchs lack Mm. transversi ventrales. My observations confirm Edgeworth (1935).

Mm. adductores arcuum branchialium (not illustrated)Mm. adductores arcuum branchialium, Vetter (1878)Mm. adductores arcuum branchialium, Edgeworth (1935)Mm. interbranchiales (not present)

Edgeworth (1935) claimed that these muscles are not present in Holocephali. My interpretation of Kesteven's (1933) description is that he indicated they are present. I have not found these muscles in my dissections.

M. cucullaris superficialis, csM. trapezius superficialis, Vetter (1878)M. levator pectoralis, Shann (1919)M. cucullaris, Kesteven (1933)M. cucullaris superficialis, Edgeworth (1935)M. protractor dorsalis pectoralis, pdpM. protractor dorsalis pectoralis, Shann (1919)M. cucullaris profundus, cpM. cucullaris profundus, Vetter (1878)M. levator arcuum branchialium posterior, Kesteven (1933)M. cucullaris profundus, Edgeworth (1935)M. subspinalis (not illustrated)M. protractor arcuum branchialium, Vetter (1878)M. levator arcuum branchialium anterior, Kesteven (1933)M. subspinalis, Edgeworth (1935)

Edgeworth also described a M. interpharyngobranchialis from pharyngobranchial 2 to pharyngobranchial 3, which I have not found.

M. coracomandibularis, cmM. coracomandibularis, Vetter (1878)M. coracomandibularis, Shann (1919)M. coracomandibularis, Kesteven (1933)M. geniocoracoideus, Edgeworth (1935)

TABLE 8—(Continued)

M. coracohyoideus, chM. coracohyoideus Vetter (1878)M. coracohyoideus Shann (1919)M. coracohyoideus Kesteven (1933)M. rectus cervicis, Edgeworth (1935)Mm. coracobranchiales, cbrMm. coracobranchiales Vetter (1878)Mm. coracobranchiales Shann (1919)Mm. coracobranchiales Kesteven (1933)Mm. coracobranchiales Edgeworth (1935)M. epaxialis, epM. retractor dorsalis pectoralis, Shann (1919)

Shann (1919) described the M. retractor dorsalis pectoralis as separate from the epaxial musculature. Although its fibers intermingle with the M. epaxialis posteriorly, its origin from the dorsal posterior edge of the scapular process seems to indicate a separate embryonic origin.

M. retractor latero-ventralis pectoralis, rlvM. retractor latero-ventralis pectoralis, Shann (1919)

This muscle is described as having two points of origin. Shann (1919) distinguished these two heads as an external and internal portion of this muscle.

M. retractor mesio-ventralis pectoralis, rmlvpM. retractor mesio-ventralis pectoralis, Shann (1919)

This muscle lies underneath the M. retractor latero-ventralis pectoralis and originates from the otic process of the cranium with the fibers running under the scapular process where they are joined by fibers from the posterior rim and medial face of the scapular process.

*M. levator anguli oris posterior*, laop (figs. 35, 38, 41, 43)

Origin: From the antorbital crest with the *M. levator anguli oris anterior*. In rhinochimaerids the posterior fibers take origin from the preorbital fascia and in chimaerids the origin is only from the preorbital fascia.

Insertion: Onto the posterior end of the superior maxillary cartilage with a small tendon inserting medially onto the connective tissue of the lip between the inferior maxillary cartilage and the premandibular cartilage.

Remarks: In rhinochimaerids and chimaerids the muscle insertion extends over the dorsal edge of the superior and inferior maxillary cartilages.

*M. labialis anterior*, la (figs. 35, 38, 41, 43)

Origin: From the anterior tip of the pre-

labial cartilage. In chimaerids this muscle originates from the prelabial portion of the premaxillary cartilage.

Insertion: Onto the posterior end of the superior maxillary cartilage.

*M. intermandibularis*, im (figs. 34, 35, 37, 41, 45)

Origin: From the posterior edge of the superior maxillary cartilage in *Callorhinchus* and from the medial side of the inferior maxillary cartilage in all other genera.

Insertion: Onto dense connective tissue surrounding the premandibular cartilages. In *Callorhinchus* this muscle inserts superficial to the interhyoideus at the anteroventral edge of the lower jaw.

Remarks: This muscle is interrupted by an insertion onto the premandibular cartilage and has been described as two separate mus-

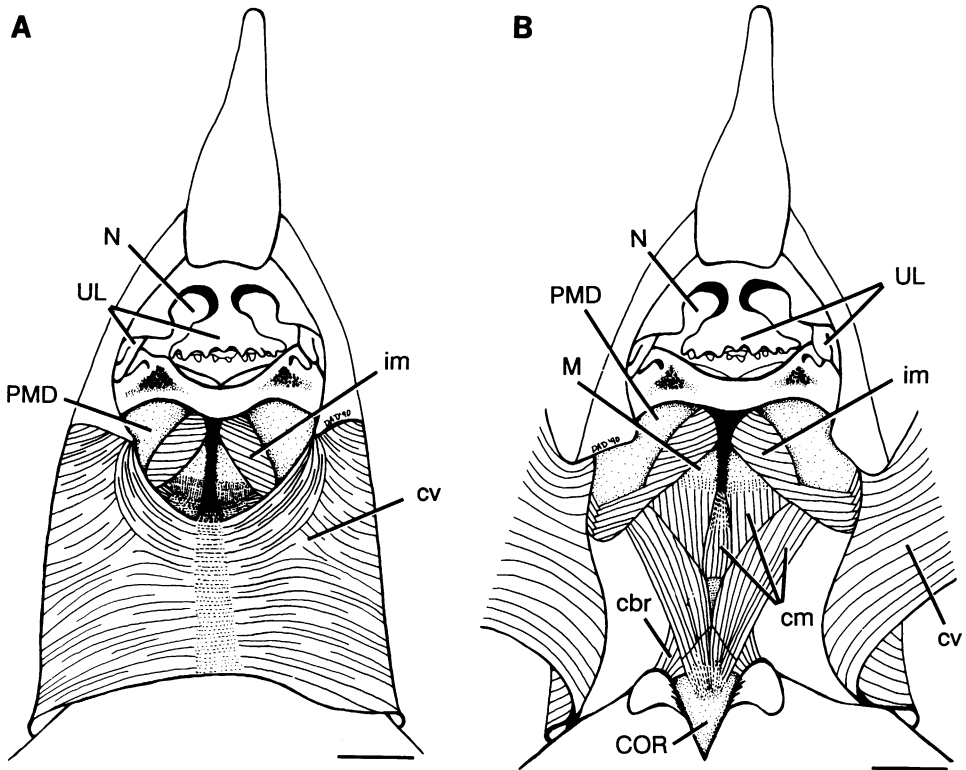


Fig. 37. Ventral muscles of *Callorhinchus milii*. A, The skin has been removed to expose superficial musculature. B, Ventral constrictor muscles have been cut to expose deep hypobranchial muscles. See text for a detailed description of the musculature. Scale bar = 2 cm.

cles (Luther, 1909; Kesteven, 1933; Edgeworth, 1935). I can find no distinct muscular connection between the premandibular cartilage and the lower jaw in *Rhinochimaera*, *Harriotta*, or *Hydrolagus* even though it is figured and described for *Hydrolagus* (Vetter, 1878; Luther, 1909; Kesteven, 1933; Edgeworth, 1935). My observations indicate that the so-called *M. labialis posterior* is actually the *M. intermandibularis* and the two parts described are one muscle that is interrupted by the premandibular cartilage. Dense connective tissue binds the ventral premandibular cartilages to the lower jaw and it is likely that the second part of the *M. intermandibularis* running from the premandibular cartilage to the lower jaw has been reduced and lost with dense connective tissue taking its place. If Luther (1909) and Vetter (1878) are correct in their figures for *Chimaera*, it seems

reasonable to assume that the *M. intermandibularis* is a single muscle interrupted by the premandibular cartilage.

*M. adductor mandibulae anterior*, ama (figs. 34, 36, 39, 41, 42, 44)

Origin: From the preorbital lamina with posterior fibers also taking origin from the preorbital fascia.

Insertion: Onto the lower jaw by a stout tendon that wraps over the lateral surface of Meckel's cartilage, forming a dense connective tissue sling around the lower jaw.

Remarks: This muscle is unusual in that its entire mass lies anterior to the orbit. The muscle fibers insert in a pinnate fashion with a thin strip of connective tissue dividing this muscle into two parts. In males the frontal tenaculum, jaws, and labial cartilages are functionally linked (Raikow and Swierczews-



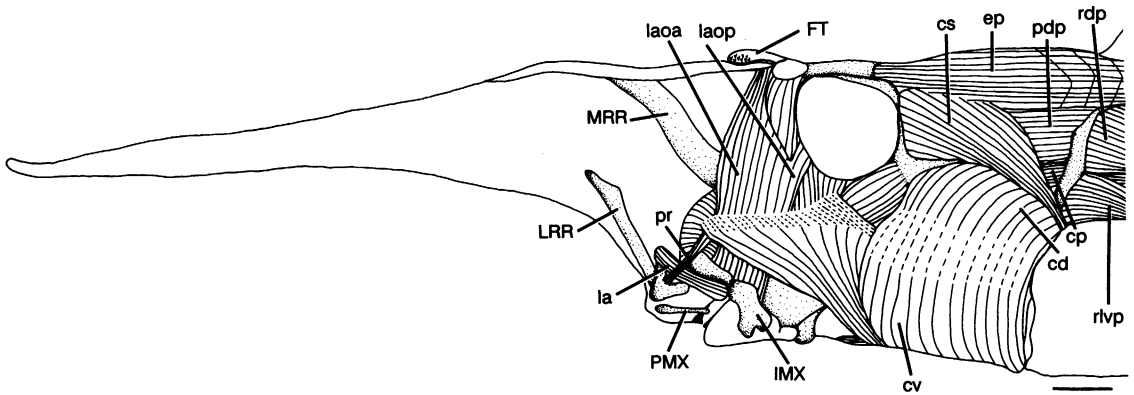


Fig. 38. Superficial muscles of the head and pectoral region of *Rhinochimaera pacifica* (AMNH 96939). Skin and connective tissue of the head and snout have been removed to expose the underlying muscles. See text for a detailed description of the musculature. Scale bar = 2 cm.

ki, 1975) and coordinated movement of the jaws and frontal tenaculum is possible. The tendon of the *M. adductor mandibulae anterior* has a dorsal connection to the frontal tenaculum with some fibers inserting onto the skin of the pocket in which the tenaculum rests. This dorsal insertion occurs via connective tissue that runs from the supraorbital crest to skin of the pocket of the frontal tenaculum. There is also a muscular connection between the labial cartilages and the frontal tenaculum (see description for *M. levator anguli oris anterior* above).

