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SYSTEMATICS OF MORONE (PISCES: MORONIDAE), WITH NOTES ON THE LOWER PERCOIDS

by

JOHN R. WALDMAN

A dissertation submitted to the Graduate Faculty
in Biology in partial fulfillment of the requirements
for the degree of Doctor of Philosophy,
The City University of New York.

1986

This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract

Systematics of Morone (Pisces: Moronidae), With Notes on the Lower Percoids

by

John R. Waldman

Adviser: Dr. C. Lavett Smith

Monogeneric classification for Morone is supported by dental characters in its four American members - americana, chrysops, mississippiensis, and saxatilis; and the two Afro-European forms - labrax and punctata, often referred to a separate genus, Dicentrarchus. Morone is unique in the possession of elongated lingual tooth plates lateral to but separate from the basihyal. These lateral tooth plates, and tooth patches anterior to the basihyal possess a previously unrecognized diagnostic value, incorporated in a dental key to the species of Morone. The presence of a single basihyal tooth patch, a primary distinguishing character for chrysops, was found to be unreliable inasmuch as many individuals showed paired patches as in saxatilis. Additionally, the fewer number of rows of vomerine teeth in the yellow bass provides a new discriminatory osteological character between it and the white perch. The proposed phylogeny, as well as renal evidence, supports marine ancestry for

Morone. Distribution of these species in relation to their phylogeny suggests the Mediterranean Sea and the Gulf of Mexico as secondary dispersal zones. Fisheries records demonstrate that the striped bass was found along much of the Texas coast into the 1930's, a westward extension of their known Gulf coast range by approximately 500 miles. Inasmuch as no evidence was found that *Morone* belongs among the Percichthyidae or any other established family, familial status as the monogeneric Moronidae is proposed. The presence of extended epioccipital processes, and features of the preopercle and scales suggest a trichotomy between *Morone*, *Lateolabrax*, and the Percidae. Characters of the dermal upper jaw, preopercle, and post-cranial region indicate that *Siniperca* is a centropomid, most probably the sister taxon to the Latinae. The fossil percoid genus *Mioplosus* is not a percid but instead, appears closely allied to the Percichthyidae. A correlation was noted among, and hypothesis of function proposed for the taxonomic distributions of an extended caudal lateral line and accessory caudal sensory canals, procurrent spur, and secondarily cycloid scales.

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My deepest gratitude to Carol, whose continuous support made this study possible.

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INTRODUCTION

Johnson (1984) cited Regan's (1913) definition of the Percoidei as those Perciformes characterized "...by the absence of the special peculiarities which characterize the other suborders of the Percomorphi = (Perciformes)." Johnson added that "seventy years of research in systematic ichthyology have failed to yield a more meaningful definition."

Progress in the classification of the lower percoids, by definition the most primitive, has in particular been minimal. The concept of lower and higher percoids is itself gradistic, and it remains unclear where the division lies or even whether a distinction should be made. Gosline (1966) in his discussion of the lower percoids included the Centropomidae, Percidae, Kuhliidae, Centrarchidae, Scorpididae, Apogonidae, Serranidae, and Percichthyidae.

Long considered a serranid, the genus Morone was placed by Gosline (1966) in his expanded Percichthyidae, but was recently removed from that group by Johnson (1984) who left its systematic placement unresolved. This study addresses the following problems regarding the systematics of Morone - resolution of the question of its monophyly, definition of relationships within the taxon, familial status, and biogeographical analysis. A second section considers relationships within the lower percoids including the sister group relations of Morone.

-MATERIALS AND METHODS-

SYSTEMATIC PROCEDURES

Relationships were evaluated using cladistic methodology, described by Nelson and Platnick (1981). Cladistics unites taxa into monophyletic groups on the basis of shared derived characters (synapomorphies). Characters are considered to be derived at the hierarchical level at which they first appear. Descendants may lose the character or reduce it, develop unique expressions of it within a portion of the original monophyletic group (new synapomorphy at a higher level), or retain it unmodified (symplesiomorphy). The determination of synapomorphy schemes results in the elucidation of patterns of relationship - nested hierarchies of monophyletic groups called cladograms. Taxa hypothesized to have shared an immediate common ancestor are termed sister groups.

There are two methods of estimating the plesiomorphic or apomorphic nature of a character. One technique is outgroup comparison. An assessment of the phylogenetic level of derivation of a character may be made by surveying its distribution in surrounding taxa, general occurrence indicating the feature is primitive at that level.

An alternative method is the use of ontogenetic information. When comparing ontogenetic transformations among taxa, the more general state may be considered plesiomorphic and the less general, derived. Both methods rest on the principle of parsimony, the preference when, given a set of competing hypotheses of varying complexity but otherwise equal likelihood, for the simplest hypothesis.

In his review of lutjanids and associated families, Johnson (1980) noted the difficulty in strict application of cladistic concepts to percoid fishes - a state of affairs also encountered in this study. As Johnson pointed out, inasmuch as relationships among the approximately fifty most generalized families are so poorly understood, it is impossible to designate a single or a limited number of outgroups. Determination of primitive and advanced character states must instead be based on a combination of knowledge of character states in the Beryciformes as well as a large number of percoids. Furthermore, synapomorphies are often in effect, conditional, that is, they can only be accepted in relation to taxa studied.

A related problem endemic to percoid systematics, particularly at the basal percoid level is the apparent dearth of shared derived characters needed to permit development of hypotheses of relationship. I concur with Johnson (1980) who believed that the many reductive states that occur among these fishes must be considered as additional evidence for relationship. As Johnson stated "The probability of co-occurrence of independent events is a multiplicative product, and thus the sharing of a number of reductive specializations in identical states is a reasonable indicator of affinity, even if each character cannot be shown to be uniquely derived."

LABORATORY METHODS

Alcohol preserved, cleared and stained, dry skeletal, and fossil specimens were used in this study. Catalogued, alcohol preserved specimens examined were from the collections of the American Museum of Natural History (AMNH), United States National Museum (USNM), Indiana University (IU), and Australian Museum of Sydney (AMS). Additional uncatalogued specimens were obtained as donations or were collected by me, some of which were later catalogued.

Wet skeletons were prepared following the technique of Dingerkus and Uhler (1977) in which bone is stained with alizarin red and cartilage with alcian blue. For ontogenetic information, size series of M. americana and M. saxatilis were cleared and stained from the AMNH Hudson River larval fish collection. A loan of previously cleared and stained percichthyid material was obtained from USNM. Dry skeletons for this study were prepared using dermestid beetles. All fossil Mioplosus material was from the AMNH collection.

Preliminary research indicated that dentition patterns would be of great value in determining intrageneric relationships of Morone. However, high intraspecific variation was noted for certain dental features. Consequently, numerous branchial skeleton preparations were made of mostly uncatalogued Morone material. Although some were cleared and stained, the majority were air-dried following fixation in formalin and preservation in ethanol. Air-drying was found to reveal dental patterns clearly, particularly of lingual teeth, by shrinking the surrounding soft tissue.

Counts and measurements were made in accordance with the procedures of Hubbs and Lagler (1958).

MATERIAL EXAMINED

Taxa	Catalogue No.	Notes
MORONE		
Morone americana		
Osteological material:	AMNH 101797	(6) alizarin preps.
	AMNH 105518	(6) alizarin preps.
	AMNH 26515	(3) alizarin preps.
	AMNH 44691	(5) alizarin preps.
	AMNH 1222	skeleton
	AMNH 22219SD	disarticulated skeleton
	AMNH 56214SD	(2) skeletons
	AMNH 56374SD	skeleton
	uncatalogued	(8) 146-183 mm gill arches only, Hudson River, NY
Alcohol preserved:	AMNH 48134	(5) 29-69 mm
	uncatalogued	(9) 40-82 mm Hudson River
	uncatalogued	(20) 44-122 mm Hudson River, NY
	uncatalogued	(12) 49-155 mm Hudson River, NY
	uncatalogued	(11) 50-208 Hudson River, NY
	uncatalogued	(12) 54-209 mm Hudson River, NY
	uncatalogued	(8) 144-225 mm Hook Creek, NY
Morone chrysops		
Osteological material:	AMNH 20973	(2) alizarin preps.
	AMNH 21590	(3) skeletons
	AMNH 22503	skeleton
	AMNH 22504	skeleton
	AMNH 22505	skeleton
	AMNH 22506	skeleton
	AMNH 22507	skeleton
	AMNH 22508	skeleton
	AMNH 22509	skeleton
	AMNH 22510	skeleton
	AMNH 22511	skeleton
	AMNH 22513	skeleton
	AMNH 22514	skeleton
	AMNH 22516	skeleton
	AMNH 22517	skeleton
	AMNH 22519	skeleton
	AMNH 22520	skeleton
	AMNH 22521	skeleton
	AMNH 22522	skeleton
	AMNH 22523	skeleton
	AMNH 22525	skeleton
	AMNH 22526	skeleton

	AMNH 22527	skeleton
	AMNH 22528	skeleton
	AMNH 22529	skeleton
	AMNH 22532	skeleton
	AMNH 22367	skeleton
	AMNH 30806	skeleton
	AMNH 30878	skeleton
Alcohol preserved:	AMNH 20960	(8) 29-43 mm
	AMNH 21042	(40) 30-72 mm
	AMNH 20973	(15) 31-43 mm
	AMNH 53567	(4) 33-63 mm
	AMNH 53754	(13) 42-67 mm
	AMNH 37281	(2) 90-110 mm
	AMNH 45966	(6) 111-132 mm
	AMNH 64566	(1) 131 mm
	AMNH 20944	(3) 131-147 mm
	AMNH 53719	(1) 142 mm
	AMNH 68264	(2) 176-192 mm
	AMNH 67136	(12) 184-211 mm
	AMNH 42443	(1) 229 mm
	AMNH 695	(1) 235 mm
	AMNH 236	(1) 236 mm
	uncatalogued	(1) 311 mm (Holston R., TN)
	uncatalogued	(1) 322 mm (L. Burlington, NC)
Morone labrax		
Osteological material:	AMNH 36832	(2) alizarin preps.
	uncatalogued	(1) skeleton
Alcohol preserved:	AMNH 32857	(5) 41-122 mm
	AMNH 36832	(9) 54-97 mm
	uncatalogued	(7) 122-188 mm, Morocco
	AMNH 192	(1) 192 mm
Morone mississippiensis		
Osteological material:	AMNH 55618SD	skeleton
	AMNH 56425SD	(3) skeletons
	uncatalogued	disarticulated skeleton (Reelfoot Lake, TN)
Alcohol preserved:	AMNH 3047	(5) 142-148 mm
	uncatalogued	(1) 122 mm (L. Ray Hubbard, TX)
	uncatalogued	(9) 120-161 mm (Reelfoot L., TN)
Morone punctata		
Osteological material:	AMNH 43094	(1) alizarin prep.
	AMNH 56343SD	(2) skeletons
Alcohol preserved:	uncatalogued	(5) 56-68 mm
	AMNH 43094	(5) 78-117
	uncatalogued	(1) 248 mm Dakar, Senegal

Morone saxatilis		
Osteological material:	AMNH 10288	(13) alizarin preps.
	AMNH 101233	(14) alizarin preps.
	AMNH 101242	(~30) alizarin preps.
	AMNH 103770	(6) alizarin preps.
	uncatalogued	(4) alizarin preps. Hudson River, NY
	AMNH 22567SD	disarticulated skeleton
	AMNH 56358SD	disarticulated skeleton
	AMNH 55916	skeleton
	uncatalogued	skeleton Long Island Sound, NY
	uncatalogued	disarticulated skeleton Montauk, NY
Alcohol preserved:	uncatalogued	(71) 49-72 mm Hudson River, NY
	uncatalogued	(3) 65-79 mm Hudson River, NY
	uncatalogued	(3) 96-120 mm Hudson River, NY
	AMNH 51028	(~55) 128-150 mm
	uncatalogued	(11) 546-838 mm gill arches only, Montauk, NY
	uncatalogued	(2) 867-914 mm gill arches only, alcohol preserved
PERCIDAE		
Ammocrypta pellucida		
Osteological material:	AMNH 43854	(1) alizarin prep.
Perca flavescens		
Osteological material:	AMNH 10155	skeleton
	AMNH 22359	skeleton
Alcohol preserved	AMNH 66936	(12) 82-196 mm
Perca fluviatilis		
Osteological material:	AMNH 56287SD	skeleton
Alcohol preserved:	AMNH 36888	(1) 119 mm
Percina caproides		
Osteological material:		
Alcohol preserved:	AMNH 39353	(2) 83-87 mm
Romanichthys valsanicola		
Alcohol preserved:	AMNH 20659	(3) 79-88 mm
Stizostedion lucioperca		
Osteological material:	AMNH 56286SD	(2) skeletons
Stizostedion vitreum		
Osteological material:	AMNH 22533	skeleton
	AMNH 64456SD	skull
Alcohol preserved:	AMNH 2003	(2) 243-309 mm

LATEOLABRAX		
Lateolabrax japonicus		
Alcohol preserved:	AMNH 37005	(2) 117-128 mm
	AMNH 13182	(2) 122-169 mm
	AMNH 26930	(1) 142 mm
	AMNH 37065	(6) 155-223 mm
	AMNH 26805	(1) 156 mm
	AMNH 37028	(1) 230 mm
CENTROPOMIDAE		
Centropomus undecimalis		
Osteological material:	AMNH 21695	skeleton
Alcohol preserved:	AMNH 35063	(1) 144 mm
Lates calcarifer		
Alcohol preserved:	AMNH 48751	(4) 145-170 mm
Lates niloticus		
Alcohol preserved:	AMNH 9546	(2) 135-200 mm
Lates sp.		
Osteological material:	AMNH 22086	skeleton
Psammoperca waigiensis		
Alcohol preserved:	AMNH 19980	(1) 105 mm
SINIPERCA		
Coreoperca kawamebari		
Alcohol preserved:	AMNH 12994	(1) 67 mm
	AMNH 34916	(1) 68 mm
	AMNH 35824	(2) 72-124 mm
Coreoperca whiteheadi		
Osteological material:	AMNH 10499	skeleton
Siniperca chuatsi		
Osteological material:	AMNH 10504	(2) skeletons
Alcohol preserved:	uncatalogued	(4) 100-102 mm Canton, China
	AMNH 10516	(1) 108 mm
	AMNH 15276	(1) 209 mm
Siniperca elongata		
Alcohol preserved:	AMNH 11649	(3) 53-68 mm
	AMNH 11076	(3) 123-137 mm
Siniperca obscura		
Osteological material:	AMNH 10512	skeleton
Siniperca sherzeri		
Alcohol preserved:	AMNH 10514	(1) 133 mm
	AMNH 11048	(2) 88-218 mm
PERCICHTHYIDAE		
Bostockia porosa		
Osteological material:	AMNH 31450SW	(24) alizarin preps.
Alcohol preserved:	AMNH 31444	(3) 32-91 mm
Edelia vittata		
Alcohol preserved:	AMNH 31346	(4) 23-43 mm
Gadopsis marmoratus		
Alcohol preserved:	AMNH 9235	(1) 161 mm

Maccullochella peeli		
Osteological material:	AMS I.15801-001	(1) alizarin prep.
Alcohol preserved:	AMS I.15806-001	(1) 186 mm
	AMS I.15792-001	(1) 340 mm
	USNM 148624	(1) 195 mm
Macquaria ambigua		
Alcohol preserved:	AMS I.21693-002	(1) 160 mm
Macquaria australasica		
Osteological material:	AMS I.19001-001	(1) alizarin prep.
Alcohol preserved:	AMS I.16626-001	(1) 195 mm
	AMS I.15794-003	(1) 268 mm
	USNM 059898	(3) 119-185 mm
	USNM 131953	(2) 274-275 mm
Nannatherina balstoni		
Alcohol preserved:	AMNH 31389SW	(18) alizarin preps.
Percalates colonorum		
Alcohol preserved:	AMS I.15413-001	(2) 174-182 mm
	USNM 059968	(2 of 3) 123-140 mm
Percalates novaemaculatus		
Osteological material:	AMS I.16607-002	(1) alizarin prep.
Alcohol preserved:	AMS I.16617-001	(2) 265-278 mm
	USNM 211324	(3 of 6) 177-230 mm
Percichthys trucha		
Alcohol preserved:	AMNH 970	(1) 98 mm
	uncatalogued	(1) 230 mm locality unknown
Percilia gillisi		
Osteological material:	IU 15516	(4) alizarin preps.
Alcohol preserved:	USNM 167727	(3 of 6) 42-63 mm
Plectroplites ambiguus		
Osteological material:	AMS I.18933-004	(1) alizarin prep.
CENTRARCHIDAE		
Ambloplites rupestris		
Osteological material:	AMNH 21536	skeleton
Alcohol preserved:	AMNH 49111	(1) 33 mm
Lepomis gulosus		
Osteological material:	AMNH 64892	(1) alizarin prep.
Micropterus dolomeiu		
Osteological material:	AMNH 22202	skull
Alcohol preserved:	AMNH 69338	(~20) 12-107 mm
Pomoxis annularis		
Alcohol preserved:	AMNH 64939	(1) 105 mm
POLYPRIONINAE		
Polyprion americanus		
Osteological material:	AMNH 22422	disarticulated skull
Alcohol preserved:	AMNH 1827	(1) 209 mm
	AMNH 30937	(1) 230 mm
Polyprion oxygenios		
Alcohol preserved:	USNM 176820	(2 of 3) 428-525 mm
Stereolepis ischnagi		
Alcohol preserved:	AMNH 4488	(1) 152 mm

SCORPIDIDAE

Scorpis aequipinnis		
Alcohol preserved:	AMNH 31314	(1) 63 mm

SERRANIDAE

Centropristis philadelphica		
Alcohol preserved:	AMNH 50482	(1) 148 mm
Centropristis striatus		
Osteological material:	AMNH 30835SD	skeleton
Cephalopholis cruentata		
Osteological material:	AMNH 21705	skeleton
Epinephelus guttatus		
Osteological material:	AMNH 21862	skeleton
	AMNH 35426SD	skeleton
Alcohol preserved:	AMNH 24302	(1) 157 mm
Epinephelus sp.		
Osteological material:	AMNH 22534	half-skull
	AMNH 22537	half-skull
Epinephelus striatus		
Osteological material:	AMNH 21865	skeleton
Niphon spinosus		
Alcohol preserved:	AMNH 3714	(1) 118 mm
Paralabrax clathratus		
Alcohol preserved:	AMNH 7934	(1) 127 mm
Rypticus subbifrenatus		
Alcohol preserved:	AMNH 35302	(1) 64 mm
Serranus hexagonatus		
Osteological material:	AMNH 22605	skeleton
Serranus tigris		
Osteological material:	AMNH 43172SW	(2) alizarin preps.

SCIAENIDAE

Aplodinotus grunniens		
Osteological material:	AMNH 27883	skeleton
Alcohol preserved:	AMNH 52501	(9) 95-138 mm
Collichthys novaeguineae		
Alcohol preserved:	AMNH 17568	(4) 45-76 mm
Cynoscion arenarius		
Osteological material:	AMNH 56266SD	skeleton
Cynoscion nebulosus		
Osteological material:	AMNH 56255SD	skeleton
Cynoscion nobilis		
Osteological material:	AMNH 27901	disarticulated skull
Cynoscion regalis		
Osteological material:	AMNH 1758SD	skeleton
Alcohol preserved:	AMNH 40708	(5) 45-52 mm
	AMNH 67	(1) 260 mm
Micropogon undulatus		
Osteological material:	AMNH 35474	skeleton
Otolithes argenteus		
Osteological material:	AMNH 55920SD	skeleton
Pogonias cromis		
Osteological material:	AMNH 21717SD	disarticulated skeleton
Umbrina cirrosa		
Alcohol preserved:	AMNH 45462	(6) 36-137 mm

LUTJANIDAE		
Apsilus dentatus		
Alcohol preserved:	AMNH 37122	(1) 80 mm
Etelis oculatus		
Alcohol preserved:	AMNH 28367	(1) 85 mm
Lutjanus apodus		
Osteological material:	AMNH 21722SD	skeleton
Alcohol preserved:	AMNH 23682	(1) 152 mm
Lutjanus aya		
Osteological material:	AMNH 55869SD	skeleton
Lutjanus campechanus		
Alcohol preserved:	AMNH 51492	(39) 30-194 mm
Lutjanus synagris		
Osteological material:	AMNH 22166	skeleton
	AMNH 22167	skeleton
HAEMULONIDAE		
Haemulon flavolineatum		
Alcohol preserved:	AMNH 24929	(3) 97-121 mm
Haemulon plumieri		
Osteological material:	AMNH 21967	skeleton
POMADASYDAE		
Pomadasys jubelini		
Alcohol preserved:	AMNH 32793	(1) 118 mm
MULLIDAE		
Mullus albula		
Osteological material:	AMNH 27908	disarticulated skull
KUHLIIDAE		
Kuhlia malo		
Osteological material:	AMNH 22068	skeleton
	AMNH 22069	skeleton
Alcohol preserved:	AMNH 331	(3) 99-106 mm
Kuhlia rupestris		
Alcohol preserved:	AMNH 17954	(2) 191-197 mm
APOGONIDAE		
Apogon exostigma		
Alcohol preserved:	AMNH 42969	(1)
Apogon novemfasciatus		
Osteological material:	AMNH 14818	(2) alizarin preps.
TERAPONIDAE		
Leipotherapon macrolepis		
Alcohol preserved:	AMNH 33976	(15) 41-63 mm
Terapon caudivittatus		
Alcohol preserved:	AMNH 35627	(6) 32-162 mm
CHANDA		
Chanda gymnocephala		
Alcohol preserved:	AMNH 32521	(16) 27-40 mm

GLOSSAMIA		
Glossamia aprion		
Alcohol preserved:	AMNH 48741	(26) 28-140 mm
SYNAGROPS		
Synagrops bella		
Alcohol preserved:	AMNH 40826	(1) 78 mm
DODERLEINIDAE		
Doderleinia berycoides		
Alcohol preserved:	AMNH 34800	(2) 220-270 mm
ARRIPIDAE		
Arripis trutta		
Alcohol preserved:	AMNH 31384	(2) 161-182 mm
BERYCIFORMES		
Holocentrus ascensionis		
Osteological material:	AMNH 56454SD	skeleton
Holocentrus rufus		
Osteological material:	AMNH 21455	(1) alizarin prep.
	AMNH 22007	skeleton
Myripristis jacobus		
Osteological material:	AMNH 21735	skeleton
Alcohol preserved:	AMNH 31071	(1) 123 mm
Myripristis parvidens		
Osteological material:	AMNH 43444SW	(2) alizarin preps.
Polymixia lowei		
Alcohol preserved:	AMNH 37335	(3) 96-104 mm
	AMNH 70602	(2) 120-123 mm
GOBIOIDAE		
Dormitator maculatus		
Alcohol preserved:	AMNH 37669	(1) 65 mm
Rhyacichthys aspro		
Alcohol preserved:	AMNH 48695	(2) 103-135 mm
SEBASTES		
Sebastes flavidus		
Osteological material:	AMNH 37944	skeleton
SPHYRAENIDAE		
Sphyraena argentea		
Osteological material:	AMNH 27949SD	skeleton
Sphyraena borealis		
Alcohol preserved:	AMNH 64416	(2) 80-173 mm

MIOPLOSUS

Mioplosus abbreviatus:

AMNH 2463	skeleton

Mioplosus labracoides:

AMNH 753	skeleton
AMNH 809	skeleton
AMNH 2457	skeleton
AMNH 2458	skeleton
AMNH 2459	skeleton
AMNH 2957	skeketon
AMNH 2973	skeleton
AMNH 2974	skeleton
AMNH 8421	skeleton
AMNH 8422	skeleton
AMNH 8425	skeleton
AMNH 8426	skeleton
AMNH 8427	skeleton
AMNH 8428	skeleton
AMNH 8429	skeleton
AMNH 10296	skeleton
AMNH 10298	skeleton

Mioplosus sp.:

AMNH 757	skeleton
AMNH 788	skeleton
AMNH 799	skeleton
AMNH 2886	skeleton
AMNH 6397	skeleton

SECTION I.

-<u>MORONE</u>-

HISTORICAL OVERVIEW OF MORONE CLASSIFICATION AND TAXONOMY

Morone comprises two eastern Atlantic species, *Morone labrax* (European bass) and *Morone punctata* (spotted bass), two western Atlantic species, *Morone americana* (white perch) and *Morone saxatilis* (striped bass), and two central North American species, *Morone chrysops* (white bass) and *Morone mississippiensis* (yellow bass).

At a higher classificatory level, *Morone* was long considered a serranid. Gosline (1966), recognizing the extreme heterogeneic nature of the Serranidae, redefined the family along substantially narrower limits while placing the accretions, including *Morone*, in a new family erected for that purpose - the Percichthyidae. Johnson (1984) redefined the percichthyids, leaving three taxa *incertae sedis* - *Morone*, *Lateolabrax* and *Siniperca*. Johnson gave *Morone* familial status as the Moronidae, a treatment previously rendered by Jordan (1923) and Smith (1981).

The six species that comprise the genus *Morone* share a history of taxonomic division and recombination. In a thorough nomenclatorial review of the generic names of this group, Whitehead and Wheeler (1966) ascribed this lack of agreement to problems stemming from nomenclatorial misimpressions and discordant systematic judgements. The authors recognized, but made no attempt to resolve disagreement among workers over their monogeneric classification.

Gill (1860) allocated the six species to four genera, placing each eastern Atlantic species in its own genus. Boulenger (1895) considered the group monogeneric, but Jordan and Eigenmann (1890) and Jordan and Evermann (1896) preferred trigeneric classification. Jordan (1923) maintained placement in three genera advocating familial status.

Berg (1949) included all six species in a single genus, *Morone*, with three subgenera, an integration that was supported by Bailey, Winn and Smith (1954). Berg provided three diagnostic generic characters: separate dorsal fins, teeth present at the base of the tongue, and the absence of a supramaxillary bone, features that when taken together serve to separate *Morone* from other percoids.

Woolcott (1957) conducted a detailed taxonomic study of the group, in part, to check the validity of monogeneric classification. Having compared the osteology of all of its species except *punctata*, Woolcott concluded that the taxon was indeed monogeneric. He also presented evidence that supported an intrageneric division into pairs synonomous with the scheme of Jordan and Eigenmann (1890), but at the subgeneric level.

Today, in North America, all six species are generally recognized as congeners, and are united under the synonym *Morone*, proposed by Mitchill in 1814 and given priority by Berg (1949), Bailey (1951), and Whitehead and Wheeler (1966). Nevertheless, Whitehead and Wheeler continued, as is common in Europe today, to use the synonym *Dicentrarchus* rather than *Morone* for the two eastern Atlantic species.

Recent work on this group includes a mitochondrial DNA analysis restricted to the American species (Bowen and Chapman 1985). This study indicated a close affinity between *chrysops* and *saxatilis*, and between *americana* and *mississippiensis*.

Two species of *Morone* have received intraspecific analysis. *M. saxatilis* has been the focus of a multitude of studies that have attempted to find morphological variation between populations as a potential fishery management tool. Meristic characters were employed for this purpose by Raney and DeSylva (1953), Raney, Woolcott and Mehring (1954), Raney and Woolcott (1955), Raney (1957), Lewis (1957), Brown (1965), and Barkuloo (1970). Morphometric variation in saxatilis was analyzed by Lund (1957) and in the annuli of their scales by Merriman (1941). A combination of meristic and morphometric characters were used by Berggren and Lieberman (1978). All of these studies succeeded in discriminating between various endemic Atlantic and Gulf coast populations to at least some degree. It does not appear that similar studies have ever been performed on the introduced Pacific coast populations, probably because of the great distance separating the two major populations which occur in San Fransisco Bay, California and Coos Bay, Oregon.

Woolcott (1962) examined meristic variation in populations of M. americana. The four remaining members of Morone do not appear to have sustained morphological comparison below the species level.

Natural hybridization within Morone was not known to occur until reported between chrysops and americana in portions of Lake Erie and connecting waters (Todd 1986), a region penetrated by americana only since the 1970's (Boileau 1985). Artificial hybridization of Morone had already received considerable attention in the United States with the recognition of the striped bass x white bass cross as an easily produced, highly desirable gamefish (Axon and Whitehurst 1985). Striped bass x white perch hybrids have also been produced but they have not been as extensively utilized. Characters for discrimination among these two artificial hybrids were provided by Kerby (1979), and between the striped bass x white bass cross and its parental species by Williams (1976). The Louisiana Department of Fish and Wildlife is currently experimenting with a striped bass x yellow bass hybrid.

-RESULTS-

OSTEOLOGY

Gregory (1933) provided illustrations of the neurocranium and branchiocranium of the striped bass. Merriman (1940) presented figures and a detailed description of the post-cranial skeleton of the striped bass, preferring not to include the cranium inasmuch as "Gregory (1933) has figured the skull alone, but has done it so perfectly that there remains little else to be added." It was revealed in the course of this research that the skull figured in Gregory's oft-cited illustration (e.g., Westin and Rogers 1978; Setzler et al. 1980) was demonstrably that of a grouper (Waldman 1984). Accurate depictions of a saxatilis skull are provided by Starks (1901) and Jordan (1905). Osteological development in larval and early juvenile stages of americana and saxatilis was described by Fritzche and Johnson (1980).

Woolcott (1957) described in detail the adult bone morphology of all Morone species except punctata, but his analysis did not discriminate between primitive and derived character states. Woolcott's subgeneric groupings and conclusion that the taxon is monophyletic were apparently based on overall similarity, but are nevertheless in agreement with this analysis. Because Woolcott adequately described the osteology of five Morone species, I will restrict my description to features of those five species omitted by him, or which I found to be in error, and to a description of punctata.

Neurocranium

As Woolcott (1957) characterized it for the other members of the genus, the nasal of Morone punctata is elongate and flatenned and encloses part of the supraorbital canal. The ventral margin of the lachrymal is serrate as in chrysops, americana, and mississippiensis, not smooth as in the other two species. Woolcott (1957) correctly noted that the third suborbital has a medially projecting shelf, but his assertion that it supports the eye may be in error, as it is not clear that this is a function of the subocular shelf (Smith and Bailey 1961). The subocular shelf reaches a more pronounced posterior point in chrysops and saxatilis than in the other species of Morone.

The shape and position of the vomer differ among the species. M. labrax, mississippiensis, and saxatilis have simple bilateral pockets posterior to the tooth-bearing vomerine wings. The condition in saxatilis is similar, but there is a groove in the medial descending arm. In chrysops, there is no medial descending arm; instead, a single cavity forms along the entire posterior margin of the tooth- bearing vomerine lobe. The vomer of punctata is highly modified in that a bone ridge medial and posterior to the tooth patch allows the tooth patch to extend posteriorly toward the parasphenoid.

The supraoccipital crest is low in punctata, as it is in saxatilis and labrax. For two punctata specimens, the mean percentage of the length of the crest into its height was 61%. The epioccipital of all six species has a flattened, posterior projection that is somewhat medially oriented, and which serves as a point of muscle attachment, as does the supraoccipital. A rather large muscle bundle inserts on a broad and often indented posterio-lateral margin of the epioccipital process; it originates from the medial septum slightly dorsal to the vertebral column over a region that includes the first three neural spines.

The ventral contour of the parasphenoid in punctata is moderately curved, as in labrax, americana, and mississippiensis.

Woolcott (1957) believed that the size and shape of the features of the otic region clearly showed interspecific relationships in Morone. He found that the greatest distortion of the otic capsule occurred in americana and mississippiensis, and that the suture between the prootic, exoccipital and basioccipital was straight. I found the suture closed between the prootic and exoccipital, but with a slight gap between the prootic and basioccipital.

For chrysops, Woolcott (1957) found an irregular suture and minimal swelling of the auditory bulla. Woolcott described saxatilis as having the least distention of the otic capsule, and an interdigitated suture between the prootic and exoccipital, as in chrysops. I observed a small but regular gap between the prootic and basioccipital.

Woolcott (1957) found the expansion of the auditory bulla in labrax to be intermediate to the American species, with most of the enlargement occurring in the prootic and basioccipital. A similar condition is found in punctata, and both labrax and punctata have an otic suture pattern that resembles the suture pattern of chrysops and saxatilis.

Branchiocranium

The *Morone* premaxilla is a tooth-bearing bone with three dorsal processes. According to Woolcott (1957), the maxillary process is located about midway on the premaxilla; in all instances, I found it to occur well posterior of the midpoint (Fig. 15C). The maxilla of *punctata* is not serrulate, serrae occur only in *chrysops* and *saxatilis*. Like all other members of *Morone*, *punctata* lacks a supramaxillary bone.

The dentary of *punctata* is similar to that of *labrax* which Woolcott (1957) described as having large sensory pores as in *americana* and *mississippiensis*, but with much denser bone like that of *chrysops* and *saxatilis*. Woolcott stated that "The suture between the epihyal and the ceratohyal is fused except in the center." It is not clear what he meant by this insamuch as in all *Morone* species the fusion between these two bones occurs medially over the central region of the suture.

Woolcott (1957) examined the ventral aspect of the urohyal and found it smooth in *saxatilis*, *labrax*, and *mississippiensis*, but with a thin median ridge in *chrysops* and some specimens of *americana*. *M. punctata* appears to lack the median ridge. I found that many *chrysops* specimens, in addition to the median ridge, also show deep, posteriorly directed fossae anterior to it.

The preopercle of *punctata* (Fig. 12A) is similar to that of *labrax*, with serrae on the posterior margin and large antrorse spines on its ventral margin. In *punctata*, the transitional spine at the angle between the two margins is sometimes bifurcated. The remaining species possess serrae on both preopercular margins (Fig. 12B). In all species of *Morone*, the preopercular portion of the preoperculomandibular sensory canal is entirely open, although only narrowly so dorsally.

The basihyal is relatively long and narrow in juveniles of all species of Morone species, but broadens characteristically to different extents in older individuals of each species. M. saxatilis, labrax and punctata show a moderate anterior expansion of this bone. M. chrysops displays a substantially broadened basihyal in adult specimens (Fig. 5A), with most, but not all, of the gain in width occurring anteriorly. Both M. americana and mississippiensis ontogenetically exhibit little change from the juvenile basihyal configuration. However, the two latter species do display an unusual feature among percoids, namely two thin flanges that jut laterally from the rear portion of the bone. In the four species of Morone that bear basihyal teeth, most specimens possess a similar lateral broadening of that region, which often supports a small portion of the tooth patch or patches. It is possible that the basihyal in americana and mississippiensis (Fig. 6B) is neotenic with development halted prior to the formation of teeth and anterior broadening.

The ventral surface of the Morone basihyal is not smooth as it is in most percoid fishes, but instead possesses longitudinal ridges and, particularly in larger specimens, anteriorly directed fossae. Surface features are visible on the ventral basihyal early in development. A 15 mm specimen of saxatilis displayed a simple, very slightly ossified rectangular basihyal which lacked teeth on its basihyal surface. However, at 23 mm, a saxatilis specimen showed significant basihyal ossification, two well-formed tooth patches, and two clearly visible ridges on the ventral basihyal surface. Fritzche and Johnson (1980) found lateral teeth in americana at 23 mm. Juveniles of chrysops, americana, labrax, and punctata also had at least two ridges (juveniles of mississippiensis were not examined).

Modal patterns in the basihyal ridges for each species were observed, but proved too variable for diagnostic purposes. The Afro-European labrax and punctata tended to possess a simple arrangement of three ridges that diverged from the posterior basihyal terminus but did not extend as far forward as in the American species. The central fold was often slightly shorter. The absence of fossae in the specimens examined of the Afro-European species may be attributable to the lack of large adult specimens available to this study, inasmuch as the fossae tend to form later in the ontogeny of saxatilis and chrysops.

M. americana and mississippiensis most often possessed a pair of ridges, or three with the middle ridge shorter than the others. These features tended to extend farther forward than in labrax and punctata, to just short of the anterior end of the bony basihyal. In both species, the ridges are often very symmetrical in shape and spacing, however, there are exceptions. One adult specimen of americana had very deep ridges that flared outwards, in addition to two large pockets that opened to the hollow interior of the bone. M. saxatilis typically possesses 2-3 ridges, sometimes more, together with numerous fossae.

The ventral basihyal surface features are most extensively developed among the genus in chrysops (Fig. 6A). There may be 5-6 main ridges together with smaller accessory ridges anteriorly, and numerous fossae over a large portion of the bone. In adults, it is not uncommon for thin bone to form between ridges, creating large, tunnel-like cavities.

The topographic features of the ventral basihyal appear to be related to its ligamentous support. There is in Morone, a thin sheet of connective tissue and ligament that extends from the protractor hyoideus to the tip of the tongue. Interior to this layer are two ligament pairs that run from the hypohyals to the anterior region of the tongue. These wide, flat bands merge medially in front of the cartilage cap, where they also meet the epithelium of the dorsal surface of the basihyal. The four ligaments provide support directly to the basihyal with numerous smaller ligaments that branch from it. These branching ligaments originate on the dorsal surface of the main ligaments and insert in the fossae and canals of the basihyal. Because the main ligaments originate somewhat ventral to the tongue, they meet it at an angle, producing a small cavity between the ligaments and the basihyal bone. This area, between the branching ligaments, is filled with a somewhat iridescent form of soft tissue.

Axial Skeleton

Woolcott (1957) stated that the characteristic number of vertebrae of Morone is 25 (12 + 13), but pointed out that an occasional specimen may have 24 (12 + 12). M. punctata also has 25 vertebrae. The punctata vertebral column is straight, as for labrax and saxatilis.