*M. adductor mandibulae posterior*, amp (figs. 36, 39, 41, 44)

Origin: From the preorbital fascia and the suborbital ridge.

Insertion: Onto the lower jaw by a stout tendon.

Remarks: In *Callorhynchus* this muscle originates from the preorbital fascia and partially overlies the *M. adductor mandibulae anterior* with some fibers inserting into the central connective tissue ventrally. In rhinochimaerids this muscle originates solely from the suborbital ridge and in chimaerids the *M.*

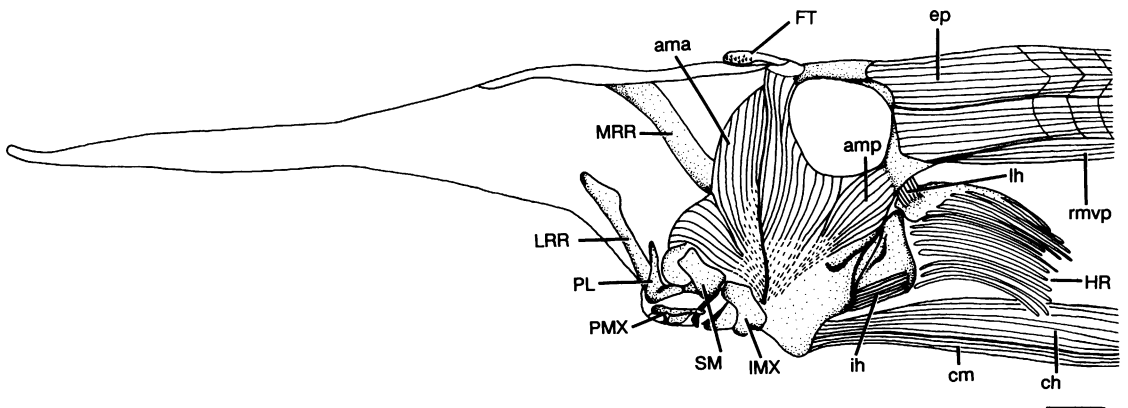


Fig. 39. Deep muscles of the head and pectoral region of *Rhinochimaera pacifica* (AMNH 96939). Superficial muscles of the jaws, labial cartilages, and opercular flap have been removed, exposing deep muscles underneath. See text for a detailed description of the musculature. Scale bar = 2 cm.

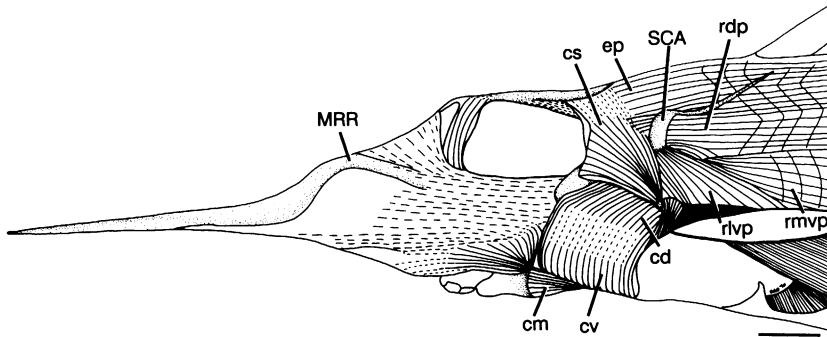


Fig. 40. Superficial muscles of the head and pectoral region of *Harriotta raleighana* (AMNH 96931). Skin and connective tissue of the head and snout have been removed to expose underlying musculature. See text for a detailed description of the musculature. Scale bar = 2 cm.

*adductor mandibulae posterior* is reduced to a small patch of muscle fibers almost completely obscured by the posteroventral edge of the *M. adductor mandibulae anterior*.

#### HYOID GROUP

The following is a description of muscles derived from the hyoid arch with VIIth cranial nerve innervation.

*M. constrictor operculi dorsalis*, cd (figs. 34, 35, 38, 40, 41, 43)

Origin: The anterior fibers originate via connective tissue from the ventral side of the notochord with posterior fibers originating from the anterior edge of the scapular process just dorsal to the articulation of the pectoral fin.

Insertion: Onto the connective tissue of the opercular flap.

Remarks: In all species examined this muscle is the same.

*M. constrictor operculi ventralis*, cv (figs. 34, 36–38, 40, 41, 43, 45)

Origin: From connective tissue of the opercular cover. Some posterior fibers are continuous with the *M. constrictor operculi dorsalis*.

Insertion: A ventral band of fascia joins this muscle to its antimer.

Remarks: Some fibers fused to the underside of this muscle sheet extend ventrally and fuse to the *M. interhyoideus* at its tendon. This is what Kesteven (1933) described as the posterior deep constrictor and I believe it to be a portion of the *M. interhyoideus*.

In all species examined there is a ventrally directed layer of muscle fibers fused to the

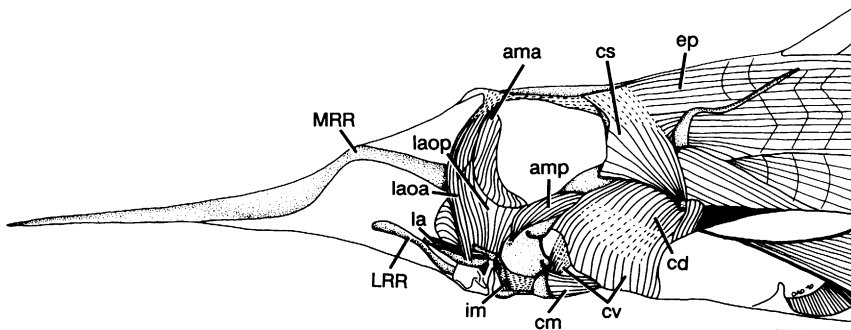


Fig. 41. Deep muscles of the head and pectoral region of *Harriotta raleighana* (AMNH 96931). Superficial musculature and connective tissue of the head and snout have been removed to reveal deep muscles underneath. See text for a detailed description of the musculature. Scale bar = 2 cm.

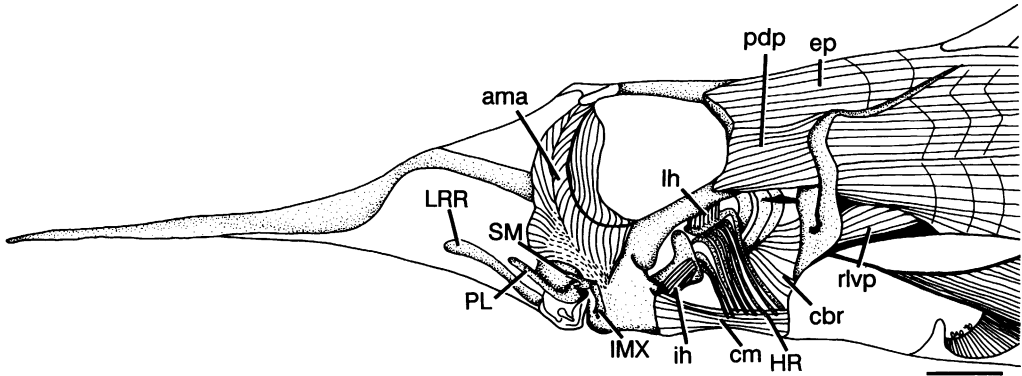


Fig. 42. Deep muscles of the head and pectoral region of *Harriotta raleighana* (AMNH 96931). Musculature of the labial cartilages and the opercular flap has been removed to expose deep muscles of the jaws and gill arches. See text for a detailed description of the musculature. Scale bar = 2 cm.

underside of this ventral constrictor muscle. In *Rhinochimaera pacifica*, *Harriotta raleighana*, and *Hydrolagus novaezealandiae* these deep fibers insert onto the posterior edge of the lower jaw where the *M. coracomandibularis* inserts. There is also a sheet of anteriorly directed muscle fibers that extends over the preorbital portion of the head and rostrum. This muscle sheet forms as anteriorly directed fibers from the *M. constrictor operculi ventralis* fuse with muscle fibers that

originate at the insertion of the *M. coracomandibularis*. This sheet of muscle inserts into the dense connective tissue just underneath the skin and ampullary canals that overlie the labial muscles and *M. adductor mandibulae anterior*. Kesteven (1933) distinguished this muscle in *Callorhynchus milii* as the *M. depressor rostri et veli* along with a deeper layer, the anterior deep constrictor. He later suggested that these layers may be part of a single muscle sheet (1933: 465). I

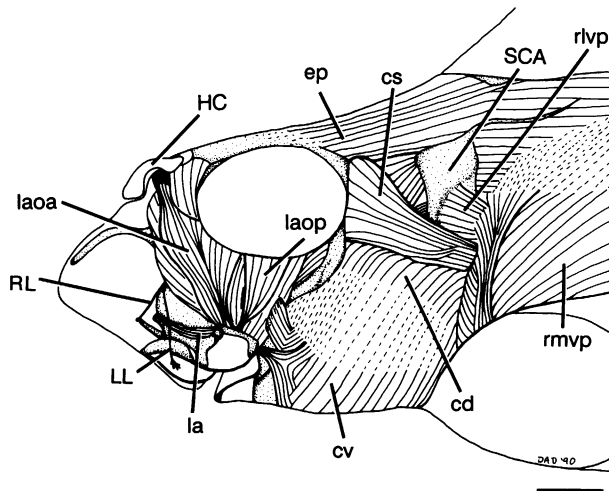


Fig. 43. Superficial muscles of the head and pectoral region of *Hydrolagus novaezealandiae*. The skin has been removed and connective tissue and ampullary organs of the snout have been cut away to reveal superficial muscles of the head. See text for a detailed description of the musculature. Scale bar = 2 cm.