The haemal arch was found by Woolcott (1957) to be completely formed at the 11th vertebra in the five species he examined. He also noted that *labrax*, and occasionally *chrysops* and *saxatilis*, have a complete haemal arch on the 10th vertebra. It appears that *punctata* has the most anterior first haemal arch (Table 1); the three specimens I examined displayed a complete arch on the ninth vertebra.

In the majority of percoids, there is at least minimal articulation between the vertebral column and the anal fin. In some taxa the extent of this contact is fairly constant while in others a range of conditions may be displayed. *Morone* appears to show a continuum in this character, ranging from slight in *labrax* to strongly developed in *americana* and *mississippiensis*, the latter two species also possessing secondarily expanded second anal spines. The configuration of the haemal spine and its associated anal pterygiophores vary to produce the range of articulation with a fairly short haemal and first anal pterygiophore (fusion of first and second pterygiophores) with little overlap in *labrax*, to somewhat more overlap in *saxatilis*, and finally to a high degree of contact in the remaining species including *punctata*.

The nature of the articulation between the anal fin and the vertebral column is such that the first pterygiophore rests in a channel on the anterior aspect of the haemal spine. Additional reinforcement is usually offered by a ligamentous attachment of the tips of the second and third anal pterygiphores to the terminus of the articulated haemal spine, and by connection with the ends of the pleural ribs of the immediately anterior haemal spine with the first pterygiphore-haemal junction. The haemal with which the anal pterygiophore articulates varies among species (Table 1).

The second anal pterygiophore of punctata is specialized as compared with the rest of the genus. In the five other species, the anterior aspect of the first anal pterygiophore is bladelike, presumably to serve as an attachment site for connective tissue, and has two lateral wings that ascend a short distance from its ventral base, the probable remnant of an independent first element. In punctata, however, the large medial blade is replaced by two laterally displaced but anteriorly oriented blades that form a channel for the reception of the swimbladder terminus. This condition is less developed but not unlike that found in Lateolabrax (Katayama 1959).

Table 1. - Vertebrae most frequently associated with first haemal arch and with anal pterygiophore in Morone.

Species	First Haemal Arch	Anal Pterygiophore
M. labrax	10	12
M. punctata	9	12
M. chrysops	11	13
M. saxatilis	11	13
M. americana	11	13
M. mississippiensis	11	13

My findings on the number of pleural spines for Morone did not agree with Woolcott's (1957). Woolcott stated that there are 12 pairs of pleural ribs in all species, but I observed 11 pairs in labrax as well as in punctata (which Woolcott did not examine), and 12 pairs in the American species. Merriman (1940) noted the presence of four epipleural ribs in saxatilis. Woolcott (1957) observed them on pleural ribs three through seven for Morone. Fritzche and Johnson

(1980) found nine or 10 pairs of pleural ribs beginning with the third vertebra and seven or eight pairs of epipleurals beginning with the first vertebra in larval and early juvenile specimens of *americana* and *saxatilis*. I found that epipleurals were consistently present on pleural ribs 1-7 in all members of *Morone*.

All *Morone* species have 17 caudal rays. However, the number of epaxial and hypaxial procurrent rays varies interspecifically. Woolcott (1957) reported the number of epaxial and hypaxial elements as follows: *saxatilis* 11+11, *chrysops* 11+9, *americana* 11+9, and *mississippiensis* 10+7. My counts, based on a limited number of specimens were generally higher: *saxatilis* 12-13+12, *chrysops* 10+9, *americana* 11+11, and *mississippiensis* 10+9. Procurrent ray counts for the eastern Atlantic species, not reported by Woolcott, were: *labrax* 14+13 and *punctata* 14+12.

Woolcott (1957) observed modal numbers of dorsal pterygiophores as follows: *saxatilis* 23, *chrysops* 25, *americana* 23, and *mississippiensis* 23. I examined a single dry skeleton of *labrax* and two of *punctata* and obtained counts of 24 in each. In all *Morone* species the first three dorsal pterygiophores remain unassociated with the dorsal fin. Woolcott noted that in regard to the insertions of dorsal pterygiophores between neural spines, both *americana* and *mississippiensis* typically lacked a pterygiophore between neural spines 10 and 11. My observations also indicated a noninfiltrated neural gap in this region for both species, but the gap sometimes occurs between the ninth and tenth neurals. Pterygiophore interdigitation patterns for the American species of *Morone* have been described by Fritzche and Johnson (1980) and Olney et al. (1983).

Dentition

The dental features of Morone have been found to bear considerable systematic significance at several taxonomic levels. The lack of any previous recognition of the importance of these unique tooth formations is surprising, given the high level of interest in this taxon, and may stem from systematic practices that did not attempt to determine the taxonomic level of origin of a character, or simply from the improper preparation of material.

The dentition of Morone is of the type found in most primitive Euteleosts and called Type 2 by Fink (1981). Mansueti (1958) provided notes on dental ontogeny in saxatilis, and Fritzche and Johnson (1980) for saxatilis and americana. All members of Morone bear teeth on the vomer, palatine, premaxillary, dentary, basibranchial, and pharyngeal bones. In addition, labrax, punctata, chrysops and saxatilis share the presence of a tooth patch or paired patches fused to the basihyal (Fig. 4).

All Morone species also possess teeth or tooth-bearing plates in the soft tissue of the tongue. One set occurs lateral to the basihyal but distinctly separated from it (Fig. 4A). A second set of teeth or tooth patches are rooted in the soft tissue anterior to the basihyal (Fig. 4A).

Gill (1860) provided some observations on lingual tooth formations in Morone. Woolcott (1957) did not provide complete descriptions of these tooth formations but he did note that "On either side of the glossohyal is a very small bone that bears teeth. These are observable only in cleared and stained specimens." Woolcott gave accurate descriptions of these lateral tooth-supporting bones in saxatilis, americana, and mississippiensis, but not in chrysops, when he noted the presence of a second tooth patch posterior to the first as if it was a regular occurrence. The lateral bone of chrysops was not observed by Woolcott, but he was aware of the large, ovate tooth patch over it. Woolcott also noted what he characterized as the occasional presence of teeth at the tip of the tongue in all of the species he studied.

Westin and Rogers (1978) provided a tabular summary of the tooth patches located at the margin of the tongue in all Morone species except punctata, largely based on the findings of Woolcott (1957). Although they vary somewhat intraspecifically, these teeth occur quite regularly in all four species in forms that are, to at least some degree, characteristic of each species.

Basihyal Teeth

In Morone the basihyal is narrow posteriorly, and broad anteriorly with a cartilaginous cap. Dentition patterns on the basihyal range from a large single patch of teeth in labrax and punctata to paired patches in chrysops and saxatilis, or the absence of basihyal teeth in americana and mississippiensis.

Of major importance in determining the significance of these differences is the question of whether basihyal teeth are of dermal, or endochondral origin. Retention of an endochondrally derived basihyal tooth patch was believed by Nelson (1969) to be plesiomorphic. Lingual teeth of dermal origin would indicate a secondary derivation.

Examination of small (35-90mm) cleared and stained specimens of the four species that bear basihyal teeth, and of adult specimens of *saxatilis* and *chrysops* indicate that these teeth are firmly fused to the underlying bone, and thus are primitive for *Morone*. Ontogenetically, they develop just before the appearance of the lateral plates, and considerably before the anterior teeth, which are the last lingual teeth to form.

Both Old World species have a single, large, basihyal tooth patch that extends from the posterior margin, where it is as broad or broader than the underlying element, forward approximately 75-90% of the distance to the cartilaginous tip of the basihyal, while tapering somewhat anteriorly. There were no notable differences in this formation between *labrax* and *punctata* in the specimens examined. Early juvenile specimens display shorter patches with much less anterior extension then do larger fish. This ontogenetic tranformation supports the hypothesis that the elongated basihyal tooth patch of *labrax* (Fig. 4C) and *punctata* (Fig. 4D) is a secondarily derived state of the primitive, posteriorly located tooth patch of the percoid basihyal.

M. saxatilis bears two consistently well separated tooth plates on its basihyal (Fig. 4E). The majority of specimens examined of *chrysops* also showed paired patches, but several common modes were identified, one of which was the presence of a single median tooth patch. In both species the plates may remain parallel or diverge slightly anteriorly, with the patches of *saxatilis* extending approximately 50% of the length of the bony portion of the basihyal, as compared with about 30% in *chrysops*. In *saxatilis* and *chrysops*, bone fills in below these patches and elevates them, possibly serving to maintain a level above the also thickening soft tissue that overlies the dorsal surface of the basihyal.

The great majority of descriptions of the white bass, as well as keys that include this species attribute a single basihyal tooth patch to the species (e.g., Jordan and Eigenmann 1890; Whitehead and Wheeler 1966; Cross and Collins 1975). However, Gill (1860) observed that "... while there are two narrow rows separated by a mesial line in Roccus lineatus, the rows are broader at the middle, in proportion, and coalescent in Roccus chrysops." Moreover, Bishop (1968) noted that some white bass may exhibit two basihyal patches, and Williams (1976) stated that specimens may possess a single rounded or heart shaped patch that has a line scribed through it. Although he recognized that some chrysops specimens have two patches at the rear of the tongue, Kerby (1979) found a single patch generally to be a reliable character.

This study showed the basihyal teeth of chrysops to be a character of great variability. Examination of 67 adult specimens from several widespread locations revealed conditions ranging from two well separated patches of equal size, to the absence of basihyal teeth.

Four primary patterns could be identified:

1. Two basihyal patches of approximately equal size that varied in proximity from well separated to contiguous (Fig. 5A). Of the 67 specimens examined, 21 (31%) were of this type.

2. Two patches of clearly unequal size, also ranging from distinctly separated to contiguous (Fig. 5B). This was the condition of 22 (33%) of the adult chrysops examined.

3. The presence of a single patch as the result of the second patch missing (Fig. 5C). Evidence for my interpretation of an absence of a second patch is that the existent patch occurs in a far lateral position on the basihyal and is of a size consistent with a typical member of a paired patch. Although it is conceivable that the second patch might have become detached from the basihyal in these fish, the absence of any intermediate states or strongly malformed tooth patches suggests that this is a developmental phenomenon. Eight (12%) of the fish examined were of this type.

4. A single, large, medial patch (Fig. 5D). Patches of this type may show indentations in their front, rear, or both, or have a completely smooth margin. Of the 67 chrysops specimens examined, 15 (22%) displayed this condition.

A fifth state, the absence of any basihyal teeth was found in only a single specimen and is probably exceedingly rare. With regard to the basihyal patches of chrysops Kerby (1979) stated that "When two patches are present, margins are more rounded and the appearance suggests an original single patch which has separated through the center...". It appears that the alternative is more likely and that the presence of a single patch is the result of a fusion between a pair of patches. Evidence for such a transformation is provided by the observation that these teeth occurred in the form of two patches in almost all of the juvenile fish I examined. A survey of 54 juvenile chrysops ranging between 29-72 mm SL from both eastern and western populations showed 51 possessing two, frequently well separated patches; two fish with one of the two patches missing; and an aberrant specimen with a large, laterally displaced, semi-divided patch. In very young white bass, basihyal tooth patches appear to form as fairly narrow tooth rows near the rear edges of the basihyal and then to broaden or migrate medially with age.

The sagittal line through a single tooth patch that Williams (1976) noted is actually a row of melanophores that often occurs in the soft tissue between the patches. Some specimens with single median patches retain a higher concentration of melanophores in the tissue that overlies the toothplate midline than occurs lateral to it.

The historical confusion over the state of basihyal teeth in chrysops can thus be attributed to two causes: failure to consider that an ontogenetic transformation occurs in these fish and, that there is variation in the timing and progression of ontogenetic events. That the two patches (when they occur) are normally much less widely separated than are the two patches of saxatilis has prevented the frequent misrepresentation of the chrysops state from being diagnostically problematical. Only since about 1970 have striped bass been heavily stocked inland within the range of the naturally allopatric white bass (Axon and Whitehurst 1985).

Neither americana nor mississippiensis possesses basihyal teeth at any developmental stage. The three primary moronid states identified - anteriorly elongated single tooth patches, paired patches, and the absence of basihyal teeth are all derived in comparison with the primitive acanthopterygian basihyal tooth patch, and therefore suggest paired subtaxa within Morone. However, inasmuch as each state could be derived in a single transformation from such a primitive patch, these teeth cannot provide a definitive resolution of relationship.

Lateral Tooth Plates

All six members of Morone share the presence of long tooth plates embedded in the distal periphery of the tongue on either side of the basihyal. The independence of these plates from the basihyal indicates that they are dermally derived.

M. labrax (Fig. 4C), punctata (Fig. 4D), and saxatilis (Fig. 4E) possess relatively smaller lateral tooth plates than do the other members of Morone, although the differences are not great. In these three species, the lateral plates extend from just posterior to the anterior tip of the basihyal to approximately 2/3 the distance toward its posterior end.

The lateral plates of chrysops (Fig. 4F) are long and broad, and often butt against the anterio-lateral ends of the basihyal. Typically, the lateral plates extend posteriorly from about the anterior tip of the basihyal 5/8 to 3/4 the distance to the posterior end, usually terminating at or just beyond the anterior margin of the basihyal patch or patches. The plates appear to broaden with age and eventually fill in much of the area on both sides of the basihyal, which itself, tends to broaden substantially as the fish matures.

The lateral tooth plates of americana (Fig. 4G) are broad with blunt, rounded ends and they extend from approximately the entire length of the basihyal to just beyond its anterior end. The lateral plates of mississippiensis (Fig. 4H) are shaped similarly to those of americana, but extend farther anteriorly than any other member of the genus.

These lateral teeth develop ontogenetically after the basihyal teeth (when present). They appear as individual teeth, one or a few at a time, and are joined ventrally by a chain- or lattice-like bony network (Fig. 4A). Complete linkage may not always occur; several saxatilis specimens showed small, isolated posterior tooth patches. Lateral tooth plates appear to form from their anterior pole posteriorly in saxatilis.

Lateral tooth plates imbedded in the soft tissue of the tongue lateral to the basihyal are unique among the taxa surveyed in this study. Lateral tooth plates are the only known autapomorphy of the taxon, and as such, serve as the single defining character of the genus.

Anterior Teeth or Tooth Patches

All members of Morone share the presence of teeth in the soft tissue of the tongue anterior to the basihyal, but variation in this character, within and between species is high.

Juvenile specimens of labrax have small teeth scattered fairly uniformly in an arc anterior to the lateral plates and basihyal near the margin of the tongue (Fig. 4C). Larger fish show consolidation of teeth to form distinct tooth patches. M. punctata (Fig. 4D) displays a similar ontogenetic change, but the consolidation occurs at a somewhat earlier stage. The anterior teeth of punctata are also more evenly sized and spaced.

M. saxatilis has the most irregular and poorly developed anterior teeth among its congeners (Fig. 4E). Some individuals apparently do not develop any anterior teeth, although most show at least a few scattered teeth near the tip of the tongue and some, particularly larger fish, may display small patches.

M. chrysops also exhibits highly variable tooth formations anterior to the basihyal (Fig. 4F), but these tend to be larger and more developed than in saxatilis. Shortly after teeth appear in this location they become organized into patches. The size of the patches varies, with large patches often occurring next to clumps of smaller ones, suggesting either that the smaller patches have yet to conglomerate or that the merging process has ceased. Although in most chrysops specimens, these teeth are restricted to the tongue's margin, one large specimen displayed two concentric arcs of large, well developed patches, the patches of the interior row being somewhat smaller.

Anterior tooth patches are best developed in americana (Fig. 4G) and mississippiensis (Fig. 4H). The anterior teeth of mississippiensis occur as blocky plates that are usually restricted towards the distal area of the tongue. In some instances these plates juxtapose, and assume an opened horseshoe shape. The anterior teeth of americana are similar, but are frequently rectangular in shape, the longer axis oriented towards the tip of the basihyal. These plates are quite large and therefore few in number, and occupy much of the lingual region forward of the basihyal.

Basibranchial Dentition

Tooth plates occur near the center of the oral cavity on or near the longitudinal midline in all species of Morone. Intraspecific variation appears to be minor, but the variation among species is significant.

Ventral gill arch dentition is least developed in americana (Fig. 8B) and mississippiensis. No teeth occur on the basibranchials. Small patches are found in the ventral epithelium of the mid-oral cavity on the three pairs of hypobranchial, but only in a lateral position, apparently as extensions of the anterior gill raker tooth patches of the hypobranchials. Others are clearly separated from their proximal gill rakers, while some may show intermediate positions. Often there is a pair of small tooth patches on the first hypobranchials that are not associated with a gill raker. On the second and third hypobranchials, dorsal dentition may consist of nothing more than the dorsal end of the gill raker being flush with the dorsal epithelium.

The mid-oral cavity dentition of chrysops and saxatilis (Fig. 8A) is more developed. Both species have tooth plates on the three hypobranchials, but their normally larger size often covers much of the dorsal surface of the underlying bony elements. The tooth patches of the first hypobranchial are rectangular and several may occur in a row, but they are occasionally absent altogether. The teeth of the second hypobranchial form as a single large patch, or several sizable fragments, both states occurring with corresponding gill rakers on the anterior surfaces of the hypobranchials. The third hypobranchial bears large ovate tooth patches approximately equal in size with the basihyal teeth, (when those teeth occur in pairs). Although the larger portion of these tooth patches are located above the hypobranchials, their medial aspects occur dorsal to the third basibranchial and to the gap between. Each third hypobranchial also retains three gill rakers on its anterior surface.

M. labrax exhibits a dental condition on the first hypobranchial similar to that of chrysops and saxatilis. In labrax, however, the second hypobranchial bears a more highly developed ovate tooth patch independent of gillrakers, and has a more longitudinal axis than do any of the North American species. The third pair of hypobranchials does not show dorsal tooth patches. Nevertheless, homologous tooth patches probably do occur on the third basibranchial. These tooth patches, although large, are closely spaced and do not contact the hypobranchials. The third hypobranchials retain several gill rakers.

M. punctata (Fig. 8C) displays by far the greatest development of buccal floor dentition in Morone. The first hypobranchial has a large tooth plate on it, as does the second. Unlike other members of the genus, punctata also possesses small patches on the second basibranchial. There may be very small patches lateral to the second basibranchial in the epithelium. Whereas the large tooth patches of the first hypobranchial occur alone, the primary patch of the second has very small patches in association with it. Unlike other Morone species, these patches also occur toward the posterior edge of the dorsal hypobranchial surface. The third hypobranchial does not possess a large tooth patch of its own in punctata, but paired patches located at the rear of the third basibranchial overlap it slightly.

Anterior to this pair of tooth patches, at the rear of the third basibranchial, are located a much larger pair of tooth patches which are closer together and more firmly fused to the underlying bone. Very small tooth patches may occur on the third basibranchial and the third ceratobranchial.

Pharyngeal Teeth

Unlike the tooth formations of the mid-buccal cavity, the pharyngeal teeth of Morone (Fig. 8A) show very little intrageneric variation. Therefore, the following description applies to the entire taxon.

Woolcott (1957) believed that Morone has only three pharyngobranchials. He also noted that the first two ceratobranchials articulate with the first pharyngobranchial. Although the latter statement is correct, there is a small bone that articulates with the distal terminus of the first epibranchial that should be considered as the first of a four member pharyngobranchial series, inasmuch as Johnson (1980) stated that the first pharyngobranchial has been modified to a suspensory function in percoid fishes. The first pharyngobranchial has been illustrated as an edentulous element in Vari (1978:Fig. 1) for the Teraponidae and Smith (1971:Fig. 2) for the Epinephelinae, and this condition may be primitive in percoids.

The first epibranchial does not bear teeth in Morone. The second epibranchial does possess an elongated, triangular tooth patch on its medial surface near its junction with the second pharyngobranchial. This tooth patch is clearly dermal in nature. The second pharyngobranchial also bears a well developed tooth patch.

Epibranchial 3 has a tooth formation similar in size and position to that which occurs on epibranchial 2, but which is fused to the underlying element by means of a distinct bony cushion. This tooth patch is oriented somewhat more anteriorly than the second epibranchial tooth patch. I have observed a similar condition of free and fused tooth patches on epibranchials 2 and 3 respectively, in Centropomus and Lutjanus.

Both the third and fourth pharyngobranchials and the fifth ceratobranchial display well developed tooth pads, with the largest teeth found on each individual occurring on all three bones with the exception of the posterior portion of the fourth pharyngobranchial.

Vomerine Teeth

Woolcott (1957) provides illustrations of the vomerine teeth of all the species of Morone except punctata. These figures show the basic form of vomer and tooth patch in these species, but only as examples of fish of the size illustrated inasmuch as the vomerine tooth patch changes in a characteristic manner during ontogeny. Additionally, Woolcott's illustration of mississippiensis showed an unusually high number of tooth rows for that species.

In very young specimens of all Morone species, the anterior margin of the vomerine tooth patch takes a straight-edged v-shape. This normally has a limited number of tooth rows, fewer than in the adult of all species except mississippiensis. In larger fish, these patches are modified into forms unique for each species, while gaining additional tooth rows and becoming broader in all but the yellow bass.

Only in americana (Fig. 7C) and mississippiensis (Fig. 7D) do vomerine teeth maintain the pattern of evenly arranged rows in adult specimens. The average number of teeth across the broadest portion of the vomer has been compared in fish of different sizes of each species (Table 2).

Table 2.- Average number of teeth across broadest portion of vomer in *Morone*.

Standard length (mm)	No. of teeth	Catalog no. or location
Morone saxatilis		
15	1	AMNH 101233
24	2	AMNH 103770
59	2	Hudson River
89	2	Hudson River
228	2-3	AMNH 55916 SD
316	3-4	Long Island Sound
914	5-8	Montauk Point
~1180	11-16	AMNH 2256
Morone chrysops		
40	2	AMNH 20973
145	3-4	AMNH 22532
233	5-6	AMNH 21590 SD
240	6-7	AMNH 22504
Morone americana		
50	2	Hudson River
104	2	AMNH 1222
206	2-3	AMNH 56214 SD
Morone mississippiensis		
125	1	Lake Ray Hubbard,TX
141	1	AMNH 55618 SD
142	1	AMNH 3047
Morone labrax		
60	3-4	AMNH 36832
160	3-4	Morocco

Morone punctata

83	5-7	AMNH 43094
225	8-10	Dakar, Senegal
236	8-10	Dakar, Senegal

M. saxatilis and *chrysops* (Fig. 7E) share similar vomerine tooth patterns. Both may acquire some posteriorly oriented curvature with increasing size, while gaining additional teeth.

The vomerine tooth patches of *americana* and *mississippiensis* are the smallest for the genus and have the lowest number of teeth. As it matures, *americana* appears to acquire additional teeth in the form of loosely arranged rows. No adult *mississippiensis* examined in this study possessed more than a single row of teeth although these were not always arranged in an even line. These teeth were the largest of vomerine teeth in relation to body size among *Morone*.

The vomerine tooth patch of *labrax* is somewhat similar to those of *saxatilis* and *chrysops*. In the other Afro-European species, *punctata* (Fig. 7A), the vomerine tooth patch is autapomorphic with regard to the rest of the genus. Although the anterior end of the patch resembles the same region in *labrax*, *punctata* possesses a long posterior extension of the patch running along the vomer towards the parasphenoid. The diagnostically useful dental features of *Morone* presented in the above sections have been arranged in the form of a key (Table 3).

Table 3.- Dental Key to species of *Morone*.

Teeth or tooth plates present in soft tissue on lateral and anterior margins of tongue .... *Morone*

1A. Teeth present on basihyal 2

1B. Teeth not present on basihyal 5

2A. Paired basihyal tooth patches, or single patch at rear of basihyal extending less than one-half distance to basihyal tip 3

2B. Single oblong basihyal tooth patch extending anteriorly at least one-half distance to basihyal tip 4

3A. Basihyal teeth in two distinctly separated parallel patches, each basihyal patch more than one-half length of lateral tooth plates, teeth on anterior margin of tongue absent or present as few scattered teeth or small patches .... *Morone saxatilis*

3B. Basihyal teeth in two slightly separated or contiguous oval patches or as single rounded or heart-shaped patch, basihyal patch or patches one-half or less than length of lateral tooth plates, teeth on anterior margin of tongue in broad patches .... *Morone chrysops*

4A. Vomerine tooth patch crescentic, without posterior extension .... *Morone labrax*

4B. Vomerine tooth patch crescentic, with posterior extension .... *Morone punctata*

5A. Vomerine teeth in two or more rows, teeth on anterior margin of tongue in broad plates often extending posteriorly near basihyal tip ...... *Morone americana*

5B. Vomerine teeth in one row, teeth on anterior margin of tongue in broad plates restricted to marginal region .... *Morone mississippiensis*

NON-OSTEOLOGICAL CHARACTERS

Pigmentation

The pigmentation patterns of *Morone* provide two synapomorphies. The most primitive pigmentation state is found in *labrax* in which adults have no secondary markings superimposed on their primary coloration. *M. punctata* has moderately sized but well separated spots that extend from its dorsal margin to about 5-6 scale rows below the lateral line.

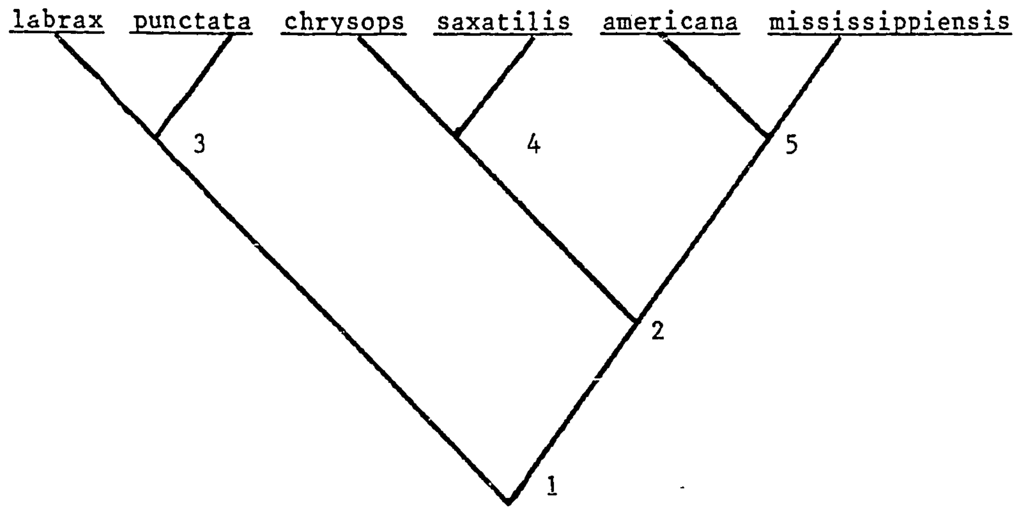
The four North American species display horizontal stripes, an apparently derived condition for the genus. It is also possible, however, that stripes are primitive for the genus, and that they have been secondarily lost or modified in the Afro-European species, but horizontal stripes are not known in juvenile *labrax*. *M. chrysops* and *saxatilis* have simple patterns, usually with approximately seven horizontal stripes that may on occasion be randomly broken or interrupted. *M. mississippiensis* has simple horizontal stripes above the lateral line, but shows a more modified pattern below it. Typically in the yellow bass, the three ventral-most stripes are strikingly displaced downward one-half the distance between stripes, in the area above the anal spines.

The coloration of *americana* resembles that of *labrax*, but faint stripes are frequently visible, indicating that a striping pattern has been secondarily lost. I collected a series of the more prominently striped *americana* specimens from the Hudson River to determine if they displayed a simple, or a modified pattern. Most specimens showed a displaced pattern closely resembling the *mississippiensis* condition, a synapomorphy between these species.

M. labrax and punctata share a pigmentation feature not found in other members of Morone - a strong dorsal spot on the opercle. This is not apomorphic, however; an opercular spot is common among percoids, particularly in juveniles. Secondary development of this feature has occurred though, in the lepomines.

MORONE INTRARELATIONSHIPS

Figure 1.--Interrelationships of Morone species.



Characters

1. anterior and lateral lingual tooth patches or plates.
2. longitudinal stripes; serrate ventral preopercular border.
3. anteriorly elongated basihyal tooth patch; spotted pigmentation pattern.
4. paired basihyal tooth patches; serrate posterior maxillary margin; subocular shelf with slight posterior process.
5. basihyal tooth patch absent; reduced vomerine tooth patch; inflated otic region with straight otic sutures; inflated cephalic sensory canals; strongly arched vertebral column; 9th or 10th interneural space lacking dorsal pterygiophore infiltration; expanded anal spines; ventral longitudinal stripes displaced.

SYSTEMATIC ACCOUNTS

MORONIDAE Jordan 1923

Diagnosis.-- Monogeneric family of percoid fishes distinguished by the following synapomorphies: distal tooth plates or patches lateral and anterior to the basihyal.

Description.-- Oblong to ovate fishes, slightly to moderately compressed; scales moderate, ctenoid; lateral line continuous, extending onto caudal fin one-third to entire with accessory lateral lines three scale rows above and two below this scale row on caudal fin.

Head moderate (3-3.5 in SL); scales on cheek, preopercle, subopercle, opercle, nape, and maxillary; snout moderate with lachrymal overlapping maxillary slightly; supramaxilla lacking; subocular shelf present; epioccipital process elongated; posterior preopercle border serrate, ventral border serrate or with large, antrorse spines; opercle with two spines, lower more pronounced; posttemporal, supracleithrum and cleithrum visible, under covering of skin.

Mouth moderate to large; gape slightly to moderately oblique, upper jaw protractile; jaws equal or lower projecting; teeth villiform, on dentary, premaxilla, vomer, palatines, and tongue; paired nares separated. Dorsal fins barely separate or slightly joined; first dorsal with 8 or 9 spines; second with 1 spine, 9-14 rays; first dorsal spine short, 3rd through 5th longest; three predorsals. Anal fin with three spines, 8-12 rays; first anal spine short, 2nd or 3rd longest.

Caudal emarginate, with 17 principal rays, 15 branched; epaxial rays 10-14, hypaxial rays 7-13; pectoral fin asymmetrical, 16 rays; pelvic fin I-5.

Vertebrae 25 (rarely 24); precaudal vertebrae 12-13, caudal 12-13; pleural ribs on first 11-12 vertebrae; epipleurals on first seven pleural ribs; caudal fin with three epurals, two uroneurals, six hypurals; procurrent spur.

Moderate to large fishes, maximum size from 2 to 60 kg. Native to central and eastern North America, western Europe, Mediterranean and Black seas, and northwest Africa.

Genus Morone Mitchill 1814

[A generic synonomy is presented in Whitehead and Wheeler (1966)]

Etymology Morone = origin unknown Gender = F

Type species = americana

Subgenus Dicentrarchus (Gill 1860)

Etymology Dicentrarchus = possessing two anal spines Gender = M

Diagnosis.-- Distinguished from other moronids by single, oblong basihyal tooth patch longer than one-half length of basihyal; lower margin of preopercle with large antrorse spines; dusky patch on opercle; flanks spotted in juveniles.

Description.-- Dorsal fins separate; anal spines graduated; anal rays 10-12; ventral margin of preopercle serrate; cephalic sensory canals moderate; otic region moderately inflated.

Morone (Dicentrarchus) labrax (Linnaeus 1758)

Etymology labrax = gluttonous

Type - BMNH no. 1853.11.12.1.

Nomenclature
Perca labrax Linnaeus 1758:X, 290.
Sciaena labrax Bloch 1792:IV, 52.
Sciaena diacantha Bloch 1792:III, 58.
Perca diacantha Bloch 1801:85.
Centropomus lupus Lacepede 1802:IV, 267.
Perca elongata Geoffroy Saint-Hilaire 1817:pl.19, f.1, Egypt.
Labrax lupus Cuvier 1828:II, 56, pl.2.
Labrax elongatus Cuvier 1828:II, 77.
Labrax diacanthus Gill 1860:110.
Labrax linnei Malm 1877:379.
Dicentrarchus labrax Jordan and Eigenmann 1890:425.
Roccus labrax Smitt 1893:I, 45 Scandinavia.
Morone labrax Boulenger 1895:I, 130.
Dicentrarchus lupus Fowler 1936:II, 742, Italy.

Diagnosis.-- Distinguished from punctata by absence of posterior extension of vomerine tooth patch; absence of spots other than opercular spot in adults.

Description.-- Body elongately ovoid; caudal slightly compressed; back not arched; mouth large, oblique, mandible even or slightly protruded; scales 66-74, approximately 10 pored lateral line scales on caudal fin, 12 on supplementary caudal lateral lines; back and upper surface brown or olivaceous, sides and belly silvery white; juveniles with numerous round dusky spots over upper 2/3 of body.

Distribution.-- Atlantic from Norway to Morocco, Canary Islands, Mediterranean, Adriatic, Black Sea.

<u>Morone</u> (<u>Dicentrarchus</u>) <u>punctata</u> (Bloch 1792)

Etymology <u>punctata</u> = dotted.

Type - lost in ZMHU

Nomenclature
<u>Sciaena punctata</u> Bloch 1792:VI, 64, Mediterranean Sea.
<u>Perca punctulata</u> Lacepede 1802:IV, 418.
<u>Perca punctata</u> Geoffroy Saint-Hilaire 1817:pl. 20, f. 2, Egypt.
<u>Bodianus punctatus</u> Bowdich 1825:236.
<u>Dicentrarchus elongatus</u> Gill 1860:111.
<u>Labrax punctatus</u> Gunther 1863:175, Gibraltar.
<u>Labrax orientalis</u> Gunther 1863:175, Alexandria.
<u>Labrax schoenleinii</u> Peters 1865:95.
<u>Dicentrarchus orientalis</u> Jordan and Eigenmann 1890:425.
<u>Dicentrarchus punctatus</u> Jordan and Eigenmann 1890:426.
<u>Morone punctata</u> Boulenger 1895:131, Portugal; Gibraltar; Alexandria.

Diagnosis.-- Distinguished from <u>labrax</u> by posterior extension of vomerine tooth patch; presence of spots in adults.

Description.-- Body elongately ovoid; caudal slightly compressed; mouth large, oblique, lower jaw even or slightly protruding; scales 60-65, approximately 40 pored lateral line scales on caudal fin, approximately 45-50 on supplementary lateral lines; color olivaceous with round black spots not disappearing with age.

Distribution.-- Atlantic from English Channel to Senegal, southern Mediterranean.

Subgenus <u>Roccus</u> Mitchill 1814

Etymology <u>Roccus</u> = latinization of rock or rockfish Gender = M

Diagnosis.-- Moronids with teeth present on base of tongue as paired patches or as single, rounded patch less than one-half length of basihyal, maxillary serrulate.

Description.-- Dorsal fins separate; anal spines graduated; anal rays 11-13; lower jaw projecting; preopercle and posterior maxillary margin serrate; cephalic sensory canal pores small; otic region slightly inflated; subocular shelf with distinct postero-medial process; vertebrae 12+13; seven or more continous or interrupted but not displaced longitudinal stripes.

Morone (_Roccus_) _chrysops_ (Rafinesque 1820)

Etymology _chrysops_ = golden eye.

Type Locality - Falls of Ohio

Nomenclature
Perca chrysops Rafinesque 1820:22, Ohio (type locality).
Lepibema chrysops Rafinesque 1820:23, Ohio.
Labrax multilineatus Cuvier 1830:488 Wabash River.
Labrax notatus Richardson 1836:III, 8, New York.
Labrax albidus DeKay 1842:13, New York.
Labrax osculati Filippi 1853:V, 1, L. Ontario.
Labrax chrysops Gill 1860:20.
Roccus chrysops Gill 1860:113 Racine; Toronto; southern Illinois.
Morone multilineata Boulenger 1895:128.

Diagnosis.-- Distinguished from _saxatilis_ by short basihyal tooth patch or patches one-half or less than length of lateral tooth plates; well-developed anterior tooth patches.

Description.-- Body deep and compressed, depth more than one-third standard length; back considerably arched; head subconical, slightly depressed at nape; mouth moderate, lower jaw somewhat projecting; scales 52-60, approximately 40 pored lateral line scales extending onto caudal fin in adults, 30-35 on supplementary lateral lines; color silvery, golden tinge below.

Distribution.-- Native to central North America.

Morone (Roccus) saxatilis (Walbaum 1792)

Etymology saxatilis = living among rocks.

Type Locality - New York

Nomenclature

Perca saxatilis Walbaum 1792:33, New York (type locality).
Sciaena lineata Bloch 1792:vi, 62, pl. 304
Perca septentrionalis Bloch and Schneider 1801:90, New York.
Centropomus lineatus Lacepede 1802:257.
Roccus striatus Mitchill 1814:25, New York.
Perca mitchilli Mitchill 1815:413, pl.3, f.4, New York.
Perca mitchilli interupta Mitchill 1815:415.
Perca mitchilli alternata Mitchill 1815:415.
Lepibema mitchilli Rafinesque 1820:23.
Labrax lineatus Cuvier 1828:79-83.
Roccus lineatus Gill 1860:112.
Lepibema lineatum Steindachner 1862:504.
Roccus saxatilis Jordan and Gilbert 1882:599.
Roccus septentrionalis Jordan 1886:72.
Morone lineata Jordan and Eigenmann 1887:295.

Diagnosis.-- Distinguished from chrysops by presence of two well-separated tooth patches on basihyal longer than one-half length of lateral tooth plates, and by relatively undeveloped anterior tooth patches.

Description.-- Body rather elongated, little compressed, depth one-third length; back little arched; head subconical; mouth large, oblique, lower jaw extending; scales 58-64, approximately 25 pored lateral line scales on caudal fin, 25-30 on supplementary lateral lines; color olivaceous, sivery, sides paler, chin sometimes bluish or rosy.

Distribution.-- Originally found on east and Gulf coasts of North America. Widely introduced.