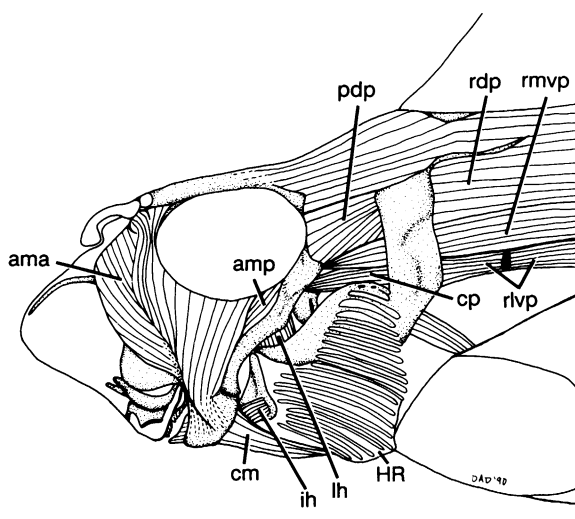


Fig. 44. Deep muscles of the head and pectoral region of *Hydrolagus novaezealandiae*. Superficial muscles of the head and opercular flap have been removed. See text for a detailed description of the musculature. Scale bar = 2 cm.

cannot separate this muscle sheet into distinct layers and therefore consider it to be a single muscle. Edgeworth (1935: 97–98) described this anterior extension of muscle fibers as derived from the hyoid constrictor sheet and its innervation by the VIIth cranial nerve confirms this hypothesis.

*M. constrictor operculi dorsalis anterior*, cda (figs. 34, 35)

Origin: From the lateral edge of the sub-orbital shelf.

Insertion: Via a tendon that extends ventrally and splits to insert anteriorly into the connective tissue sheet that covers the rostrum and posteriorly wraps around the jaw joint.

Remarks: I have only found this muscle in *Callorhynchus milii*. This muscle seems to be derived as part of the *M. constrictor operculi dorsalis*, yet it is distinctly separate except at its very dorsal end where some muscle fibers intermingle with the *M. constrictor operculi dorsalis*. Kesteven (1933: 457) called this muscle a part of the *M. depressor mandibuli superior* (D.m.s., Kesteven, 1933: 458, fig. 6) and described its insertion onto the lower jaw and floor of the mouth. He also stated that it is innervated by the VIIth cranial nerve. Nowhere does he describe the unique tendon

associated with this muscle and Edgeworth (1935) does not mention this muscle.

*M. levator hyoideus*, lh (figs. 35, 39, 42, 44)

Origin: From the underside of the neurocranium ventral to the orbit.

Insertion: Onto the dorsal edge of the epihyal.

Remarks: Edgeworth (1935) described this muscle as being derived from the hyoid constrictor muscle sheet.

*M. interhyoideus*, ih (figs. 35, 39, 42, 44)

Origin: From the posterior edge of the lower jaw at the symphysis, deep to the insertion of the *M. coracomandibularis*.

Insertion: Onto the lateral face of the ceratohyal at its ventral angle.

Remarks: This muscle is also derived from the hyoid constrictor muscle sheet (Edgeworth, 1935). Based on positional information only, this muscle may be functionally analogous to the mandibular depressor muscle of lungfishes and correlated with the evolution of autostyly in both of these lineages (Bemis, 1987a, b; Didier, 1988).

#### BRANCHIAL MUSCLES

The following is a description of all branchial and epibranchial muscles innervated by nerves IX and X.

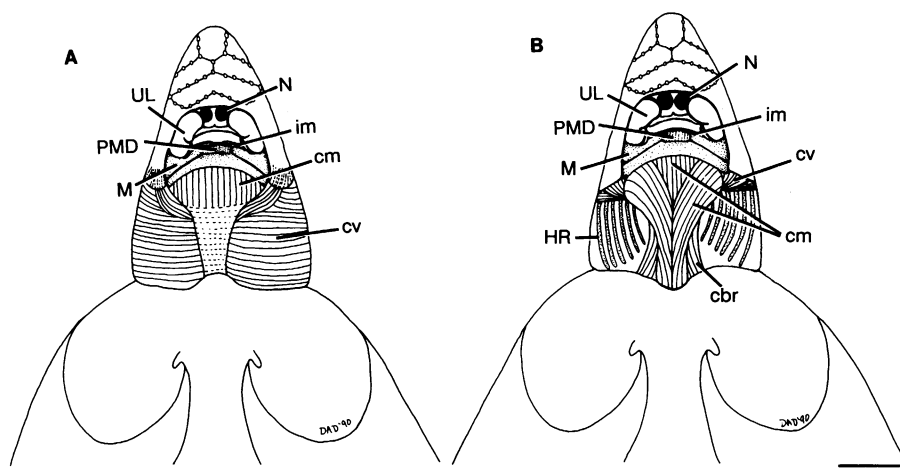


Fig. 45. Ventral muscles of *Hydrolagus novaezealandiae*. A, The skin has been removed to reveal the superficial musculature. B, Ventral constrictor muscles have been removed to expose deep hypobranchial muscles. See text for a detailed description of the musculature. Scale bar = 2 cm.

*Mm. constrictores branchiales*, cb (fig. 36)

Origin: From epibranchials 1–3.

Insertion: Onto ceratobranchials 1–3.

Remarks: I found only three branchial constrictors. Edgeworth (1935: 137) described a fourth branchial constrictor that lies between the fifth gill cleft and the *M. coracobranchialis*. In *Rhinochimaera pacifica* I found only the first branchial constrictor, but it is assumed that the pattern follows that of *Callorhynchus*. For *Chimaera* Edgeworth (1935: 137) described these muscles as extending from ceratobranchials to epibranchials of the following arches. This may explain why Vetter (1878) named these muscles *Mm. interbranchiales*.

*Mm. adductores arcuum branchialium*, aac (not shown)

Origin: From epibranchials 1–3 and the pharyngobranchial complex of branchial arches 4 and 5.

Insertion: Onto ceratobranchials 1–4.

Remarks: These small muscles lie on the medial side of the branchial arches and four are always present. Edgeworth (1935: 137, 166) claimed that the most caudal adductor is developed into a *M. constrictor oesophagi* that originates in chimaeroids from the third pharyngobranchial and inserts onto the penultimate basibranchial. I have found this

muscle and it originates from the pharyngobranchial complex and inserts onto the fourth basibranchial. I follow Edgeworth (1935) in calling this last branchial constrictor the *M. constrictor oesophagi*.

*M. cucullaris superficialis*, cs (figs. 34, 38, 40, 42, 43)

Origin: From the postorbital crest and posteriorly from a connective tissue sheet that overlies the epaxial muscles.

Insertion: Onto the lateral face of the scapular process.

Remarks: This muscle is present in all taxa examined. It angles ventrally from its origin to its insertion. There is often a raised ridge or protuberance at the site of insertion and it is especially prominent in *Harriotta*. In *Hydrolagus novaezealandiae* some muscle fibers run under the scapular process and insert onto its ventral side.

*M. protractor dorsalis pectoralis*, pdp (figs. 35, 38, 42, 44)

Origin: From the postorbital ridge and the otic capsule deep to the *M. cucullaris superficialis*.

Insertion: Onto the scapular process along the anterior edge and medial surface.

Remarks: This muscle was first described by Shann (1919); however, Edgeworth (1935)

made no reference to this muscle as part of the cucullaris complex in *Holocephali*.

*M. cucullaris profundus*, cp (figs. 36, 38, 44)

Origin: From the underside of the otic shelf.

Insertion: Onto the posterior end of the pharyngobranchial complex of branchial arches 4 and 5.

#### EPIBRANCHIAL SPINAL MUSCLES

The following is a description of epibranchial musculature with spinal nerve innervation.

*M. subspinalis* (not shown)

Origin: From the underside of the otic shelf medial to the *M. cucullaris profundus*.

Insertion: Onto pharyngobranchials 1 and 2.

Remarks: A single *M. interpharyngobranchialis* is found in all taxa examined. It runs from pharyngobranchial 2 to pharyngobranchial 3 (Edgeworth, 1935).

#### HYPOBRANCHIAL SPINAL MUSCLES

The following description includes ventral branchial muscles of myotomic origin with spinal innervation.

*M. coracomandibularis*, cm (figs. 35–37, 39, 40, 42, 44, 45)

Origin: From a central depression on the anterior face of the coracoid with some bundles of muscle fibers taking origin lateral and dorsal to this depression.

Insertion: Onto the posterior edge of the lower jaw lateral to the symphysis.

Remarks: This large muscle mass originates on the ventral surface of the coracoid. Just cranial to the origin the muscle is divided by a V-shaped septum of connective tissue at which point the mass divides into several muscle bundles. Two bundles insert on the lower jaw laterally, ventral to the jaw joint, and a central sheet of muscle inserts along the posterior rim of the lower jaw. This muscle pattern is found in all chimaeroids I have examined and is described by Shann (1919), but the V-shaped septum is not present in *Callorhynchus*. In *Callorhynchus* a central bundle of muscle heads anteriorly and ends in a long tendon that splits as it reaches the anterior edge of the lower jaw; the tendon

inserts onto the right and left sides of the lower jaw.