Subgenus Morone Mitchill 1814

Diagnosis.-- Moronid fishes lacking teeth on basihyal; dorsal pterygiophore lacking between 9th or 10th neural gap, vomerine tooth patch narrow in adults.

Description.-- Dorsal fins slightly joined at base; dorsal and anal spines very robust; 2nd anal spine as long or longer than 3rd; anal rays 8-10; jaws approximately equal; preopercle serrate; cephalic sensory canal pores large; otic region greatly inflated; vertebrae 12+13; longitudinal stripes when visible displaced dorsally on ventral flanks above anal spines.

Morone (Morone) americana (Gmelin 1788)

Etymology americana = American.

Type Locality - New York

Nomenclature
Perca americana Gmelin 1788:1308, New York (type locality).
Perca immaculata Walbaum 1792:330.
Perca americanus Bloch 1801:88, New York.
Morone pallida Mitchill 1814:17, New York.
Morone rufa Mitchill 1814:18, New York.
Centropomus albus Rafinesque 1814:19.
Bodianus pallidus Mitchill 1815:420, New York.
Bodianus rufus Mitchill 1815:420.
Perca mucronata Rafinesque 1818:204.
Labrax mucronatus Cuvier 1828:86, Massachusetts.
Labrax rufus DeKay 1842:9, New York.
Labrax pallidus DeKay 1842:11, New York.
Labrax nigricans DeKay 1842:12, New York.
Labrax americanus Holbrook 1855?:21, South Carolina.
Morone americana Gill 1860:116.
Lepibema americanus Steindachner 1862:504.
Roccus americanus Jordan and Gilbert 1883:530.

Diagnosis.-- Distinguished from _mississippiensis_ by vomerine tooth patch with two or more tooth rows.

Description.-- Body oblong-ovate; back elevated; mouth small, lower jaw even or slightly protruding; scales 46-51, approximately 10 pored lateral line scales extending onto caudal fin, 15-20 on supplementary lateral lines; color olivaceous, varying from from greenish black, to brassy or silvery, faint stripes on flanks.

Distribution.-- Atlantic coast North America.

Morone (_Morone_) _mississippiensis_ Jordan and Eigenmann 1887

Etymology _mississippiensis_ = pertaining to the Mississippi.

Type Localities - St. Louis, New Orleans

Nomenclature

Labrax chrysops Girard (non-Rafinesque) 1859:29, St. Louis; New Orleans.
Lepibema interruptum Steindachner 1862:504.
Roccus interruptus Jordan and Gilbert 1882:530.
Morone mississippiensis Jordan and Eigenmann 1887:295.

Diagnosis.-- Distinguished from _americana_ by vomerine tooth patch with less than two tooth rows.

Description.-- Body oblong-ovate; back arched; snout somewhat pointed; mouth small, somewhat oblique, lower jaw even or slightly protruding; scales 49-51, approximately 12 lateral line scales on caudal fin, 15-20 on supplementary lateral lines; color yellowish to brassy.

Distribution.-- Central North America.

BIOGEOGRAPHY AND DISTRIBUTION

There are two alternative approaches to historical biogeographical analysis - the vicariance method (Platnick and Nelson 1978), and the panbiogeographic method (Croizat 1964). Vicariance biogeography does not necessarily imply that vicariance is the causative distributional process, but instead recognizes repeated spatial pattern to be indicative of a shared process having governed the distribution of those groups. Biogeographic pattern is analyzed by first erecting cladograms, then constructing area cladograms by including each taxon's distribution, and then restricting the branching diagram to endemic taxa. The cladogram may then be compared to cladograms of other taxa from the same geographic areas. Repetition of pattern becomes increasingly statistically unlikely, indicating non-randomness for that distributional pattern. Finally, corroborated pattern may be correlated to known geological history.

The interrelationships of *Morone* suggest two area relationships: 1) that central and eastern North America are more closely related to each other than either is to Europe and northwestern Africa, and 2) that Europe and northwestern Africa show a greater affinity towards each other than either does to North America. In an attempt to better understand the area relationships of North America through its ichthyofauna, Patterson (1981) analyzed existing cladograms using the vicariance method. Although cladistic information on a large number of piscine taxa were reviewed, only one group, *Umbra* (Nelson 1972), showed area relationships equivalent to *Morone*. Patterson considered the ranges of the two American *Umbra* species to be eastern North America, but it is clear that *U. limi*, restricted to the Mississippi

River and Great Lakes systems (Lee et al., 1980), has what could be considered a central North American distribution. U. pygmaea is native to the Atlantic coastal plain. The two species are more closely related to each other than to the European species U. krameri (Nelson 1972), a pattern consistent with that seen in Morone.

The biotic relationship between Europe and North America coincides with the known geologic history of these areas. As recognized by Patterson (1981), during the Cretaceous the two continents were diverging from each other but remained linked via Greenland, which remained temperate until the Eocene and possibly the Miocene.

Panbiogeography is a method involving the analysis of tracks between ranges of closely related taxa. This approach is based on the premise that the earth and its biota evolved together, and consequently, that all extant taxa are the products of evolution in concert with vicariant processes over time. The panbiogeographic method unites species or groups by means of graphically illustrated tracks with the aim of identification of repeated pattern. Unlike vicariance biogeography, panbiogeography deals with both endemic and widespread taxa. The area relationships implied by the phylogenetic intrarelationships of Morone show complete concordance with Croizat's (1964) tracks (Fig. 3D). Major taxic disjunctions appear to have occurred between Europe and northern Africa; Europe and eastern North America; and eastern and central North America, results that are largely consistent with the vicariance approach. Therefore, it appears that moronid distributions were not the product of random dispersal, but were instead influenced by geological processes that also governed the distributions of other taxa.

Additional information may be obtained from moronid distributions if an allopatric speciation model is assumed. Nelson and Platnick (1981), among others, recognized that whereas higher taxonomic categories frequently show sympatric distributions, closely related species normally do not. Patterson (1981) stated that if speciation is allopatric, then sympatry is evidence of secondary dispersal. Of the native ranges of the two American species pairs, one shows complete allopatry and the other, a zone of secondary contact.

M. americana and *mississippiensis* have remained completely isolated from each other (Fig. 3B). The pattern of sister species or close relationship between lowland taxa occurring in the Mississippi Valley and the Atlantic coastal plain is a common one, and can be seen in esocids, ictalurids, percids, and centrarchids. However, that the representative east of the Appalachians should be predominantly estuarine rather than lacustrine is unusual.

M. chrysops and *saxatilis* (Fig. 3A) occurred together in the lower Mississippi River system westward along the Gulf coast to near the Mexican border. Although sympatric in this region, the two species may have been spatially or ecologically segregated within these river systems. Both species also occur in the St. Lawrence River, but the presence of *chrysops* there appears to be a recent phenomenon there (Scott and Crossman 1973).

M. labrax and *punctata* (Fig. 3C) are broadly sympatric over the Mediterranean and the coasts of Iberia and northwest Africa. If we accept the geologically well-supported theory that the Mediterranean became isolated and either largely or completely evaporated during the late Miocene, and then reopened to the Atlantic in the early Pliocene

(Ruggieri 1967), secondary dispersal of one or both species would account for the their present distribution.

Phylogeny provides a contextual framework in which to analyze biogeography. The importance of a resolved cladogram as a biogeographical tool is particularly important for taxa that occur in a full range of alternative habitats, thereby permitting polarization of habitudinal transformations among taxa. Within *Morone*, *labrax* spawns at sea with juveniles entering estuaries and ascending the lower reaches of rivers before they take up a coastal existence as adults (Russell 1935; Kennedy and Fitzmaurice 1972; Holden and Williams 1974). Although not nearly as well documented, *punctata* appears to exhibit a similar life cycle (Smith 1981).

Among the American species, *saxatilis* also leads an essentially coastal existence, although populations at the extremes of its range may be largely to completely riverine. Unlike *labrax* and *punctata*, however, the striped bass spawns in rivers with adjacent estuaries serving as nursery grounds (Raney 1952). Largely sympatric with *saxatilis*, *americana* also spawns in fresh or slightly brackish water but it tends to complete its life cycle within estuaries (Mansueti 1964). The two central North American species are restricted to freshwaters. *M. chrysops* and *mississippiensis* are both lentic species that normally ascend feeder streams for spawning purposes. Given the phylogenetic relationships outlined in Fig. 1, a general transformation from a largely marine life cycle, to intermediate estuarine stages, to completion of the life cycle in freshwater is suggested for *Morone*.

Additional evidence for a marine to freshwater polarization was presented in the analysis of kidney structure by Beitch (1963) of two moronids. Beitch noted that purely marine teleosts lack or have poorly developed glomeruli and no distal segments in their kidneys and that euryhaline forms generally possess well developed glomeruli and distal segments. Beitch found that both *americana* and *saxatilis* have fully developed glomeruli but only proximal tubules, and he interpreted this as evidence of marine ancestry. Additionally, Beitch noted that in *americana*, a species that tends to inhabit waters of lower salinities than *saxatilis*, the glomeruli averaged about 20% larger than in the latter species, except for landlocked populations of *saxatilis* in which the glomeruli were about the same size as in *americana*.

On the Atlantic coast, the native range of *saxatilis* extended from the St. Lawrence River estuary (Scott and Crossman 1973) to Lake Washington in the St. Johns River system in Florida (Barkuloo 1970). Riverine populations from South Carolina southward appear to be nonmigratory. Striped bass stocks from North Carolina to the Hudson River, New York tend to make extensive northward movements in spring with many of the fish returning in autumn (Merriman 1941). Striped bass from north of the Hudson River to the Canadian Maritimes appear to be a mixture of southern migrants and local resident stocks. Based on meristic evidence, Lewis (1957) cited Raney's belief that stocks in Nova Scotia, New Brunswick and the St. Lawrence River were semi-endemic but had been drawn from post-Pleistocene northward movements of the Chesapeake population.

M. saxatilis is the only moronid which showed a significant disjunction in its native range, with Gulf and Atlantic coast populations separated by the major portion of the Floridian penninsula. Given the distribution of the sister taxon of the American moronids on the European coast, and the restriction of *americana* to the western Atlantic, it seems probable that *saxatilis* also was native to the Atlantic coast. Less clear, however, is its presence in the Gulf of Mexico. Two possibilities exist: 1) that the striped bass had a continuous range from the North Atlantic to the western Gulf which became interrupted by the emergence of the Floridian penninsula and the closing of the Straits of Florida (McLane 1958); or 2) that its presence in the Gulf was due to dispersal either around the penninsula or through the Florida straits. The minor meristic divergence between the two disjunctive stocks indicates recency for the separation by whatever means. That the striped bass is the only *Morone* species to achieve such a wide distribution may be related to its strongly migratory character. In contrast, *americana* and *mississippiensis* do not approach any overlap in their natural ranges and appear to be the least migratory of moronids.

Various western limits of the native range of *saxatilis* in waters bordering the Gulf of Mexico have been reported. Bean (1884) noted their occurrence in the Alabama River near Montgomery, Alabama, and the Tangipahoa River (which also enters Louisiana) near Osyka, Mississippi. McIlwain (1968) documented the fish's distribution in Mississippi waters in all major river systems from the Pascagoula River west to the Tangipahoa. In Louisiana, Pearson (1938) noted their occurrence in the Tchefuncta River, and Raney (1952) reported an endemic population in the Tickfauw River.

In a review of striped bass distribution in southeast and Gulf states, McIlwain (1980) stated that historically they occurred as far west along the Gulf coast as Lake Ponchartrain, Louisiana. There was no indication that saxatilis might have ranged farther westward until Matlock, Hysmith, and Colura (1984), in a report on recent stocking efforts in Texas bays and estuaries, noted that there had been catch records of striped bass from Texas in the late 1800's (Collins 1892; Townsend 1900) and early 1930's (Fieldler 1936). In reviewing the studies cited by Matlock, Hysmith, and Colura (1984), it became clear that a species called striped bass had been taken in quantities approaching 10,000 lbs. yearly by seining in the brackish waters of the Texas coast as far west as about Corpus Christi, approximately 28°N latitude. Positive identification that these fish were indeed saxatilis is provided by Stevenson (1893). In his review of Texas coast fisheries, Stevenson described methods and locations of brackish water fisheries, but only discussed the two or three most important species landed at each port. However, Stevenson also provided plates of the Texas coastal species he observed which included an illustration of saxatilis (Plate 18), referred to as "Roccus lineatus - striped bass or rockfish."

Therefore, it appears that striped bass had a much broader native range along the coast of the Gulf of Mexico than has been realized, as much as 500 miles farther west than the previously reported extreme western limit of Louisiana. Although Gulf coast populations have decreased significantly in general (McIlwain 1980), striped bass in Texas waters appear to have been eliminated completely sometime in the 1930's. An hypothesis worthy of further analysis is that decreased flow conditions in Texas coastal rivers during the 1930's, a period of unusually arid climatological conditions in that region which was responsible for the creation of the "dust bowl", was a contributing factor to the demise of striped bass in Texas waters. Recolonization may not have occurred because of the absence of coastal migration of Gulf stocks (McIlwain 1980).

M. saxatilis was introduced to the Pacific coast in San Fransisco Bay in 1879 and 1882 (Pearson 1938). Within 20 years of the initial plantings, striped bass had extended their range to Oregon, and a few years later to the Columbia River (Forrester, Peden, and Wilson 1972). Individuals have been captured as far north as Barkley Sound, British Columbia (Forrester, Peden and Wilson 1972), and as far south as Ensenada, Mexico (Setzler et al. 1980).

Since it has been recognized that saxatilis can prosper in large freshwater reservoirs, the fish has been widely introduced across the United States (Axon and Whitehurst 1985). Striped bass also have been introduced into the U.S.S.R., France, and Portugal (Setzler et al. 1980).

The natural range of the chrysops is central North America from Gulf drainages to the Great Lakes system. Bailey and Smith (1981) postulated a Mississippian refugium for chrysops during the Pleistocene, with dispersal into the Great Lakes through an interconnection approximately 1400 yrs. bp, prior to the shift of the Great Lakes to an entirely Atlantic drainage. Preglacial remains of chrysops have been discovered, a part of the Sand Draw fauna of western Nebraska, somewhat west of what is understood to be their recent natural range (Smith and Lundberg 1972).

The native distribution of americana is the Atlantic coast from New

Brunswick and Prince Edward Island to South Carolina (Scott and Crossman 1973). Although the species occurs on the Atlantic coastal plain in both naturally landlocked and introduced populations, (Scott and Crossman 1973), it has not been introduced west of the Appalachians with the exception of Nebraska (Hergenrader and Bliss 1971). However, the white perch has successfully invaded the Great Lakes via the Hudson-Mohawk and Erie Barge Canal systems, and is now found as far west as Saginaw Bay in Lake Michigan and as far east as the St. Lawrence River. The sequence of its colonization has been chronicled by Larsen (1954), Scott and Christie (1963), Busch, Davies, and Nepszy (1977), and Boileau (1985).

M. mississippiensis is endemic to the central United States. Greene (1935) stated that the native range of the yellow bass was restricted to the Mississippi River and its tributaries extending from southern portions of Wisconsin and Minnesota through Louisiana and eastern Texas. Clay (1975) found that this range included the lower Tennessee River, but Stroud (1947) believed the species to be absent from its tributaries and upstream reaches. Starnes, McDonough and Colwell (1982) documented the range expansion of mississippiensis upstream through the Tennessee Valley Authority reservoir system.

To summarize, the available evidence indicates that the American and Old World moronids diverged along with the separation of the Laurasian landmasses. It is not clear what may have spurred speciation in the eastern forms, but the distributional overlap and complex geological history of the Mediterranean suggest that it may have occurred in that region.

The two American species pairs show roughly sympatric distributions between the sister species of each pair, but largely allopatric distributions within the pairs, suggesting that both species pairs responded to similar geological pertubations. However, with evidence in favor of a marine ancestry for these fishes, it seems likely that the central North American freshwater forms diverged from coastal ancestors. It is not clear whether their initial presence in the Mississippi Valley was the result of penetration from the sea or adaptation to freshwater conditions as an inland marine embayment receded. The largely sympatric freshwater sciaenid, *Aplodinotus grunniens*, may have evolved in a similar fashion.

SECTION II.

THE LOWER PERCOIDS

OVERVIEW OF HISTORICAL CLASSIFICATIONS OF LOWER PERCOIDS

Two primary problems have remained unsolved with regard to the lower percoids: 1) what are the relationships of the taxa included in its most primitive family (the Serranidae prior to 1966, the Percichthyidae since then), and 2) what are the relationships among their families? Which percoid taxa should be considered as "lower" is debatable, but the groups discussed by Gosline (1966) serve as a reasonable core. According to Gosline, they consist of his expanded Percichthyidae in addition to the Centropomidae, Percidae, Kuhliidae, Centrarchidae, Scorpididae, Apogonidae, and his restricted Serranidae. The conclusion he reached was that none of the aforementioned taxa share any unique features with the percichthyids, but that the serranids were probably closely related on the basis of a common lack of derived characters.

Gosline was not able to employ any synapomorphic characters to define the Percichthyidae and could only provide a diagnosis that served to distinguish them from other percoid fishes. Given his rationale for a restriction of the Serranidae, mainly the presence of a third opercular spine ventral to the longer central spine, a character that seems firmly apomorphic to the percichthyids, Gosline concluded that "...the serranids are either more specialized or that they and the percichthyids have both evolved in different directions from a proto-percoid ancestor". Although this statement suggests sister group status, neither Gosline nor anyone else has provided evidence for this relationship.

Gosline's revision, although a gross manipulation, did serve to redefine the first problem by substantially lowering the number of species left unresolved at the very base of the percoid lineage, with the removal of the members of the speciose and now relatively well-defined Serranidae. This left a considerably smaller "wastebasket" group, the Percichthyidae, that were united on the basis of a common lack of specializations that would permit elevation to higher taxa. The problem has received some attention since that 1966. Gosline (1966) had placed the monotypic genus *Niphon* in the Percichthyidae because it possessed two opercular spines, even though he noted that it exhibited certain serranid affinities, but Rivas and Cook (1968) after a phenetic analysis placed this fish among the Centropomidae. Greenwood (1977) strongly criticized the latter study and suggested *Niphon* be left in the Percichthyidae pending further analysis. More recently, Johnson (1983), in addition to providing further evidence for serranid monophyly, showed that *Niphon* is a serranid and most likely the sister group to the Epinephelinae.

MacDonald (1978) examined morphologic and protein variation among six Australian percichthyid species. He found that three genera, *Plectroplites*, *Percalates*, and *Macquaria* form a monophyletic group and he assigned all of them to *Macquaria*. A fourth genus, *Maccullochella*, although left a percichthyid by MacDonald, was found to share a number of character states with the serranids. Johnson (1984) later redefined the Percichthyidae by a series of nested hierarchies in which *Morone*, *Lateolabrax*, and *Siniperca* were left *incertae sedis*.