*M. coracohyoideus*, ch (fig. 39)

Origin: From the connective tissue septum of the *M. coracomandibularis* complex.

Insertion: Onto the ventral surface of the basihyal cartilage.

Remarks: This paired muscle runs deep to the central portion of the *M. coracomandibularis*. Further studies are needed to verify the presence or absence of the V-shaped septum in *Callorhynchus* and *Rhinochimaera* and will establish if this muscle does indeed take origin from the septum or the coracoid.

#### VENTRAL BRANCHIAL MUSCLES

The following muscle complex is developed from the branchial muscle plate and in all chondrichthyans has spinal nerve innervation that is considered to be secondarily derived (Edgeworth, 1935).

*Mm. coracobranchiales*, cbr (figs. 37, 42, 45)

Origin: As separate slips of muscle from the ventral edges of the ceratobranchial cartilages.

Insertion: Onto the anterior edge of the coracoid lateral to the origin of the *M. coracomandibularis*.

#### TRUNK MUSCLES

The following includes a description of the epaxial musculature as well as myotomic trunk muscles.

*M. epaxialis*, ep (figs. 34–36, 38–40, 42, 43)

Origin: From the top of head dorsal to the orbit.

Insertion: Continues posteriorly into the myomeres of the dorsal body musculature.

*M. retractor dorsalis pectoralis*, rdp (figs. 34, 36, 38, 40, 44)

Origin: From the dorsal end of the scapular process along its posterior edge.

Insertion: Continues into myomeres of the dorsal body musculature.

*M. retractor latero-ventralis pectoralis*, rlvp (figs. 34, 38, 40, 42, 44)

Origin: As two heads from the lateral and medial face of the scapular process ventral to the *M. protractor dorsalis pectoralis*.

Insertion: Continues deep to the *M. retractor mesio-ventralis pectoralis* as a large muscle bundle that forms the dorsal muscle mass of the body cavity.

Remarks: This muscle was described by Shann (1919) as having two portions, an external and internal division, corresponding to the two heads of origin I have described. It is found in all taxa studied.

*M. retractor mesio-ventralis pectoralis*, rmvp (figs. 34–36, 39, 40, 43, 44)

Origin: Originates as a sheet of muscle from the posterior edge of the pectoral girdle, ventral to the origin of the *M. retractor dorsalis pectoralis*, and extends around the coracoid ventrally.

Insertion: This muscle sheet fans out to form the lateral and ventral body wall.

Remarks: The description given by Shann (1919) indicates a superficial, medial, and inferior division of this muscle. The superficial portion originates just dorsal to the articulation of the pectoral fin and fans out over the trunk to insert into connective tissue of the transverse septum. In rhinochimaerids this muscle is indistinguishable. I find that the medial portion consists of some deep fibers that originate as a discrete bundle via a tendon from the posterior edge of the otic process. These fibers continue under the scapular process where they join fibers originating from the posterior edge of the scapular process before fanning out to form the lateral musculature of the body wall. The inferior portion originates from the posterior edge of the coracoid, just dorsal to the articulation of the pectoral fin, and extends posteriorly, forming the ventral body musculature.

#### LIGAMENTS

There are two large ligaments in the snout. These have only been observed and described for *Callorhinchus*, but comparable ligaments may be found in other chimaeroids when more detailed investigation of the snout is completed.

*ligamentum labialis*, ll (figs. 18A, 35)

Origin: From the top of the nasal capsule.

Insertion: Into the connective tissue of the

upper lip at the base of the snout just ventral to the prelabial cartilage.

Remarks: I have not found this ligament in any chimaerids or rhinochimaerids. Kesteven (1933: 459) called this the *ligamentum radialis rostri*.

*ligamentum rostralis*, rl (fig. 18A)

Origin: From the anterior tip of the prelabial cartilage.

Insertion: Onto the lateral rostral rod.

Remarks: I have found this ligament only in *Callorhinchus*. Kesteven (1933: 458) described the lateral ligament of the rostrum as originating from the nasal capsule and inserting on the rostral spine (median rostral rod); however, my observations indicate that this ligament originates from the anterior tip of the prelabial cartilage and inserts onto the lateral rostral rod. In *Hydrolagus* I have found a comparable ligament, but it originates from the dorsal surface of the nasal capsule and inserts on the small lateral rostral rods. I have not found a *ligamentum rostralis* in the snouts of rhinochimaerids and chimaerids.

#### CHARACTER ANALYSIS

The phylogenetic conclusions about the relationships of living chimaeroids are shown in figure 46. My purpose is to resolve relationships among extant chimaeroids, and the following discussion will assess shared derived characters (synapomorphies) only as they relate to living forms. It is understood that many taxa known only from fossils (e.g., *Ischyodus*) probably belong to Chimaeroidei, but the systematic position of fossil forms is beyond the scope of this study.

The following character scheme is organized around the families Callorhynchidae, Rhinochimaeridae, and Chimaeridae and their genera. Many of the characters listed are new or are redefined from previous accounts. The synapomorphies of Chondrichthyes, Holocephali, and Chimaeriformes are listed in tables 1 and 5 and will not be treated further in this analysis.

#### SYNAPOMORPHIES OF CHIMAEROIDEI

49. REDUCTION OF TRABECULAR DENTINE IN THE LATERAL WALLS OF THE FIN SPINE. Pat-

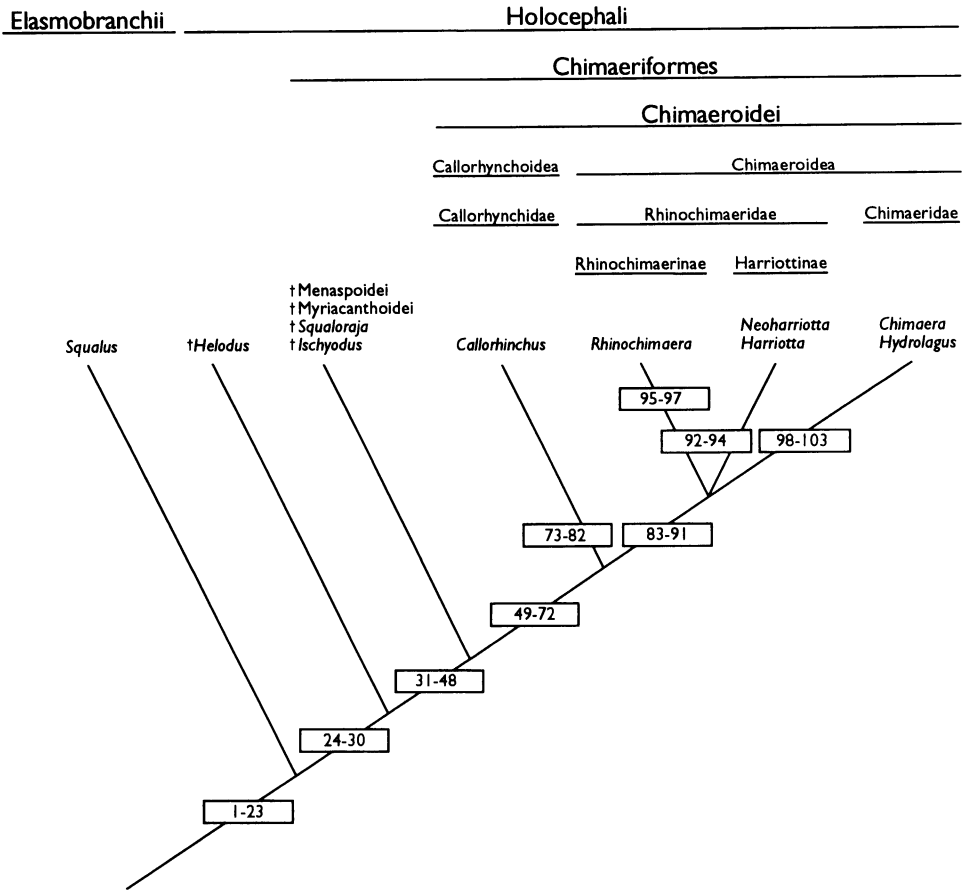


Fig. 46. Phylogenetic relationships of extant chimaeroids. In this first cladistic interpretation of relationships among the living forms, callorhynchids represent the most primitive living chimaeroids and the chimaerids, *Chimaera* and *Hydrolagus*, are derived forms. The rhinochimaerids are illustrated as a polychotomy with both lineages sharing characters 92–94. There are three apomorphies of *Rhinochimaera* (characters 95–97) and no synapomorphies uniting *Harriotta* and *Neoharriotta*. Although these problematic relationships could also have been represented as a Y-shaped branching, I have here used a polychotomy to emphasize the distinction between *Rhinochimaera* and the Harriottines (*Harriotta* plus *Neoharriotta*). Based on characters 92–94 alone, it is not clear that Rhinochimaeridae is necessarily a monophyletic group. See text for further discussion and description of characters.

terson (1965: 197) described a narrow zone of tissue, which he defined as osteodentine, in the fin spines of Recent chimaeroids and hypothesized that the thick layer of osteodentine found in extinct chimaeriforms was replaced by lamellar tissue in the modern forms. Because of this histological difference, Patterson (1965) interpreted the fin spine of Recent chimaeroids to be a recently evolved feature from a spineless form, not homologous to the fin spine of fossil forms such as *Helodus*. According to Maisey (1986), the lack

of trabecular dentine (“osteodentine”) is a synapomorphy of living chimaeroids (see table 5). A comparative investigation of the fin spines of Recent and fossil holocephalans indicates that they are homologous on the basis of morphological and developmental similarities and Recent forms are characterized not by the absence of trabecular dentine in the fin spine, but by a reduction in the amount of trabecular dentine present (Maisey, unpubl. Ph.D. diss., 1974; personal commun.).

50. SCAPULOCORACOIDS ARE FUSED



VENTRALLY (MAISEY, 1986: J20). This character also occurs in some Recent elasmobranchs and is considered by Compagno (1973) to be a derived character of neoselachians. Because this feature is not present in hexanchoids, *Chlamydoselachus*, and some fossil holocephalans, its occurrence in elasmobranchs and holocephalans is convergent (Maisey, 1984, 1986).

51. VENTRAL LOBE OF THE PITUITARY IS ISOLATED EXTERNAL TO THE CRANIUM (Maisey, 1986: J22). According to Maisey (1986) this is probably a convergent feature of elasmobranchs and chimaeroids. A similar modification of the pituitary is also found in coelacanth (Lagios, 1979). Most workers agree that it has been independently derived in all of these lineages; however, more study of this character is needed.

52. ALL OF THE TOOTH PLATES ARE COMPOSED OF TRABECULAR DENTINE AND HAVE HYPERMINERALIZED REGIONS (TRITORS) IN LARGE DISCONTINUOUS PATCHES. Aspects of this character have been discussed by many workers (e.g., Nielsen, 1932; Bargmann, 1933, 1941; Peyer, 1968; Ørvig, 1985); however, this character has historically been problematic because of the complex and confusing terminology related to the tooth plates and their tissues (e.g., Kemp [1984] for a review). Fossil holocephalans (e.g., *Helodus*, cochliodonts) have tooth plates in which the entire crown is covered with hypermineralized trabecular dentine; however, other fossil taxa (e.g., *Myriacanthus*) exhibit a reduction in the amount of hypermineralized tissue in the crown of only the upper anterior tooth plates that have characteristic patches of hypermineralized tissue. Therefore, I interpret tooth plates in which the hypermineralized tissue does not cover the entire crown as derived for Chimaeriformes and the presence of discrete patches of hypermineralized tissue in all tooth plates as derived for Chimaeroidei.

53. A DESCENDING LAMINA IS PRESENT ON THE ABORAL SURFACE OF THE TOOTH PLATES. The descending lamina of chimaeroid tooth plates has been described by Patterson (1992). A descending lamina is present, at the very least, in the mandibular and palatine tooth plates of many fossil forms, including *Ischyodus* and *Myriacanthus*, and is well developed in all tooth plates of *Callorhinchus*

*milii*. I agree with Patterson (1992) that a well-developed descending lamina is primitive for chimaeroids. This character certainly applies to more than just the living forms; however, a closer examination of this character in all tooth plates of the fossil forms is beyond the scope of this analysis and the distribution of this character among fossil taxa is not indicated on my cladogram.

54. A MORPHOLOGICALLY COMPLETE HYOID ARCH THAT INCLUDES A PHARYNGOHYAL ELEMENT IS PRESENT. Chimaeroids are the only living vertebrates with this character. Because the pharyngohyal is cartilaginous and small in size, it is difficult (or impossible) to assess in fossils. Outgroup comparison and embryological and paleontological evidence suggest that this is a derived feature related to the evolution of autostyly in this lineage.

55. JAW JOINT IS ANTERIOR TO THE EYE WITH JAW MUSCLES ORIGINATING ANTERIOR TO THE EYE. This character is not known in fossils and is correlated with the evolution of autostyly. The adductor muscles of *Heterodontus* also lie anterior to the eye and superficially they resemble chimaeroid fishes in this respect. I interpret this as a convergent feature of heterodontids and chimaeroids.

56. FUSED PHARYNGO-EPIBRANCHIAL PLATE ASSOCIATED WITH THE THIRD, FOURTH, AND FIFTH BRANCHIAL ARCHES. This element articulates with both the notochord and pectoral girdle via a strong ligament, and also articulates with the third epibranchial and fourth and fifth ceratobranchials. Although this feature has been noted by many workers (e.g., figured by Garman, 1904), its phylogenetic significance has never been considered. I have found this skeletal element in all genera of extant chimaeroids and consider it to be a synapomorphy of Chimaeroidei. I have found no reference to this character in any other vertebrate taxa.

57. THE FIRST EPIBRANCHIAL ARTICULATES WITH THE HYOID ARCH. An articulation between the first epibranchial and the hyoid arch is found in all extant chimaeroids. This character is probably related to the presence of a complete hyoid arch in holocephalans. It is likely that this is a synapomorphy of Holocephali, although this feature is not known for any fossil taxa due to poor preservation of the gill arches. It is considered a

synapomorphy of Chimaeroidei based on this study.

58. PRESENCE OF A FLESHY OPERCULUM THAT IS FORMED BY THE DORSAL AND VENTRAL CONSTRICTOR MUSCLES AND SUPPORTED BY AN OPERCULAR CARTILAGE AND HYOID RAYS. Among Recent Chondrichthyes, this character appears to be unique to chimaeroid fishes. The opercular cartilage, formed by the fusion of dorsal hyoid rays, articulates at the joint between the epihyal and ceratohyal elements of the hyoid arch and supports a series of filamentous hyoid rays ventrally. A series of hyoid rays is also present along the posterior edge of the ceratohyal. These hyoid rays lie directly underneath (and support) the fleshy opercular flap that is formed by the dorsal and ventral constrictor muscles. Holmgren (1942: 207) claimed that hyoid rays were present in galeoid sharks and rays; however, among living chondrichthyans, only chimaeroids possess a fleshy operculum supported by hyoid rays. It has been suggested that the presence of a fleshy operculum is a convergent feature among Chondrichthyes (Dean, 1909; Lund, 1977; Maisey, 1986), and the presence of long hyoid rays in some xenacanth and symmoriids indicates that a fleshy operculum may have been present in some fossil forms.

59. THE *M. LEVATOR HYOIDEUS* ORIGINATES FROM THE SUBORBITAL SHELF ANTERIOR TO THE OTIC CAPSULE. This muscle is not homologous to the *M. levator hyoideus* of elasmobranchs, which originates from the otic capsule (Holmgren, 1942: 210). According to Edgeworth (1935), the *M. levator hyoideus* in holocephalans is derived from the constrictor sheet and is homologous to the levator in dipnoans. This is probably a convergent feature in dipnoans and chimaeroids related to the independent evolution of autostyly and the presence of a nonsuspensory hyomandibula in both of these lineages. This character cannot be assessed in the fossil Holocephali; however, it may be a synapomorphy at that level since it is associated with autostyly.

60. THE PRESENCE OF A HYOID ARCH MUSCLE THAT EXTENDS ANTERIOR TO THE ORBIT. Portions of the dorsal constrictor sheet, innervated by the VIIth nerve (Allis, 1916, unpubl.; Edgeworth, 1935), extend into connective tissue of the snout in all chim-

aeroids. Its origin varies among chimaeroids and I interpret the development of a secondary origin from the lower jaw to be derived among Chimaeroidei. This character has not previously been described for chimaeroids and is a unique feature of this lineage. This muscle may play a functional role in movement of the large snout in these fishes.

61. SIX PAIRS OF LABIAL CARTILAGES ARE PRESENT. Elasmobranchs also possess labial cartilages, but never more than three pairs are present in modern forms. The complexity and degree of development of the labial cartilages is unique to chimaeroids among living chondrichthyans. The presence of well-developed, complex labial cartilages in *Hybodus basanus* (Maisey, 1983) is intriguing in that it suggests that complex labial cartilages may be a primitive feature shared by chimaeroids and elasmobranchs; however, further study will be required to test this hypothesis. For this analysis I accept the interpretation of Holmgren (1942: 246) that the presence of six labial cartilages is the primitive condition in chimaeroids.

62. PREPELVIC TENACULA WITH INDEPENDENT CARTILAGINOUS SKELETON PRESENT IN BOTH MALES AND FEMALES. The prepelvic tenacula articulate with the anterior edge of the pelvic girdle and are housed in small pouches anterior to the pelvic fins. This character is unique to chimaeroid fishes and has generally been considered to be a sexually dimorphic characteristic; however, there are rudimentary prepelvic tenacula and prepelvic pouches in all female callorhynchids.

63. PRESENCE OF A FRONTAL TENACULUM. A frontal tenaculum is unique to chimaeroid fishes and in all male chimaeroids this is a median, unpaired structure armed with denticles at the bulbous tip and housed in a small groove atop the head just anterior to the antorbital crest. This structure is present but remains undeveloped (beneath the skin) in females. The evolution and significance of the frontal tenaculum has been studied by several workers (e.g., Reis, 1895; Dean, 1906; Patterson, 1965; Raikow and Swierczewski, 1975). It has been hypothesized that the unpaired frontal tenaculum in chimaeroids evolved from paired structures (Reis, 1895; Patterson, 1965).

64. FUSED ANTERIOR RADIALS ARTICULATE

WITH THE PROPTERYGIUM OF THE PECTORAL FIN. This feature characterizes the pectoral fins of all extant chimaeroids and is probably related to the presence of a dibasal fin.

65. THE FIRST TWO OR THREE RADIALS OF THE PELVIC FIN ARE FUSED WITH THE BASIPTERYGIUM. The basipterygium of the pelvic fin in all extant chimaeroids has a characteristic process along the anterior margin formed by the fusion of the first few pelvic radials. Present in all extant chimaeroids, this feature is considered to be derived in this lineage.

66. THE OTIC CAPSULES HAVE A MEMBRANOUS MEDIAN WALL. The otic capsules of chimaeroids have only a membranous inner wall (Holmgren 1942: 195), whereas in elasmobranchs the inner wall of the otic capsules is cartilaginous. A membranous inner wall of the otic capsule is considered to be a derived feature of chimaeroids.

67. THE SPIRACLE IS ABSENT IN ADULTS DUE TO ONTOGENETIC LOSS. A spiracle is lacking in all chimaeroids, although a small spiracle is present in early developmental stages (the only taxa surveyed to date are *Callorhinchus* and *Hydrolagus*). The early ontogenetic closure of the spiracle is probably related to the development of the operculum. Loss of the spiracle is derived in Chimaeroidei, although it is a convergent feature found in other lineages (e.g., dipnoans, scaphyrhynchine sturgeons, and neopterygians).