I examined a large number of lower percoid taxa in search of phylogenetic relationships among them. Two approaches were taken. First, characters that had received description and analysis prior to this study were surveyed for cladistic information. Examples include the configuration of the ceratohyal (Gosline 1966; McAllister 1968) and the procurrent spur (Johnson 1975). In many of these instances, I examined these characters in additional taxa not included in the original study. Second, characters that have received little or no attention were surveyed , including such examples as the lateral ethmoid-lachrymal articulation and ventral surficial features of the basihyal.

Many of the notes I provided on the expression and distribution of characters did not yield information of immediate value in the development of hypotheses of phylogenetic relationship, but nevertheless, were included to expand the data base for future studies on these fishes. The distributions of several of the characters examined: caudal lateral line extensions, the procurrent spur, and cycloid scales, were found to show a significant degree of correlation to each other, and a hypothesis of function is proposed to explain the correlation.

Certain characters did suggest probable relationships among lower percoids, primarily for the three taxa left _incertae sedis_ from the Percichthyidae by Johnson (1984): _Morone_, _Lateolabrax_, and _Siniperca_. _Mioplosus_, a fossil genus from the Eocene was also examined because it was observed by Cope (1877) to resemble the striped bass, but was classified as a percid by Jordan (1923) and Grande (1980). My analysis does not support either moronid or percid affinities for _Mioplosus_. Several suggestions are offered for directions in future research on phylogenetic relationships among the lower percoids.

Epioccipital Process

Katayama (1959:Figure 16) noted and illustrated the prominent epioccipital processes of Lateolabrax japonicus (Fig. 9C). Among lower percoids, a similar process occurs in all members of Morone (Fig. 9A), and in primitive percids (well developed in Stizostedion (Fig. 9B), reduced in Perca).

An extended epioccipital process of this type is normally very thin and fimbriated around its posterior margin, and is directed somewhat inwards. It appears to function as the attachment site for a large muscle bundle of the first myomere. These fibers originate at the medial septum in the region of the predorsals and first neural spine.

Probably homologous epioccipital processes occur in the Sciaenidae, although they are sometimes modified in more apomorphic genera. The epioccipital process of Cynoscion is long and fairly broad in comparison with other sciaenids. They are strand-like in both Otolithes and Micropogon, long in the former and somewhat shorter in the latter.

Epioccipital processes that are most likely non-homologous to the moronid type are found in at least two other taxa. A mullid, Mullus, has a pair of epioccipital processes that are narrow proximal to the neurocranium, but then broaden considerably into a spatulate shape with a fimbriated rear margin. Sphyraenids possess extremely elongated, multi-filamented epioccipital processes. They differ from the aforementioned taxa in that the processes take an almost vertical orientation.

Second Neural Expansion

In his review of the Centropomidae, Greenwood (1976) found a markedly antero-posteriorly expanded second vertebral spine to be a synapomorphy of the family. The degree of anterior expansion of the second neural varies among the genera (Greenwood 1976:Figure 25). In *Centropomus* (Fig. 10A), it completely envelops the posterior margin of the first neural. There is less contact between these elements in *Lates* and *Luciolates*, and articulation occurs primarily between the ventral and central regions of each spine. *Psammoperca* (Fig. 10B) shows the least association with the first neural contacting but not inserting inside the second.

The inflated second neural of the Centropomidae appears to be part of a suite of modifications that reinforce the anterior axial skeleton and posterior neurocranium. The medial plane above the vertebral centra in centropomids is infiltrated by an unusually tough, somewhat ligamentous, vertical skeletaginous septum. Osteological expansions and translocations appear to serve as points of attachment for local intensifications of these ligaments. Expansion of the base of the third neural anteriorly serves as the origin for attachment to the long, first dorsal pterygiophore that inserts in front of it. The anterior blade of the first pterygiophore is unusually long anteriorly. This same pterygiophore is joined anteriorly by a ligamentous sheet emanating from the inflated second neural. The second neural is bound to the first neural by ligament, and in most centropomid taxa, by direct articulation. The first and second neurals are supported anteriorly by ligamentous tissue from the supraoccipital. The predorsals are also embedded within the general ligamentous sheet.

In a review of latine osteology, Greenwood (1976) did not illustrate or discuss the fourth neural spine. However, it too, is modified in Lates. The anterior margin of the fourth neural is deeply grooved, presumably to provide additional reinforcement of the third dorsal pterygiophore that inserts in front of it. The third dorsal pterygiophore is closely associated with the second, the pair inserting as a single unit into the gap between the third and fourth neurals. It seems, therefore, that an inflated second neural, while perhaps the most obvious and noteworthy specialization, is only part of a complex of structural modifications that reinforce this region.

Although parallel, unmodified vertebra are almost certainly plesiomorphic for percoids, many taxa exhibit slightly expanded second neurals. In most instances, these do not appear homologous with the centropomid condition. For example, a sciaenid, Otolithes, has a well developed, anteriorly inflated second neural that overlaps the first neural. Both the first and second neurals are tilted somewhat forward, leaving a large gap between the second and third neural elements. Otolithes also retains extended epioccipital processes. All of these specializations provide reinforcement to the pectoral region, however,the neural modifications are convergent to the centropomid condition, and appear in Otolithes to be apomorphic for sciaenids.

An homologous condition to the centropomid state does exist in Siniperca (Fig. 11). This genus possesses a virtually identical arrangement of dorsal pterygiophores, predorsals, and neural spines, together with similar osteological expansions and translocations as in Lates. The degree of second neural expansion is not extreme in Siniperca, approximating the condition in Psammoperca.

Suspensorium

Johnson (1980) discussed the morphology of the percoid suspensorium and concluded that it might be of considerable value in delineating relationships within the Percoidei. The results of the present investigation support Johnson's view.

Examination of the preopercle revealed two systematically significant features at the basal percoid level: the nature of its sensory canal and the configuration of the ventral margin of the horizontal limb. Two gross conditions of the preoperculomandibular sensory canal occur as it passes through the preopercle, either an "open gutter" type, or an enclosed canal. In most percoid taxa, however, the condition is at least somewhat intermediate between these.

The degree of exposure of the preopercular canal tends to be quite stable at the family level in these fishes. The centropomids , however, are an exception. In _Centropomus_, the canal is open with a wide gap between the flange of the preopercular ridge and its medial portion on the ventral arm, and it gradually narrows and closes along its ascending arm. In _Psammoperca_ and _Lates_ (Fig. 12E), however, the preopercular canal is enclosed by a dense bony layer. Greenwood (1976) interpreted the open canal condition of _Centropomus_ as autapomorphic in relation to the other members of the family. Accepting his placement of _Centropomus_ as the primitive sister group to the Latinae, the implication must be that he considered an open canal to be a derived condition, and that an enclosed canal is plesiomorphic for the Centropomidae.

Greenwood's (1976) polarization of the degree of exposure of the preopercular sensory canal is contrary to my observations. Gadiiforms and beryciforms possess open or largely open canals. When a transformation occurs within percoid taxa, it appears to be toward the enclosure of the canal. For example, within the Serranidae (sensu Gosline 1966), primitive genera such as *Centropristis* and *Serranus* possess semi-exposed canals, whereas apomorphic forms like *Epinephelus* and *Cephalopholis* display closed canals with only small pores to facilitate sensory function. Ontogenetically, in taxa with open canals such as *Morone*, the preopercle in postlarval specimens as small as 15 mm shows the open condition.

Most lower percoids display open or predominantly open preopercular sensory canals. Such taxa type: *Morone* (Figs. 12A,B), and the Percichthyidae (sensu Johnson 1984), Percidae, *Lateolabrax*, *Kuhlia*, Sciaenidae, Centrarchidae, and Lutjanidae. Fishes with an enclosed preopercular canal include: Latinae, *Siniperca*, *Coreoperca*, Polyprioninae, *Niphon*, *Plectropomus*, *Variola*, *Epinephelus*, and *Cephalopholis*.

The degree of exposure of the preopercular canal agrees closely with the general extent of cephalic sensory canal development, the sciaenids serving as an example of extreme sensory canal expansion.

Ornamentation of the ventral preopercle, while often illustrated and used as a diagnostic feature, appears not to have been the subject of phylogenetic analysis. The most likely reason for this is that it seems to be an unstable character with numerous secondary gains and losses of both serrae and spines. Nevertheless, I believe this character may be of use in certain instances.

The first is when an ornamentation pattern shared between or among groups is truly unique. Greenwood (1976), in discussing the preopercle of *Lates* (Fig. 12E), noted that the presence of large and discrete spines on its horizontal limb and angle are extremely rare in other lower percoids, occurring only in *Percalates* and *Siniperca*. I do not concur with Greenwood's characterization of the *Percalates* condition which appears to me to be much more finely serrate. However, the horizontal preopercular limb of *Siniperca* (Fig. 12F) does very closely resemble that of *Lates*.

The second approach, one which applies some directional rigor to an apparently mosaic character distribution is to ascertain the polarity of transformation within families in which resolved cladograms have been determined. If the primitive intrafamilial states can be identified, then intrafamilial comparisons can be attempted. Although serrate horizontal preopercular limbs are common among percoids, long antrorse spines are not and occur only in certain moronids, percids, *Lateolabrax*, and *Bostockia* (an apomorphic percichthyid). Intrafamilial analysis revealed that these spines only occur in the basal members of *Morone* (*labrax* and *punctata*) and the Percidae (*Stizostedion*, reduced in *Perca fluviatilis*, further reduced in *P. flavescens*). This suggests that this somewhat specialized pattern of ornamentation may be synapomorphic for these groups. However, since they are secondarily reduced in more apomorphic forms of these taxa, lack of this ornamentation pattern does not exclude membership in the group.

Although the preoperculomandibular sensory canal and ornamentation patterns of the horizontal limb have been discussed separately, they are consistent with the groupings suggested above. The Latini and

Siniperca have almost identical, highly derived preopercles. In addition to the ventral margin of the horizontal limb, Morone (Fig. 12A,B)), certain percids (Fig. 12C) and Lateolabrax (Fig. 12D) possess very similar, open preopercular canals.

One other feature of the suspensorium suggests an affinity between Siniperca and the Latinae. Johnson (1980) described the plesiomorphic condition of the symplectic as being simple and strutlike. In Stizostedion (Fig. 12C) and most percoid taxa, the symplectic originates near the hyomandibular facet at a sharp angle and continues ventrally as an almost straight but tapering strut. In the Latinae (Fig. 12E) and Siniperca (Fig. 12F), the symplectic continues downward from the hyomandibular at a less marked angle and then abruptly (in parallel with the preopercle), turns somewhat anteriorly before inserting in the quadrate. In these fishes, the symplectic does not taper but instead remains approximately even or broadens slightly at the angle, before tapering within the quadrate insertion. Within both the Latinae and Siniperca, the symplectic may also show channeling or a step-like margin along its ventral surface.

Dermal Upper Jaw

Several features of the dermal upper jaw show significant and correlated variation at the phylogenetic level of the basal percoids. Both reductions of beryciform conditions and translocations towards the more apomorphic general percoid state are visible in these fishes.

There is a strong trend within the basal percoids toward a reduction or loss of the supramaxillary bone. In primitive beryciforms two well developed supramaxillae are present - a large posterior plate-like supramaxilla with a short dorso-anterior process for articulation with the much smaller anterior supramaxillary element (Patterson 1964). No percoids retain the anterior supramaxilla. Some, however, retain the posterior element in an at least partly reduced form.

Reduction of the supramaxilla occurs in two ways. Probably its most plesiomorphic condition is seen in primitive percichthyids in which the bone is dorsally reduced but the dorso-anterior process is retained. In Percalates (Fig. 13A), the supramaxilla is essentially a straight bar which tapers upwards at its anterior terminus. A second mode of reduction is one in which the dorso-anterior process is lost while the supramaxilla is anteriorly and somewhat dorsally reduced (as in Micropterus, Fig. 13B). Further reductions approaching the vestigial state may occur as in Percilia (the bone erroneously considered absent by Eigenmann 1927 and Norman 1957). In some taxa such as Stizostedion that have lost the supramaxillary bone, there has been secondary expansion of the maxilla in that region.

Inasmuch as it is a reductive feature, the condition of the supramaxilla does not provide unambiguous synapomorphies, nevertheless it does contain some systematic information. In the Centropomidae (Fig. 13C), the supramaxilla is quite long and narrow and has a very well defined dorso-anterior process. Its condition in Siniperca (Fig. 13D) is similar but the process is not as distinctly formed. It is possible, but not certain that there has been at least some secondary anterior extension of the supramaxilla in these fishes.

The supramaxilla is consistently present in the: Centropomidae, Siniperca, Percichthyidae (sensu Johnson 1984), Lateolabrax (reduced), and Polyprioninae. The supramaxilla is consistently absent in: Morone, Percidae, Sciaenidae, and Lutjanidae. The supramaxilla is both present and absent in the Centrarchidae and Serranidae.

Two primary states of the premaxillary were noted in this investigation. In the first condition, found only among the Centropomidae and Siniperca (Fig. 15A), the premaxilla has a relatively short ascending process and a maxillary process located near the midpoint of the horizontal limb. Unlike the situation in Morone and other basal percoids, the ascending and articular processes are closely bound. This arrangement of premaxillary processes seems to mirror fairly closely the beryciform state described by Patterson (1964), and is of a type that provides minimal protrusibility of the premaxilla. Gregory (1933) in fact, used Lates (Fig. 15B) as an example of a percoid that displays a primitive development of the percoid upper jaw.

Greater protrusibility of the upper jaw has been attained in most lower percoids. Gregory (1933) noted several means by which this has occurred, including lengthening of the ascending process of the premaxilla and translocation of the connective tissue attachment from the coronoidal process further anteriorly on the maxilla - thereby creating greater leverage on the maxilla and premaxilla. Gregory did not discuss the effect of this increased leverage on the maxillary process, but it appears that it too was modified in response to these changes. Greater premaxillary protrusion increased the possibility of the maxillary process to prevent dislocation presumably would have required some modification of the palatine. Instead, the maxillary process shifted posteriorly along the horizontal premaxillary limb where it is found in almost all lower percoids (Fig. 15C). It should be noted, however, that in the Centropomidae and Siniperca, this caused a reduction in the large tissue pad at the angle of the jaw which lay in the cavity behind the premaxillary process when the jaw was closed.

Lateral Ethmoid-Lachrymal Articulation

Although the lateral ethmoid articulates with both the palatine and lachrymal in percoid fishes, Gosline (1966) discussed only the former. However, significant changes in the latter have also occurred between berycoids and percoids. In holocentrids, the most lateral condyles on the lateral ethmoid are directed ventrally where they articulate with a dorsally oriented cusp-like process of the first suborbital. The lateral ethmoid in these fishes does not extend far laterally. Essentially the same condition is seen in centropomids; the articulation remains in a primarily horizontal plane, with some lateral contact made on each side. Siniperca displays a similar state but without the articulation on the medial condylar face. The lateral ethmoid-lachrymal articulation in Percalates and Micropterus resembles that of Siniperca, but the lateral arm is further extended and the articular facet anteroposteriorly compressed.

In Morone, the condyle has swung upwards so that all contact with the lachrymal facet is in a vertical plane. This translocation of the condyle has resulted in its becoming more distal to the more medial condyle for support of the palatine, and so a narrow support bridge has formed. In some species, such as *Morone labrax* and *M. punctatus*, the bridge shows open, cancellous bone on its ventral margin. In *M. americana*, the bridge has narrowed into a thin ridge. Similar transformations have occurred within the percids. Sciaenids possess a broad lateral ethmoid, but the flat surfaced condyle is directed downwards, at 45°.

Ceratohyal

The configuration of the ceratohyal takes several common forms among percoids and associated taxa. Of primary systematic value is the dorsal region of the ceratohyal midsection. In many beryciforms and zeiforms, there is an oblong foramen between the latitudinal midline and the upper border, with the dorsal margin of the foramen exhibiting a bony projection. This perforation, termed the "beryciform foramen" by McAllister (1968) has been retained within the Perciformes, mainly in some lower percoids.

Gosline (1966) discussed the ceratohyal in relation to lower percoids and attributed the dorsal strut over the foramen to a need for bony protection for a nerve that traverses the ceratohyal and epihyal. MacDonald (1978) characterized it similarly in a review of several Australian percichthyids in which he employed many of Gosline's (1966) characters. McAllister (1968), however, in a detailed analysis of the branchiostegals and related structures, attributed the function of the groove that occurs on the dorsal ceratohyal region to serve as a pathway for the hyoid artery - as did Patterson (1964).

Two discrete reductive states from the perforated ceratohyal (Type I) were described by Katayama (1959) for the extended (pre-Gosline 1966) Serranidae. In Type II, the dorsal strut has been partially or completely eliminated, leaving a deep hollow in the ceratohyal together with a channel across its upper margin. Type III serranids have a shallow, slightly concave upper ceratohyal margin which lacks a latitudinal fossa but sometimes possesses a channel in the bone on both sides where the hyoid artery enters and exits across the upper ceratohyal gap.

These three patterns appear to represent a transformation series from a well developed bony strut across the ceratohyal to the complete absence of any bridge, a return to the pre-beryciform condition judging from the results of McAllister (1968). Further support for the polarity of this transformation is offered by the uncommon, but occasional changes that exist within taxa. For example, within MacDonald's (1978) _Macquaria_ group, _Percalates_, (considered the most primitive member), shows the Type I pattern, while _Plectroplites_ and _Macquaria_ display an incomplete foramen. A similar transformation occurs within the Centrarchidae.

I found that although the Type I configuration is relatively unambiguous, allocation of fishes to types II and III was difficult as there appears to be a continuum between these states. Katayama (1959) found _Niphon_, _Siniperca_, and _Stereolepis_ to possess a ceratohyal foramen. To this list I would add, among the lower percoids, _Micropterus_, _Polyprion_, _Percilia_, _Lates_, _Centropomus_, and

Psammoperca. Katayama (1959) placed *Lateolabrax* in his Type II group, and *Epinephelus* in his Type III. I found *Morone*, *Perca*, *Stizostedion*, *Percichthys*, *Serranus*, and *Lutjanus* to show partial infiltration of the lateral grooves across the upper margin of the ceratohyal concavity.

Subocular Shelf

The subocular shelf is a bony lamina that extends medially from the suborbital series of bones. Although previously used as a character in systematic studies (e.g., by Boulenger 1895 and Katayama 1959), the taxonomic distribution and function of the subocular shelf were first examined in detail by Smith and Bailey (1962). Their interest arose from a dissatisfaction with the common explanation for its function as a support for the eye, since it was apparent that many fish at the same phylogenetic level which lack the shelf have equivalent optical function.

Smith and Bailey (1962) found that the subocular shelf first appeared in the Beryciformes and that it was modified within the Perciformes. In most taxa, the shelf occurs on the third suborbital (counting posteriorly with the lachrymal as suborbital 1). Smith and Bailey (1962) noted a trend in the Beryciformes towards increased stiffening of the suborbital ring with the development of sutures between individual elements, followed by expansion to form the subocular shelf. They hypothesized that the shelf is a response to a need for strengthening the subocular region rather than simple eyeball support. In addition to the relative inflexibility produced by these modifications, they also noted, particularly with regard to Centropomus which has a posteriorly extended process on its subocular shelf, that the shelf may serve as a site for ligamentous attachment to other branchiocranial elements.