68. TWO LATERAL LINE CANALS ARE PRESENT ABOVE THE MOUTH. Lateral line canals have been described and discussed by several workers, in particular Garman (1888) for *Chimaera monstrosa* and *Callorhinchus antarcticus*; Garman (1904) for *Rhinochimaera pacifica*; Reese (1910) for *Chimaera monstrosa*; Bigelow and Schroeder (1953) for North Atlantic species; as well as Bullis and Carpenter (1966) and Compagno et al. (1990) for rhinochimaerids. The lateral line canals are compared among all genera of chimaeroids for the first time in this study. The pattern of lateral line canals is unknown in fossil forms. This feature is present in all extant forms and is thus considered here as a synapomorphy of Chimaeroidei.

69. THE FIRST THREE BASIBRANCHIAL CARTILAGES ARE REDUCED TO LUMPS OF FIBRO-CARTILAGE. In all extant chimaeroids these

are unpaired ventral elements that do not articulate directly with the corresponding hypobranchial cartilages, but are instead interconnected to each other and to the hypobranchial elements by connective tissue. These three cartilages remain uncalcified even in the largest and most mature fish.

70. LARGE EGG CASES WITH A BROAD, RIBBED LATERAL WEB EXTENDING AROUND THE BULBOUS CENTRAL SPINDLE. This type of egg case is common to all callorhynchids and rhinochimaerids, and egg cases with a broad lateral web are identified here as a plesiomorphic character for all Recent chimaeroids. The reduction of the lateral web in egg cases of several species of chimaerids had been documented by Dean (1912) and I agree with his interpretation that a large lateral web is primitive. Although it is impossible to discriminate species based solely on egg cases, the discovery of fossil egg capsules resembling those of callorhynchids (Brown, 1946) is intriguing evidence for the potential usefulness of this character for higher level phylogenetic analysis when considered in conjunction with other fossil evidence, embryological studies, and when compared with egg cases of living forms.

71. AT LEAST THIRTEEN DISTINCT AMPULLARY PORE FIELDS ARE PRESENT ON THE HEAD AND SNOUT. The distribution of the pores of the ampullary organs with respect to the lateral line canals appears to be very unusual in chimaeroids in comparison to those gnathostomes in which the ampullary organs have been carefully studied (e.g., *Ambystoma*, Northcutt, 1990, Northcutt et al., 1994; elasmobranchs, Bodznick and Boord, 1986; *Polyodon*, Bemis and Northcutt, personal commun.). Specifically, it appears that the openings in a particular ampullary field are located only on one side of the adjacent lateral line canal rather than flanking it as in these other taxa.

72. ORBITS LIE DORSAL TO THE TELENCEPHALON AND ARE SEPARATED BY A MEMBRANOUS INTERORBITAL SEPTUM. Chimaeroids are unusual in that the orbit is located dorsal to the telencephalon, which extends anteriorly as the olfactory tracts run ventral to the eyes into the ethmoid region. Embryological studies indicate that the skull is shaped by development of the eyes, and early development

of large eyes in these fishes plays an important role in the development of a membranous interorbital septum that is present only in this lineage.

#### SYNAPOMORPHIES OF CALLORHYNCHOIDEA

73. **CALCIFIED RINGS ARE NOT PRESENT IN THE NOTOCHORDAL SHEATH.** All juveniles lack calcified rings in the notochordal sheath, but callorhynchids are the only chimaeroids that do not develop notochordal calcifications as adults. Notochordal calcifications are almost certainly a synapomorphy of Holocephali as this feature is present in all Recent chimaeroids (except *Callorhinchus*) as well as several fossil taxa (e.g., myriacanthoids and *Squaloraja*). The absence of notochordal calcifications in callorhynchids is interpreted as a synapomorphy of this lineage, although some extinct genera with calcified notochordal rings have been classified as callorhynchids (Stahl, personal commun.).

74. **ANGULAR AND ORAL CANALS BRANCH SEPARATELY FROM THE INFRAORBITAL CANAL.** In all other chimaeroids the angular and oral canals share a common branch (the horizontal canal) that is lacking in callorhynchids.

75. **PELVIC CLASPERS ARE IN THE FORM OF CARTILAGINOUS SCROLLS THAT LACK DENTICLES.** Scrolled claspers are also present in many Recent elasmobranchs (Compagno, 1973, 1977); however, this type of clasper morphology is probably independently derived in callorhynchids and elasmobranchs based on comparisons with fossil chondrichthyan taxa, which have claspers in the form of several jointed cartilages (e.g., Zangerl, 1981). The rodlike pelvic claspers of rhinochimaerids are morphologically very different from the scrolled rods of callorhynchids and the presence of denticles on rhinochimaerid claspers distinguishes them from those of callorhynchids. Pelvic claspers are known in a few fossil forms, but their morphology is not well known. I consider these smooth, scroll-like claspers to be primitive for chimaeroids, although it is possible that denticulated pelvic claspers are primitive for chimaeroids, and this feature is an apomorphy of callorhynchids.

76. **COMPLEX PREPELVIC TENACULA.** The prepelvic tenacula of callorhynchids consist

of a large spatulate blade of cartilage armed with flat scalloped denticles and a scrolled cartilaginous tube. Two fleshy, frilled lobes and a gland are also associated with the prepelvic tenacula, and the entire complex is housed within prepelvic pouches. Correlated with the presence of complex prepelvic tenacula are large anterior processes of the pelvic girdle with open vacuities. Among living fishes only chimaeroids have prepelvic tenacula. Based on the scanty fossil evidence, it appears that retractable prepelvic tenacula and prepelvic pouches are recent specializations of chimaeroids. Patterson (1965) considered the articulated, skeletally supported prepelvic tenacula of Recent chimaeroids to be derived from groups of enlarged scales with no skeletal support. I consider the presence of complex prepelvic tenacula in male callorhynchids and the presence of rudimentary prepelvic cartilages in females to be primitive. It is equally likely that this feature is an apomorphy of callorhynchids and simple prepelvic tenacula are primitive, but this cannot be resolved until further paleontological and embryological studies are completed.

77. **THE ROSTRUM IS FORMED INTO A PLOW-SHAPE.** The three rostral rods are almost equal in length and support a fleshy flap of tissue at their distal ends.

78. **THE SUPERFICIALIS MUSCLE.** This thin sheet of muscle lies just underneath the skin of the head and is located anterior to the orbit. It is found only in *Callorhinchus*.

79. **PRESENCE OF THE *M. CONSTRICTOR OPERCULI DORSALIS ANTERIOR*.** This muscle is derived from the anterior edge of the dorsal constrictor and inserts via tendons into connective tissue of the rostrum and onto the lower jaw. It is present only in *Callorhinchus*.

80. **PRESENCE OF THE *LIGAMENTUM LABIALIS* AND *LIGAMENTUM ROSTRALIS*.** These ligaments are found only in *Callorhinchus*. The polarity of this character is difficult to state with certainty. I interpret the presence of these ligaments in *Callorhinchus* as a derived feature related to the presence of a plow-shaped snout; however, these may be present in reduced form in other chimaeroids.

81. **HETEROCERCAL TAIL.** A heterocercal tail is a primitive gnathostome feature and among chimaeroids is present only in *Callorhinchus*. The condition of the tail is not known

for fossil holocephalans. Preliminary developmental studies indicate that a heterocercal tail may be secondarily derived in this lineage because initially a straight (nonheterocercal) tail is formed and only after hatching does the tail develop a heterocercal shape; however, this hypothesis is still inconclusive and I will consider a heterocercal tail to be primitive for chimaeroids until further analysis can be completed.

82. ANAL FIN WITH INTERNAL CARTILAGINOUS SUPPORT. Among chimaeroids only *Callorhynchus* and *Neoharriotta* have an anal fin. I consider this anal fin to be correlated with the development of a heterocercal tail and primitive for chimaeroids. I interpret the presence of an anal fin in *Neoharriotta* to be a convergent feature.

#### SYNAPOMORPHIES OF CHIMAEROIDEA

83. A LONG, WHIPLIKE TAIL WITH SUPRA-CAUDAL AND SUBCAUDAL LOBES THAT ARE ALMOST EQUAL IN SIZE AND SHAPE. The tail ends in a long filament that may almost equal body length in some species (e.g., *Hydrolagus mirabilis*). The supracaudal and subcaudal lobes are usually equal in size with a fin web composed only of ceratotrichia, sometimes supported by a few tiny radial cartilages.

84. THE ABSENCE OF AN ANAL FIN WITH AN INDEPENDENT CARTILAGINOUS SUPPORT AT ITS BASE. An anal fin with an internal cartilaginous support is a primitive gnathostome feature present in elasmobranchs as well as *Callorhynchus* and *Neoharriotta*. For reasons of parsimony, I have assessed this character to be a loss at this node with the secondary derivation of an anal fin in *Neoharriotta* rather than a loss in all taxa except *Neoharriotta*. *Chimaera* and *Hydrolagus* are often said to be distinguished by the presence of an anal fin in *Chimaera* and its absence in *Hydrolagus*. This "anal fin" has no independent cartilaginous support, and thus by definition is not homologous to the anal fins of other gnathostomes, elasmobranchs, and chimaeroids. The "anal fin" of *Chimaera* is formed by ceratotrichia, which are separated from the subcaudal lobe by a notch, and this feature in chimaerids is of questionable phylogenetic significance.

85. LOSS OF THE PREPELVIC TENACULA AND PREPELVIC POUCHES IN FEMALES. Only males have prepelvic tenacula, which are housed in prepelvic pouches. Females do not have prepelvic pouches nor are any rudimentary prepelvic claspers present. I consider the loss of this feature in females to be derived for chimaeroids.