Although Smith and Bailey (1962) were most likely correct in their assertion that increased stiffening of the suborbital series occurs as a result of the development of the L-shaped lamina, it is also apparent that the shelf serves a major role as a point of attachment for ligamentous support of the entire suborbital ring. I examined the subocular shelf of specimens representative of numerous berycoid and perciform families and found that in all instances, the shelf was strongly bonded to the suspensorium by connective tissue. In Holocentrus and Myripristis, the narrow but multi-elemental subocular shelf is the site for the attachment of thin tissue to the metapterygoid and ectopterygoid. Both Percichthys and Lateolabrax have a broad ligament running from the shelf anterior to the ectopterygoid and a posterior ligament to the metapterygoid. In Morone, however, the posteriorly attached connective tissue also joins the hyomandibula. In the aforementioned taxa the connective tissue generally appears as a thin sheet with localized ligamentous intensification, but in Centropomus and Lates the posterior connective extensions occur as distinct ligamentous bundles, a single bundle to the metapterygoid in Centropomus, and a forked ligament to the metapterygoid and hyomandibula in Lates. In contrast, Epinephelus and Lutjanus showed separate posterior ligaments attached to those elements. Although the role of the subocular shelf as an attachment site for the connective support of the suborbital series seems clear, the variation in origin of its associated connective tissue suggests that the shelf and its modes of reinforcement might prove worthy of phylogenetic analysis, particularly given its origin and wide distribution among the acanthopterygians.

The subocular shelf, much like the procurrent spur (Johnson 1975), shows a pattern of loss in certain percoid families. Smith and Bailey (1962) found that the families which lack the shelf probably did not comprise a single lineage, and hypothesized therefore, that its secondary loss has occurred several times. Whereas Smith and Bailey attributed these apparently independent losses among well-separated families to several hypotheses involving functional processes, Johnson (1980) believed that the losses of this character were already established at the family level and that functional rationales would be better studied by examining intra-taxic losses. It seems that the systematic value of the presence or absence of the subocular shelf at the intrafamilial level will not begin to become apparent until hypotheses of relationship based on other characters are proposed, thus making possible reciprocal analyses of its phylogenetic distribution.

Ventral Surficial Features of the Basihyal

Certain percoid taxa display basihyals with ventral modifications. *Morone*, for example, exhibits a basihyal with varying degrees of ventral relief (discussed in detail in Section I - Branchiocranium), ranging from multiple ridges in *americana* and *mississippiensis* to deeply pocketed fossae and diverticulating ridges in *chrysops*. A similar pattern of fossae and ridges occurs in *Polyprion*, a taxon that possesses a large basihyal tooth patch and, frequently, tooth patches located anterior to the basihyal.

Most lutjanids possess a large basihyal tooth patch and some (Rivas 1966) a second patch anterior to the first. *L. campechanus*, which possesses two basihyal tooth patches has a ventrally smooth basihyal. *L. griseus* and *L. synagris*, both of which have single basihyal tooth patches, may show very small fossae, slight surficial irregularities, or a very modest median ridge on the basihyal's lower side. *Haemulon*, allied to the Lutjanidae (Johnson 1980), lacks basihyal teeth but displays a median ventral ridge.

The centrarchids show little modification of the ventral basihyal even in species that possess basihyal teeth. *Ambloplites* and *Micropterus*, both with tooth patches on the posterior basihyal, may show very slight troughlike depressions, and *Pomoxis*, which also possesses a basihyal tooth patch has a smooth ventral basihyal.

Most, but not all of the percoids that lack basihyal teeth, have basihyals that are smooth on their ventral surfaces. Exceptions are *Epinephelus*, which may have a slight median ridge, and *Stizostedion*, which sometimes shows an irregular central trough. *Kuhlia* has a highly specialized median keel that flares posteriorly to form two large, anteriorly directed cavities. *Centropomus*, *Lates*, *Siniperca*, and *Centropristis* all lack basihyal teeth and have a smooth basihyal underside.

It appears that a basihyal highly modified for ventral ligamentous reinforcement is correlated with the presence of dental specializations on the tongue. In *Morone*, the degree of specializations for basihyal attachment corresponds to some extent to the total area covered by lingual tooth plates with less in *americana* and *mississippiensis* and more in *chrysops*. *Polyprion* appears to parallel *Morone* in this respect.

This correlation, however, does not hold for other percoid taxa. Lutjanids with less basihyal dentition may possess a median ridge while more dentally endowed species of snappers may show smooth attachment surfaces. Centrarchids also display little ventral basihyal variation between taxa that possess or lack the primitive percoid tooth patch. It is not clear whether taxa that lack basihyal teeth (presumably lost at some ancestral level) and that have some surficial relief on the ventral basihyal do so through retention of a primitive condition, or through a need for greater ligamentous support for non-dental functions.

Accessory Subpelvic Keel

In some percoids, there is a ridge on the ventral surface of each pelvic bone that Katayama (1959) termed the accessory subpelvic keel. Johnson (1980) believed that its presence in beryciforms, lower percoids such as *Symphysanodon* and some percichthyids indicate it is a primitive percoid character. Among the Lutjanidae, Johnson (1980) found it in etelines, in a reduced form in apsilines, and absent in other lutjanoids.

Katayama (1959) noted its presence in *Lateolabrax*, *Coreoperca*, *Stereolepis* and *Synagrops*, and in what he termed the *Franzia* stem of the Serranidae which includes relatively specialized serranid genera such as *Plectranthias*, *Tosana*, and *Franzia*.

I surveyed a number of lower percoids and found the keel present in: Siniperca, Centropomus, Polyprion, Cynoscion, Perca, Stizostedion, Percina, Ammocrypta (reduced), and Morone (vestigial); and absent in: Centrarchidae, Lates, Aplodinotus, and Centropristes.

These results support Johnson's (1980) belief that the accessory subpelvic keel, when present in percoids, is primitive. Like lutjanids, intra-familial losses of this character within the Percidae and Sciaenidae seem to occur among the more derived members.

Dentition

A number of apomorphic dental features were noted in this investigation; however, all are almost certainly autapomorphic at the familial level.

The tooth plates lateral to the basihyal in Morone appear to be unique among percoids. The condition most similar to it that I identified occurs as an autapomorphy of a scombrid, Gymnosarda unicolor which possesses two large dermal tooth patches overlying most of the basihyal and extending laterally beyond it (Collette and Chao 1975). Morone also possesses teeth in the soft tissue of the tongue anterior to the basihyal. A condition resembling this is found in Polyprion, most specimens of which display several discrete, moronid-like tooth patches between the tip of the tongue and the basihyal. Polyprion, however, does not possess lateral plates, the probable precursor to the anterior tooth formations in the progression shown by Morone. It should be noted that none of the findings of this study

Polyprioninae. A single tooth plate also occurs anterior to the basihyal in some lutjanids (Rivas 1966).

Morone punctata possesses a secondarily derived, posteriorly extended vomerine tooth patch. A similar, nonhomologous condition exists in certain lutjanids (Rivas 1966).

Morone retains a basihyal tooth patch, a condition that is primitive for percoids (Nelson 1969), but which is modified into a paired patch in some members. A centrarchid, *Lepomis gulosus*, also shows a paired (sometimes horseshoe-shaped) basihyal patch, an autapomorphy of that species.

The teeth of the branchial skeleton were not helpful in delineating intrafamial relationships in basal percoids. Endopterygoidal teeth are retained in *Percalates*, centropomids, and primitive centrarchids.

Procurrent Spur

Johnson (1975) discussed the distribution and phylogenetic significance of the procurrent spur. This structure is a ventrally directed projection that occurs anteriorly on the first ventral procurrent ray of the caudal fin (Fig. 14). It is usually, but not always, accompanied by a preceding ray that is basally shortened, and which often originates slightly posterior to the spur. The distribution of these features in taxa relevant to this study appears in Table 4.

This spur only occurs in perciform fishes. Johnson (1975) found it in approximately 30 percoid families, and in the Polynemidae, Sphyraenidae, and Stromateiodei. Johnson compared the apparent adaptive significance of the spur with the lifestyle of fishes that possess it or lack it in an attempt to determine whether it was acquired independently by various taxa or as a specialization of unique origin. It was his conclusion that the spur had not been gained independently inasmuch as he found no correlation between swimming mode and the spur's presence, both sedentary and pelagic taxa possessing it while a similar ecological range was found for groups that lacked it. Further support for the monophyly of taxa possessing the spur was its strong constancy within families. However, it also was clear that the spur and the associated shortening of its proximal ventral ray have been lost completely within some groups (e.g., Sciaenidae, Centrolophidae), so that no information is to be gained from groups that lack it. Apparently intermediate states also exist (e.g., Siniperca, Scombrolabrax).

Similar structures have been found in certain perciform taxa that lack the procurrent spur. In most perciforms, the usual number of principal caudal rays is 17. However, ventral spurs have been found in one or more of the principal caudal rays in certain groups with less than 17 principal rays, including the Scorpaeniformes, Blennioidei, and Gobioidei, all of which lack the procurrent spur. Johnson (1975) believed that the absence of the procurrent spur in these taxa strengthened the argument for a unique derivation of this feature, but it appears to me that the possibility of homology between the two types of spur warrants consideration.

Anal Spines

Johnson (1980), among many others, considered the presence of three anal spines primitive for percoids. Although most percoids exhibit this character, many taxa have less, and a few, more than three.

That three anal spines are plesiomorphic at this level is supported by at least one intrafamilial transformation. Micropterus, which is generally considered to be the most primitive centrarchid (Smith and Bailey 1961; Mok 1981), possesses three anal spines, whereas more derived centrarchids such as Acantharcus (5) and Archoplites (7) show higher counts.

Among taxa sometimes treated as basal percoids, Johnson (1984) found the following to possess two anal spines: Apogonidae, Percidae, Sciaenidae (some), and Serranidae (some).

Johnson (1984) described two patterns of reduction in the number of anal spines. In the plesiomorphic condition of three anal spines, two spines occur in supernumary fashion on the same pterygiophore followed by a third spine on the next pterygiophore in serial association. In one type of anal spine loss, such as that which occurs in sciaenids, both anal spines occur in supernumary fashion. Johnson believed this kind of reduction was due to failure of the third serial element to transform into a spine. In contrast, in percids and apogonids the two anal spines occur in serial association, suggesting that the first spine has been lost. However, both types of reduction may occur within a family. Ammocrypta, a highly derived percid has only one anal spine, the second serial element failing to transform.

Scaly Pelvic Axillary Process

The scaly pelvic axillary process has been utilized as a primary subdivisional character in at least two percoid classificatory schemes (Regan 1913; Norman 1957). Gosline (1966) noted that although it may serve as a convenient taxonomic marker, its variability of expresssion from minimal to well developed, and its irregular occurrence within some taxa (e.g., Sciaenidae) render this character difficult to evaluate.

Examination of two beryciforms showed the presence of a scaly pelvic axillary process in both. Myripristis jacobus has a well developed medial process, while Polymixia lowei possesses an axillary process that bifurcates along the medial margins of the pelvic fin. Given its presence in beryciforms, it seems likely that the scaly axillary process is primitive for percoids. Norman (1957) listed the Centropomidae, Lutianidae, Scorpididae, and Sciaenidae as displaying this feature and the Centrarchidae, Serranidae, Kuhliidae, and Percidae as lacking it.

Scales

McCully (1961) investigated the anatomy of serranid scales. Employing numerous scale characters, he divided the Serranidae into four subgroups, the first of which included the majority of Gosline's (1966) Percichthyidae. Within group I, McCully united Lateolabrax with Roccus to form the subfamily Roccinae, one of five subfamilies that included the Niphonidae, Polyprioninae, Doderleininae, and Percichthyinae. The remainder of the serranids were allocated to three other groups that with the exception of the pseudochromids, approximate the Serranidae of Gosline (1966).

McCully (1961) found the scales of Lateolabrax to be so similar to Roccus "that a detailed description would be redundant." At that time he maintained that "The quadrangular truncated scalelets that are regular in both shape and arrangement and that have both the proximal and distal margins square and straight, are of a type that is found nowhere else". Not long afterwards, McCully (1962) determined that the Percidae share a similar posterior scalelet morphology and placement and postulated that the three taxa diverged from a common ancestor during the Cretaceous.

The placement of the Centrarchidae was also considered by McCully (1962) who found that they share a number of scale features with his Percichthyinae. This subfamily of freshwater serranids included Percichthys, Percilia, Maccullochella, Percalates, Plectroplites, Macquaria, and Siniperca.

McCully's Percichthyinae, minus Siniperca, comprise the basal members of Johnson's (1984) restricted Percichthyidae. Although Siniperca is the only genus within this grouping that lacks ctenii, McCully included it on the basis of characters found elsewhere in certain scales, and on characters of the vertebral column presented in tabular form by McCully who was following Boulenger (1895). While Siniperca appears to be intermediate in several respects to the remainder of McCully's Percichthyinae, it is not clear whether the various types of vertebral counts displayed are meaningful at this level. Johnson (1983) considered vertebral counts in a number of lower percoid taxa and found them to have little apparent significance. In his re-examination of Gosline's Percichthyidae, Johnson (1984) removed Siniperca and left it unresolved despite McCully's inclusion.

Johnson (1984) discussed the gross morphology of percoid scales, and described three basic types. A number of percoids have a ctenoid-like scale type, also found in myctophids and beryciforms, that is the product of continous spinous projections from the lateral surface and posterior margin of the scale. The majority of percoid taxa, however, have true ctenii formed by separate bony plates called scalelets. The patterns formed by scalelets as the scale grows and additional scalelets are formed are highly diagnostic. A third type, the cycloid scale, is found in some percoid families and is probably a secondary derivation in most, if not all of these.

Siniperca is the only genus among Gosline's percichthyids that lacks scalelets in the posterior field. All other members of this group add scalelets to their posterior scale margins in one of several characteristic ways as it enlarges. In most of these families, the posterior field fills with remnants of old ctenii which appear amputated to some degree, as new ctenii are added (McCully 1970). I restricted my analysis to these features of the posterior scale field and found three primary patterns within the percichthyids and several closely related taxa.

One pattern shows the posterior scalelets in an imbricated arrangement. This pattern (Fig. 16A) is found in percichthyids, centrarchids), centropomids, and the Polyprioninae. Scalelets of this type are only slightly amputated, retaining the typical triangular shape but minus the tip.

A second pattern (Fig. 16B) is characteristic of serranids. In these scales the margin bears complete ctenii but old ctenii are strongly amputated, the remainder appearing as little more than rounded mounds. The placement of these scalelets is of the same alternating pattern as the first type, with gaps maintained between scalelets.

McCully (1961) noted the regularity in shape and position of the amputated scalelets of *Morone* and *Lateolabrax*, that form examples of a third pattern (Fig. 16C). I found similar patterns in the Percidae (as indicated by McCully 1962), sciaenids, and lutjanids. Scales of this type are characterized by the linearity of both the individual scalelet replacements and of the marginal rows. Old scalelets are amputated (or as Johnson 1984 suggested, resorbed) thus leaving a block shaped remnant that is bordered on all four sides by contiguous amputated scalelets.

It is not clear what the relationship is between the spinous projections of myctophids, beryciforms and some percoid groups, and the "true" ctenii of the majority of percoid taxa. If the former represent a primitively homologous condition, then their alternating pattern suggests that the alternating pattern found in the percichthyids, serranids, and several other groups is probably primitive for true ctenoid scales and that the regular block-like pattern found in the third group is derived. The more complete amputation of serranid scalelets also appears to be a derivation in relation to the first group.

Caudal Fin Lateral Line Extension

The lateral line of most percoids terminates posteriorly on scales near the hypural plate or a few scales beyond. Nevertheless, a considerable number of percoids have lateral lines that either extend towards or reach the rear margin of the caudal fin. Of those species with partial to complete caudal extensions, some also have accessory sensory canals on the fin. None of these canals lie within the fin membranes; they are features belonging to the very small scales that radiate outwards from the caudal peduncle between the caudal rays.

All members of Morone possess a lateral line that extends at least one third of the way onto the caudal fin and, in addition, accessory lateral lines that occur three caudal rays above and two below the central line (Fig. 17). A similar condition is found in the Luciopercinae (Collette and Banarescu 1977), and certain lutjanids (Rivas 1966) and gobioids (Springer 1983), although the accessory lines may occur a different number of scale rows from the medial row. Greenwood (1976) described in detail the specializations of the sensory canals of the caudal region, and suggested the possibility of a relationship with sciaenids on the basis of this. Springer (1983) called attention to the diversity of the perciforms that exhibit accessory lateral lines on the caudal fin. Johnson (1984) also noted the presence of these specializations among a number of percoid families and he supported the view of Springer (1983), that these features may be primitive for perciforms.

Caudal, sensory canal specializations among lower percoids were surveyed and are presented in Table 4.