86. PREPELVIC TENACULA IN MALES ARE SIMPLY DENTICULATE BLADES OF CARTILAGE. The denticles occur in a single row or sometimes appear as a small patch. Unlike the prepelvic tenacula of callorhynchids, these prepelvic tenacula are reduced in size and complexity and are not associated with any glands in the prepelvic pouches. The possibility that this condition may be primitive, and complex prepelvic tenacula apomorphic in callorhynchids, has been considered (see character 76).

87. PEDICULAR LABIAL CARTILAGES ARE ABSENT. Only five pairs of labial cartilages are present. This loss of the pedicular cartilage may actually represent the fusion of the pedicular cartilage to the prelabial cartilage, which is a relatively elongate element in rhinochimaerids and chimaerids. I interpret the reduction of labial cartilages as derived among chimaeroids (see character 61).

88. THE ANTERIOR PORTION OF THE HYOID CONSTRICTOR MUSCLE ORIGINATES FROM THE RETROARTICULAR PROCESS. In callorhynchids this muscle is an extension of fibers from the constrictor muscles of the opercular flap. The derived condition for this muscle is separation from the constrictor sheet and origin from the retroarticular process of the lower jaw. This origin is at the lateral edge of the *M. coracomandibularis* insertion.

89. TOOTH PLATES THAT HAVE HYPERMINERALIZED TISSUE IN THE FORM OF DISCRETE RODS. The hypermineralized tissues in the tooth plates occur in the form of isolated rods as well as hypermineralized pads. The histological distinction between hypermineralized rods and the plesiomorphic hypermineralized pads has most recently been discussed by Ørvig (1985) and is not considered in this analysis. The hypermineralized rods and pads can be distinguished morphologically and the external morphology of rods of hypermineralized tissue is regarded as a derived feature. Outgroup comparison with fossils indicates that the reduction of hyper-

mineralized tissue on the surface of the tooth plates is a general trend among Holocephali.

90. **THE PELVIC GIRDLE ARTICULATES AT THE SYMPHYSIS.** The two halves of the pelvic girdle are separate but closely articulated with each other in the ventral midline. This contrasts with the condition in *Callorhinchus* where the two halves of the pectoral girdle are united by a sheet of dense connective tissue. The polarity of this character cannot be determined with certainty. I have interpreted the articulated pelvic girdle as derived. It is equally likely, however, that the condition in *Callorhinchus* is an apomorphy of callorhynchids.

91. **LOSS OF THE DESCENDING LAMINA IN THE VOMERINE TOOTH PLATES AND REDUCED DESCENDING LAMINA IN THE PALATINE AND MANDIBULAR TOOTH PLATES.** The presence of a well-developed descending lamina in all tooth plates is considered primitive for chimaeroids on the basis of comparison with fossil taxa. I interpret the reduction and loss of this feature to be derived in Chimaeroidea. The descending lamina is clearly related to the mode of growth of the tooth plates (Patterson, 1992; Didier et al., 1994) and its reduction and loss in Chimaeroidea is related to a pattern of growth in which the tooth plates are arranged in a more sectorial dentition.

#### SYNAPOMORPHIES OF RHINOCHIMAERIDAE

92. **PRESENCE OF AN ELONGATE FLESHY SNOUT THAT TAPERS DISTALLY.** The elongate rostrum in rhinochimaerids is supported by a single long medial rostral rod that extends to the tip of the snout. The large rostrum found in some Jurassic forms is thought to be functionally related to the large frontal clasper found in these forms (Patterson, 1965). The presence of an elongate rostrum is primitive for chimaeroids and on the basis of this feature alone it is possible to consider rhinochimaerids to be primitive chimaeroids and the synapomorphies of callorhynchids would then be apomorphies.

93. **THE EGG CASES HAVE A CONSTRICTED CENTRAL SPINDLE.** This type of egg case morphology is found only among the rhinochimaerids. Although not illustrated, represen-

tative egg cases are figured in Bigelow and Schroeder (1953). The central spindle portion of rhinochimaerid egg cases has a prominent constriction. This feature is difficult to assess, but comparative study shows a general trend toward reduction of the central spindle and lateral web (see character 70). Another possibility is that this is an apomorphy of this lineage. If one accepts this interpretation, then egg cases are apomorphic in all chimaeroid lineages.

94. **PELVIC CLASPERS THAT ARE SIMPLE RODS WITH A FLESHY DENTICULATE TIP.** The distal tip of the smooth clasper rod is an expanded fleshy bulb and placoid denticles are found only on this portion of the clasper. Only rhinochimaerids possess claspers of this morphology. For polarity of clasper characters, see character 75 and the discussion below.

#### APOMORPHIES OF RHINOCHIMAERA

95. **LOSS OF ALL HYPERMINERALIZED TISSUE IN THE TOOTH PLATES.** *Rhinochimaera* is the only holocephalan known to lack hypermineralized tissue in the tooth plates and there is no evidence to suggest that hypermineralized tissue is ever present. This is the only species of chimaeroid that lacks hypermineralized tissue; therefore, I consider it an apomorphy of this genus.

96. **TUBERCLES DEVELOP ON THE SUPRA-CAUDAL LOBE OF THE TAIL IN MALES.** At sexual maturity numerous paired denticulations develop along the dorsal edge of the supracaudal lobe of the tail in adult males of *Rhinochimaera*. This feature is not present in any other chimaeroid nor is there evidence of this feature in any fossil form. These denticles are not homologous to placoid scales and their histological structure has yet to be examined in detail.

97. **THE *M. RETRACTOR MESIOVENTRALIS PECTORALIS* IS NOT A SEPARATE MUSCLE.** This soft tissue character cannot be assessed in any fossils, but its singular presence in *Rhinochimaera* is interpreted as an apomorphy of this genus.

#### SYNAPOMORPHIES OF CHIMAERIDAE

98. **CRANIAL LATERAL LINE CANALS ON THE ROSTRUM ARE ENLARGED AND HAVE EXPANDED**

**DILATIONS.** The lateral line canals continuing onto the rostrum (the supraorbital canal, infraorbital canal, nasal canal, and subrostral canal) become widened and have enlarged dilations that occur at regular intervals along the canals. This feature is found only in species of *Chimaera* and *Hydrolagus* and is derived in this family.

**99. THE BLUNT ROSTRUM IS SUPPORTED BY REDUCED ROSTRAL CARTILAGES.** The lateral rostral rods are reduced to tiny prongs lying just medial to the nasal capsules. The medial rostral rod is a short, narrow cartilaginous rod that supports only the dorsal edge of the fleshy rostrum. I consider the reduced rostral cartilages and correlated reduction in size of the snout to be a derived feature of chimaeroids.

**100. THE EGG CASES ARE SPINDLE-SHAPED WITH A PROMINENT DORSAL KEEL AND LACKING A LATERAL WEB.** The egg cases of *Chimaera* and *Hydrolagus* are simpler and smaller than those found in callorhynchids and rhinochimaerids. This is considered to be a derived feature (see characters 70 and 93).

**101. THE PELVIC CLASPERS ARE BIFID OR TRIFID WITH A SHAGREEN OF DENTICLES.** The posterior clasper cartilage is divided in chimaerids. The distal arms of the clasper are fleshy with numerous placoid denticles. In forms that have trifid claspers the third arm is smooth with fleshy denticulate tissue only at the distal end. Pelvic claspers of this complexity are unknown among chondrichthyans and I consider them to be derived.

**102. A FLESHY POSTANAL PAD IS PRESENT IN MALES AND FEMALES. AMONG CHIMAEROIDS A POSTANAL PAD IS FOUND ONLY IN CHIMAERIDS.** I interpret this character to be a derived feature of chimaerids. Its function is unknown.

**103. VOMERINE TOOTH PLATES WITH SEVERAL ROWS OF PARALLEL RIDGES EXPOSED ON THE POSTERIOR FACE OF THE OCCLUSAL SURFACE.** Although other chimaeroids possess incisorlike vomerine tooth plates, the presence of transverse ridges on the posterior oral surface is a feature found only in the vomerine tooth plates of chimaerids. Developmental studies will be required to determine if perhaps these ridges are related to growth of the tooth plates in a manner analogous to development of growth rings.

## DISCUSSION

Figure 46 is a cladogram illustrating the results of this phylogenetic analysis of living chimaeroids. There are several aspects of this analysis that warrant further discussion. Polarity of characters in my analysis is difficult to assess, which results from focusing solely on living forms (i.e., soft tissue features cannot be studied in fossil forms). Other characters that may be known in some fossils are equally difficult to polarize because of the scanty nature of the fossil record for chimaeroid fishes. For example, the pattern of lateral line canals is not known from fossils, although the calcified rings associated with lateral line canals have been identified. Still, it is impossible to determine whether these calcified rings supported an open or closed lateral line canal. On the basis of comparison with extant elasmobranchs, which all have closed lateral line canals, I have interpreted the closed canals of *Callorhinchus* as primitive and open lateral line canals as derived in Chimaeroidea.

Tooth plate characters are of particular significance because the pattern of hypermineralized tissues on the surface of the tooth plates is used to identify and distinguish fossil taxa (e.g., Ward, 1973; Ward and McNamara, 1977; Duffin, 1984). Developmental, micro-anatomical, and histological studies of tooth plates indicate that the structure of the hypermineralized tissue may be more complex than external morphology alone would indicate. Until more is understood about the development of the tooth plates and the relationship between the hypermineralized pad and rods, these features are considered in this study as separate characters based on external morphology alone.

Callorhynchids are interpreted as primitive chimaeroids and Callorhynchoidea is erected as the sister group to derived chimaeroids of the superfamily Chimaeroidea on the basis of 10 synapomorphies (characters 73–82). It is not clear that all of these characters are synapomorphies of this lineage; instead, some characters, such as the presence of a heterocercal tail and anal fin, may be symplesiomorphies, whereas others may be apomorphies of *Callorhinchus*. For example, the presence of complex prepelvic

tenacula is here interpreted as a synapomorphy of Callorhynchoidea and simple prepelvic tenacula are derived in Chimaeroidea. This feature is impossible to assess among living outgroups because chimaeroids are the only fishes to have prepelvic tenacula. The prepelvic region of fossils is poorly known, but evidence suggests simple prepelvic tenacula may have been present in some fossil taxa. On the basis of this observation, simple prepelvic tenacula may instead be interpreted as a primitive chimaeroid feature and complex prepelvic tenacula would then be apomorphic in callorhynchoids.

Pelvic claspers are difficult to assess for the same reason. The presence of three morphologically distinct pelvic claspers clearly corresponds to the three families of chimaeroids; however, because this feature is poorly known in any fossil chimaeroids, this character is difficult to polarize and one could interpret each discrete morphological type as an apomorphy for each family. Based on comparisons with living elasmobranchs, which possess pelvic claspers that are morphologically similar to those of *Callorhynchus*, I interpret simple pelvic claspers as primitive and more complex claspers, such as those of chimaerids, to be derived.

Egg capsule morphology is another difficult character to assess. As with pelvic claspers, the egg cases exhibit three distinct morphologies that clearly correspond to the familial grouping of chimaeroids. One interpretation and polarization of this character is discussed above (character 70).

The most problematic aspect of this analysis is the grouping of all rhinochimaerids on the basis of morphology of the snout, egg cases, and pelvic claspers (characters 92–94). Although these features are shared by all members of this family and are stated as synapomorphies in this work, the problematic nature of these characters has been discussed above. *Neoharriotta* and *Harriotta* undoubtedly belong to Chimaeroidea, but *Rhinochimaera* is a difficult genus to characterize because it exhibits some features of Chimaeroidea, such as open lateral line canals, but also exhibits some features unique to chimaeroids (95–97). The most important of these three apomorphies is the absence of hypermineralized tissue in the tooth plates of

*Rhinochimaera*. Another problematic aspect of this lineage is the separation of *Harriotta* and *Neoharriotta* into a separate subfamily. This distinction among rhinochimaerids was first suggested by Gill (1898). Dean (1904b) later proposed the family Harriottidae to distinguish *Harriotta* from *Rhinochimaera*. I was unable to find any synapomorphies to unite *Harriotta* and *Neoharriotta* that were not shared by *Rhinochimaera*; however, the morphological differences among rhinochimaerids are significant enough to warrant such a separation.

Two alternative interpretations of rhinochimaerid relationships are possible. *Rhinochimaera* could be interpreted as a primitive form (suggested by Holmgren, 1942), either a sister lineage to Callorhynchoidea or within Chimaeroidea, as the sister group to *Harriotta* plus *Neoharriotta*. As a primitive chimaeroid, either sister group to Callorhynchoidea or Chimaeroidea, *Rhinochimaera* would have independently derived all of the features of Chimaeroidea (characters 83–91) as well as the three rhinochimaerid synapomorphies (characters 92–94), and would have lost hypermineralized tissue and descending lamina in the tooth plates. A more likely alternative, which is illustrated here, is to keep *Rhinochimaera* within Rhinochimaeridae on the basis of characters 92–94. Of the two alternatives, this is the most parsimonious because it requires only the independent derivation (or convergence) of rhinochimaerid features (92–94) and independent derivation of characters 95–97. Although *Neoharriotta* and *Harriotta* are not united by any synapomorphies, I have illustrated them as a sister lineage to *Rhinochimaera* within Rhinochimaeridae. This reflects the fact that although these forms are convergent, they exhibit morphological distinctions worthy of taxonomic recognition, which is reflected in this phylogenetic interpretation as well as the classification of chimaeroid fishes. Despite my assessment of characters 92–94 as synapomorphies, I have illustrated rhinochimaerid relationships as a polychotomy because these three characters could be convergent. Unfortunately, polarity is impossible to determine from this study. This clade could also be illustrated as a Y-shaped branch, with no synapomorphies uniting



*Harriotta* plus *Neoharriotta*; however, I think a polychotomy more accurately conveys the problematic nature of rhinochimaerid monophyly.

The similarity of the neurocranial structure in *Harriotta*, *Neoharriotta*, *Chimaera*, and *Hydrolagus* is worthy of note. All have short ethmoid and otic regions and large orbits. This similarity is clearly convergent because chimaerids are united by six synapomorphies (characters 98–103) not present in *Harriotta* and *Neoharriotta*. However, this interesting convergence follows a general trend observed among derived chimaeroids, Chimaeroidea, which are characterized by a general reduction in features. For example, such features include reduction in the snout length, reduction of the tail to a tapering whip, and reduction in length of the neurocranium. The phylogenetic significance of these observations is undetermined and may be insignificant; however, further developmental studies may provide insight into the interpretation of these general morphological trends in chimaeroids.

### TAXONOMIC SUMMARY

Below is a brief diagnosis of the three families and two subfamilies of extant chimaeroids. Each description lists a mix of primitive and derived characters and is intended to describe the general morphotype for each lineage of chimaeroid fishes.

#### CALLORHYNCHIDAE

The members of this monogeneric family are the most plesiomorphic chimaeroids. The four living species of *Callorhynchus* are restricted to the Southern Hemisphere. Externally, callorhynchids are characterized by an elongate snout with a fleshy plow-shaped flap, closed lateral line canals, small eyes, a heterocercal tail, and an anal fin. The tooth plates are large and robust with hypermineralized tissue in the form of a tritor pad. Males have simple scroll-like pelvic claspers lacking denticles; a broad, flat frontal tenaculum with tiny denticles at the tip; and complex prepelvic tenacula housed in prepelvic pouches. Prepelvic pouches are present in females, as are rudimentary prepelvic tenacula. Females

lay large ovoid egg cases with a wide, ribbed lateral web.

#### RHINOCHIMAERIDAE

The three genera *Rhinochimaera*, *Harriotta*, and *Neoharriotta* and seven species of the family Rhinochimaeridae have a worldwide distribution in deep oceanic waters. All rhinochimaerids possess an elongate tapering snout, lateral line canals in the form of open grooves, and a leptocercal tail. The tooth plates are smooth, without hypermineralized tritors, or have hypermineralized tissue in the form of tritor pads and rods. Males have simple rodlike pelvic claspers with a fleshy denticulate bulb at the distal end, and prepelvic tenacula that are simple spatulate blades of cartilage with one to three rows of denticles on the medial edge. Females lay ovoid egg cases with a ribbed lateral web and constricted central spindle. I have divided this family into two subfamilies on the basis of certain morphological distinctions.

The subfamily Rhinochimaerinae (new subfamily) includes the genus *Rhinochimaera*. Members of this subfamily have smooth, thin tooth plates that lack hypermineralized tissue. The ethmoid region of the neurocranium is elongate and orbits are small. The elongate snout is fleshy and lacks tubercles at its tip. In adult males the supracaudal fin possesses horny denticles and the frontal tenaculum is robust and nearly flat dorsally.

The subfamily Harriottinae Gill, 1898, includes two genera: *Harriotta* and *Neoharriotta*. Members of this subfamily have thick tooth plates with hypermineralized tissue in the form of tritor pads and rods, and the anterior edges of the tooth plates occlude to form sharp nipping blades. The ethmoid region of the neurocranium is short and the orbits are large. The frontal tenaculum is slender with a distinct dorsal curve. Mature males of the genus *Harriotta* have knobs on the tip of the snout. An anal fin is present in *Neoharriotta*.

#### CHIMAERIDAE

The family Chimaeridae has a worldwide oceanic distribution with the greatest diversity of species known from the Pacific off the

coasts of Japan and New Zealand. There are two genera, *Chimaera* and *Hydrolagus*. This is by far the most speciose family of chimaeroid fishes with 6 species of *Chimaera* and 17 species of *Hydrolagus*. All members of this family have a blunt, fleshy snout, lateral line canals are open grooves and in the snout region these grooves become widened with large open dilations along their length. The tail is leptocercal and a cartilage-supported anal fin is lacking. The tooth plates are bladelike and occlude along their anterior edges to form a sharp nipping beak. The hypermineralized tissue is in the form of tritor rods and a small tritor pad. The hypermineralized pad may be large (e.g., *Chimaera monstrosa*) or not visible on the surface of the tooth plate (e.g., *Hydrolagus collieri*). Females lay elongate, spindle-shaped egg cases that lack a lateral web.

Based on my comparative study of all six genera of extant chimaeroids I propose the following new classification:

- Class Holocephali Müller, 1834
  - Order Chimaeriformes Patterson, 1965
    - Suborder Chimaeroidei Patterson, 1965
      - Superfamily Callorhynchoidea
        - Family Callorhynchidae Garman, 1901
          - Callorhynchus* Lacépède, 1798
  - Superfamily Chimaeroidea
    - Family Rhinochimaeridae Garman, 1901

#### Subfamily Rhinochimaerinae

*Rhinochimaera* Garman, 1901

#### Subfamily Harriottinae Gill, 1898

*Harriotta* Goode and Bean, 1895

*Neoharriotta* Bigelow and Schroeder, 1950

#### Family Chimaeridae Bonaparte, 1831

*Chimaera* Linnaeus, 1758

*Hydrolagus* Gill, 1862

Two new superfamilies, Chimaeroidea and Callorhynchoidea, have been erected. Callorhynchoidea includes a single genus, *Callorhynchus*, and members of this lineage are primitive chimaeroids. Chimaeroidea includes *Rhinochimaera*, *Harriotta*, *Neoharriotta*, *Chimaera*, and *Hydrolagus* and is supported by 9 synapomorphies (characters 83–91). Within Chimaeroidea the family Rhinochimaeridae has been divided into two subfamilies, Rhinochimaerinae and Harriottinae, based on morphological differences as well as apomorphic features of *Rhinochimaera* that are not present in *Harriotta* and *Neoharriotta*.

The phylogenetic conclusions of this study are by no means complete nor has my character analysis been exhaustive; however, the value of this phylogenetic hypothesis is as a framework for future studies.

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