Table 4. - Lateral line extensions on the caudal fin and procurrent spurs in lower percoid taxa. (r=reduced)

Taxon	Percent Extension Beyond Hypural to Caudal Margin	Lateral Lines No. Rays Above Above(+) Below(-)	Procurrent Spur	Reduced Proximal Ray
PERCICHTHYIDAE				
Percalates colonorum	~25	--	+	+
Macquaria australasica	~20	--	+	+
Macquaria ambigua	~25	--	+	+
Maccullochella peeli	0	--	-	-
Percichthys trucha	~10	--	+	+
Edelia vittata	0	--	-	-
Bostockia porosa	0	--	-	-
Gadopsis marmoratus	0	--	-	-
SINIPERCA				
Siniperca chuatsi	0	--	r	+
Coreoperca kawamebari	0	--	r	+
CENTRARCHIDAE				
Micropterus dolumei	0	--	-	-
Amboplites rupestris	~5	--	-	-
Pomoxis nigromaculatus	~5	--	-	-
CENTROPOMIDAE				
Psammoperca waigiensis	100	--	+	+
Centropomus undecimalis	100	--	+	+
Lates calcarifer	100	+3 -2	+	+
POLYPRIONINAE				
Stereolepis ischnagi	~20	--	+	+
LUTJANIDAE				
Etelis oculatus	~25	--	-	-
Apsilus dentatus	<5	--	-	-
Lutjanus apodus	~15	--	-	-
Lutjanus campechanus	~35	+4 -3	-	-

SCIAENIDAE				
Cynoscion regalis	100	--	+	+
Aplodinotus grunniens	100	--	+	-
Umbrina cirrosa	100	--	r	-
PERCIDAE				
Stizostedion vitreum	~35	+4 -4	-	-
Romanichthys valsanicola	~20	+3-4 -3-4	-	-
Perca flavescens	0	--	-	-
Perca fluviatilus	0	--	-	-
LATEOLABRAX				
Lateolabrax japonicus	~30	--	+	+
MORONE				
Morone labrax	~30	+3 -2	+	+
Morone punctata	100	+3 -2	+	+
Morone saxatilis	~40	+3 -2	+	+
Morone chrysops	~70	+3 -2	+	+
Morone americana	~40	+3 -2	+	+
Morone mississippiensis	~25	+3 -2	+	+
KUHLIIDAE				
Kuhlia rupestris	~35	--	+	+
SERRANIDAE				
Centropristis philadelphica	~20	--	-	-
Paralabrax clathratus	~20	--	-	-
Niphon spinosus	0	--	-	-
Epinephelus guttatus	0	--	-	-
Rypticus subbifrenatus	0	--	-	-
APOGONIDAE				
Apogon exostigma	~40	--	-	-
TERAPONIDAE				
Terapon caudivittatus	~25	--	+	+
Leipotherapon macrolepis	0	--	+	+

POMADASYDAE				
Pomadasys jubelini	~45	--	+	+
HAEMULONIDAE				
Haemulon flavolineatum	~45	--	+	+
SCORPIDIDAE				
Scorpis aequipinnis	~40	--	+	+
GOBIOIDAE				
Rhyacichthys aspro	~35	+1 -2	-	-

Several patterns can be discerned. Percichthyids appear primitively to possess a somewhat extended central line which has been lost in the more specialized members, assuming the accuracy of Johnson's (1984) arrangement in which he placed the *Macquaria* group at the base of the group and *Edelia*, *Bostockia* and *Gadopsis* near its terminus. Two of the three genera Johnson excluded from the Percichthyidae (*Morone* and *Lateolabrax*), possess at least some degree of lateral line extension, but *Siniperca* does not. In the Polyprioninae, considered percichthyids by Gosline (1966) but often treated as a separate bigeneric family, *Stereolepis* shows a slight extension of the medial canal, but *Polyprion* does not. The percids show a pattern of loss from the derived state. Collette and Banarescu (1977) found a lateral line extending onto the caudal fin with supplementary lines above and below it in *Stizostedion*, *Zingel* and *Romanichthys*, but they noted that *Romanichthys*, the most derived member of the subfamily Luciopercinae, occasionally lacked the supplementary canals. I found the accessory canals of *Romanichthys* to be rudimentary and that the number of scale rows separating the central row of modified scales from the supplementary scale rows was sometimes different on either side of individual specimens. Among the Percinae, accessory lateral lines are absent in all genera with the occasional exception of _Gymnocephalus_. Lutjanids also display two states: a complete lack of caudal modifications and a partial medial extension with supplemental canals. The lack of an available phylogenetic analysis prevented any determination of the polarization of this character in the Lutjanidae.

Air Bladder

The air bladders of lower percoids show a number of peculiarities. Gosline (1966) made use of two apparent specializations of the air bladder to define the Percichthyidae. MacDonald (1978) defended the synapomorphic value of an anteriorly bilobed and interhaemally extended air bladder, when the two characters are taken together.

Although Gosline (1966) noted that holocentrids and kuhliids also possess anteriorly bilobed air bladders, he considered them to show distinct states of this character based on their relationship to Baudelot´s ligament. He also recognized, however, that that not all percichthyid taxa possess either specialization. Johnson (1983) reconsidered these characters but thought them "too variable" for systematic work at this level.

Dissection to study the air bladder was not performed, but information was available from several sources, and is presented in Table 5. Among taxa under consideration, only _Lateolabrax_ possesses a well developed posterior extension onto the first anal pterygiophore, although *Morone punctata* shows what appears to be a precursory stage of this condition.

Table 5. -- Anterior configuration of the air bladder in lower percoid taxa.

Blunt or Rounded		Anteriorly Bilobed	
Taxa	Source(s)	Taxa	Source
Morone	Dobbin (1941) Gosline (1966)	*Percalates*	MacDonald (1978)
		Plectroplites	MacDonald (1978)
Perca	Dobbin (1941)	*Macquaria*	MacDonald (1978)
Percichthys	Gosline (1966)	*Maccullochella*	MacDonald (1978)
Percilia	Gosline (1966)	*Stereolepis*	Katayama (1959)
Centrarchidae	Dobbin (1941)	*Lates*	Katayama (1956)
Niphon	Katayama (1959)	*Siniperca*	Katayama (1959)
Epinephelus	Katayama (1959)	*Coreoperca*	Katayama (1959)
Teraponidae	Vari (1978)	*Lateolabrax*	Katayama (1959)

In holocentrids and *Kuhlia* the anterior prongs of the air bladder extend beyond Baudelot's ligament, but this does not appear to be true for the taxa that possess an anteriorly bilobed air bladder in Table 5. In *Percalates* and *Lateolabrax* at least, the relatively small lobes do not penetrate forward beyond the exoccipital-vertebral junction, and fall short of Baudelot's ligament.

The systematic significance of the anteriorly bilobed air bladder remains unclear. It may represent, at the lower percoid level, a derivation from the simple, blunt-ended form. Alternatively, a moderately bilobed air bladder may represent a reduced state of the more extreme beryciform type, which would suggest that a simple anterior terminus is derived relative to the bilobed one. Gosline (1966) noted that the serranid trend towards a reduced Baudelot's ligament or one absent altogether, and its replacement by a posteriorly derived muscular support would preclude any air bladder-inner ear connection of the type found in holocentrids, for example.

Ramus Lateralis Accessorius

Freihofer (1962) described the patterns of a facial nerve, the ramus lateralis accessorius (RLA), as found in 21 orders and 130 families of fishes. Freihofer believed that these nerve patterns held strong systematic significance. Of the 16 patterns described, thepatterns he designated as numbers 8, 9, and 10 were found to occur in many percoid families, with some percoid taxa showing partial to complete loss of the nerve.

These patterns were distributed among the taxa relevant to this study in the following manner:

Pattern 8 - (Roccus-Perca Pattern): Morone, Lateolabrax, Percidae (reduced in Stizostedion and Percina), Sciaenidae, Macquaria, Percalates, Coreoperca, Siniperca, Scorpis, Acropoma, Haemulonidae, Pomadasydae (majority).

Pattern 9 - (Polycentrus-Serranus Pattern): Gadopsis, Centropomidae, Centrarchidae, Malakichthys, Serraninae, Hapalogenys.

Pattern 10 - (Kuhliid Pattern): Kuhliidae, Theraponidae, Girellidae, Scorpididae (except Scorpis).

RLA absent: Beryciformes, *Niphon*, Epinephelinae, *Stereolepis*, Apogonidae, *Glaucosoma*, Gobioidea.

Other taxa not listed also possess patterns 8, 9, and 10.

Freihofer (1962) compared the anatomical relationships among these patterns and concluded that Pattern 8 is most likely primitive in relation to patterns 9 and 10. In Pattern 8, RLA exits through the parietal foramen, while in patterns 9 and 10, it exits through the trigeminal foramen, an apparent specialization. Freihofer believed that similarities between Pattern 8 and patterns found in pre-percomorph fishes indicated that Pattern 8 may have evolved earlier than did patterns 9 and 10 and that patterns 9 and 10 are quite similar. He also assumed that Pattern 8 species must have evolved from Pattern 8 forebears and Pattern 9 species from Pattern 9 forebears, but no evidence for this was provided. With regard to the Serranidae as then constituted, Freihofer advocated removal of Pattern 8 genera to a separate group with *Roccus*, a treatment that presaged Gosline's (1966) erection of the Percichthyidae, justified on other grounds.

If Freihofer's assertion that patterns 8 and 9 (and presumably Pattern 10) represent distinct lineages is accepted, then three extensive lower percoid clades are suggested. Absence of RLA was considered a loss and therefore not a unifying character, so it is conceivable that a species lacking RLA might belong to any one of the three groups. Although groups defined by RLA pattern in many instances support current notions of percoid classification at low taxonomic levels, the absence of independently derived higher level classifications means that Freihofer´s results for the percoids are still untested hypotheses. It appears, at least in relation to the taxa listed above, that patterns 8 and 9 form groups that are supported to a fair extent by the results of my study. Conflicts do occur, however, and they suggest that taxa displaying patterns interpreted as patterns 9 or 10 may have originated directly from ancestors with Pattern 8.

-DISCUSSION-

A Functional Hypothesis Regarding the Taxonomic Distribution of Caudal Lateral Line Extensions, the Procurrent Spur, and Cycloid Scales

What seem to be meaningful associations were noted between the presence of certain characters never before considered in relation to one another. An apparently inviolate correlation at the basal percoid level is that taxa with cycloid scales do not display any lateral line extension onto the caudal fin as well as showing a general reduction in the extent of scalation on the caudal fin. The lateral line in these fishes normally terminates near the hypural plate, well before the posteriormost scales. The scale rows that radiate outward from the caudal peduncle in many ctenoid-scaled percoids are not as extensive as in cycloid-scaled taxa like *Siniperca*, which are thickened by significant development of the muscles that insert on and control the caudal rays. Moreover, the procurrent spur is not normally developed in these cycloid-scaled taxa, having been lost in *Maccullochella*, *Gadopsis*, *Bostockia*, and *Edelia*, and reduced in *Siniperca*.

The association between a reduced or absent procurrent spur and a nonextended caudal lateral line also exists in many ctenoid-scaled percoids. Taxa of this type include centrarchids, serranids, and most percids. However, some groups lacking the procurrent spur have a posteriorly extended lateral line. Examples of fishes with extreme caudal lateral line development but lacking the procurrent spur include _Stizostedion_ and certain lutjanids.

The distribution of these features suggests a functional hypothesis for the observed correlations. A significantly extended caudal line with accessory canals is found in active predatory forms such as _Morone_, _Centropomus_, _Lates_, and some lutjanids. This condition is also found in pelagic members of the Luciopercinae, but is reduced or lost in its more benthic and sedentary taxa. The presence of caudal sensory canal modifications undoubtedly increases the efficacy of proximal mechanoreception. In _Morone saxatilis_, the post-hypural sensory canals increase the total post-opercular sensory canal system by approximately 20%.

Most groups with significant caudal fin lateral line development possess the procurrent spur. Johnson (1975) considered the functional significance of the spur and its shortened adjacent ray, and concluded that it most likely facilitates abduction of the last procurrent ray and, through connective association, all the ventral rays of the caudal fin. This would occur by means of the generation of increased leverage through the translocation of the tendon insertion on the lateral surface of the ray to the spur. Shortening of the preceding ray could allow further abduction of the spur and hence, the caudal fin, however, not all taxa that possess a spur have the shortened associated ray. Maximal abduction of the caudal fin is most likely important to active predatory fishes in that it increases the aspect ratio (Fin span^2/Fin area), to make possible more efficient forward thrust. Groups possessing caudal lateral line extensions have extended scale rows between the caudal rays. If not compensated for, these extended scale rows must produce additional rigidity against horizontal flexion of the caudal fin.

A different mode of life is seen in most lower percoid fishes that lack a significantly extended caudal lateral line and supplementary canals as well as a procurrent spur. Centrarchids and serranids are primarily sedentary fishes that tend to hover around structures. Although they are capable of short bursts of speed, feeding is probably most often accomplished by means of visual or lateral line perception of prey as it enters their home territory, instead of an active searching pattern.

Close alliance to structure may preclude or at least diminish the functional value of increased caudal lateral line development. In addition to a anteriorly directed trophic orientation, a lifestyle of this type may include the need for frequent finely adjusted movements as prey is stalked or backwards retreat is necessitated, and not for continual strong locomotion. Therefore it seems likely that a flexible caudal fin capable of fine movements is favored in these taxa. Both the procurrent spur and significant caudal scalation would decrease the range of caudal motility. Fine caudal movements would be further assisted by the apparent increase in post-hypural musculature present in some of these fishes.

The correlated distribution of caudal fin lateral line patterns, to the presence of the procurrent spur, and the loss of ctenii provides additional insight into the systematic significance of these characters. Johnson (1975) defended a monophyletic origin for the procurrent spur and subsequently suggested (Johnson 1984) that cycloid scales in percoid fishes are independent secondary losses (supported by this analysis). The question of monophyletic derivation for caudal lateral line specializations has not been addressed at this level.

Intrafamilial patterns are revealing. Within the Centropomidae, the Centropomini, primitive sister group of the Psammopercini and Latini possesses a complete extension to the caudal margin but lacks supplementary canals. The dichotomous Latinae shows the centropomine state in Psammoperca, and a complete lateral line extension with accessory canals in Lates. Eolates, an extinct latine also lacked accessory canals, and this suggests that a fully extended lateral line without supplementary lateral lines is primitive for the Centropomidae. Two anomolous conditions are seen. Siniperca, considered a sister taxon of the Latinae in this study, exhibits a posterior lateral line extension reduced back to the caudal peduncle, cycloid scales, and a reduced procurrent spur. Luciolates, a derived latine, possesses supplementary canals that curve anteriorly to meet the primary lateral line at the hypural region (Greenwood 1976). As Greenwood stated, it is not clear whether this is an intermediate state in the derivation of accessory canals, or a unique secondary condition.

Within the Percidae, considerable caudal lateral line extension with supplementary canals occurs only among the more plesiomorphic but active pelagic members of the Luciopercinae, features that have been lost among its more derived, benthophagic taxa (Collette et al. 1977). The pattern within Morone, in most instances, consists of moderate lateral line extension with supplementary canals, with the highly apomorphic M. punctata showing a complete caudal extension of the medial lateral line. However, the supplementary canals do not occur between the same caudal rays in moronids as in percids. Certain lutjanids approximate the general moronid condition. Sciaenids, despite their great sensory canal development, do not possess accessory caudal canals, but they do tend to show a medially extended caudal fin and this increases the length of the lateral line (Trewavas 1977).

Most lower percoids do not show highly specialized posterior sensory canals like these. Nevertheless, many of the most basal members display at least a partial extension of the medial canal onto the caudal fin, and when they do not, its absence usually coincides with the loss of the procurrent spur and sometimes the loss of ctenii as well.

Given the distributions noted, and the relationships indicated by this study, the following hypothesis is suggested regarding the origin of specializations of the caudal fin lateral line:

1. The ancestral condition of the basal percoids was a partial caudal lateral line extension, lacking supplementary canals.

2. Complete lateral line extension has occurred independently in centropomids, sciaenids, and M. punctata.

3. Accessory canals in centropomids have been acquired independently from those occurring in moronids, percids, and lutjanids. Although there is a greater possibility of homology between moronid, percid, and lutjanid accessory canals, their absence in sciaenids and Lateolabrax, hypothesized to comprise a monophyletic group or a paraphyletic group including all of these taxa, favors independent derivation of these features.

4. Reduction of the caudal lateral line extension has occurred in many taxa, frequently in concert with loss of the procurrent spur and development of cycloid scales.

Additionally, it was observed that secondary reduction of ctenoid scales to a cycloid state seems to include thickening of the overlaying mucosal layer. This thickening may negate the function of marginal ctenii, a state seen clearly within Morone as americana has both the thickest mucosal coating and the least developed ctenii.

Relationships of Moronidae, Percidae, and Lateolabracidae

The results of this study indicate that the Moronidae, Percidae, and Lateolabracidae form a monophyletic group, as suggested by McCully (1962). However, resolution of this proposed trichotomy awaits further analysis. Three synapomorphies unite these fishes - unique expressions of the epioccipital processes, preopercular ornamentation, and scale morphology. Although not synapomorphic for these taxa, several other characters show approximately equivalent development or reduction from plesiomorphic conditions. They include RLA pattern, the premaxilla, supramaxilla (reduced or absent), ceratohyal, and lateral ethmoid-lachrymal articulation.

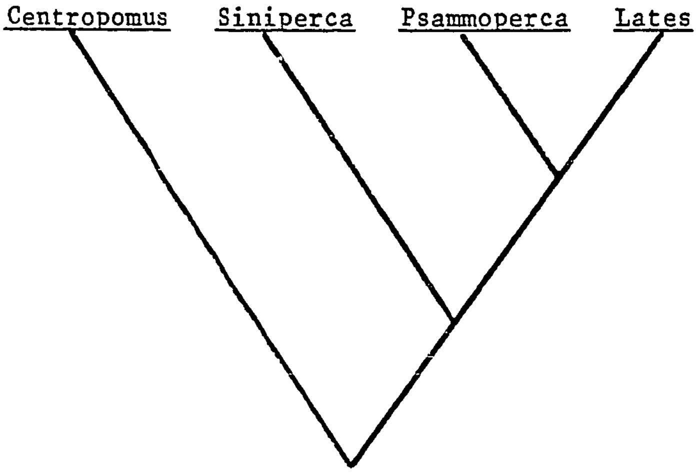
No synapomorphies were found between any two of the three taxa. Both the Moronidae and Percidae possess supplementary lateral line canals on the caudal fin, but the homology of this character is uncertain. Even if homologous, accessory canals would probably be plesiomorphic for such a union. These two taxa also share the complete loss of the supramaxilla, anteriorly rounded air bladders, and a largely parapatric distribution over two continents.

Moronids and Lateolabrax retain the subocular shelf, procurrent spur, and three anal spines. Both taxa also share the two alternative pigmentation patterns found in each. Members of Morone exhibit a longitudinally striped pattern and a spotted pattern. Within the bispecific genus Lateolabrax, L. japonicus shows a spotted pattern similar to M. punctatus, while L. latus has horizontal stripes (Katayama 1957) that resemble those of the American Moronidae. However, juvenile specimens of M. saxatilis (Scott and Crossman 1973), and possibly other moronids as well, show 6-10 vertical bars similar to those found in primitive percids.

Relationships of Siniperca

Greenwood (1976) presented a cladogram for the subfamilies of the Centropomidae. The results of this study indicate that Siniperca (and Coreoperca) comprise a heretofore unrecognized centropomid subfamily. The inclusion of Siniperca among the Centropomidae and its close alliance with the Latinae is strongly suggested by its possession of an entire suite of characters associated with the antero-posterior expansion of the second neural, unique ornamentation of the preopercle, enclosure of the preopercular portion of the preoperculomandibular canal by bone, and the derived form of the symplectic. Retention of two uroneural pairs suggests placement in Greenwood's (1976) cladogram as the sister taxon of the Latinae (Fig. 2). Shared retention of conditions normally lost or reduced in lower percoids are found for the configurations of the premaxilla and supramaxilla, primarily ventrally directed lateral ethmoid - lachrymal articulation, ceratohyal foramen, and anteriorly bilobed air bladder.

Figure 2.--Hypothesized position of Siniperca among the Centropomidae.



Two possible homoplasies are known. Freihofer (1963) placed Siniperca among his Pattern 8 group, and centropomids among Pattern 9. However, he noted several conflicts between his patterns and classification schemes of that time, and it is still not clear which groupings, if any, are correct. Johnson (1984) placed Gadopsis (Pattern 9) among the Percichthyidae (Pattern 8) despite the conflict in RLA state. A second homoplasious condition is that Siniperca lacks supralamellar teeth. Greenwood (1976) found these specialized teeth at the border between the gill filaments and supporting elements in both centropomid subfamilies. I believe their absence in Siniperca is a secondary reduction or loss. Close examination of specimens has revealed what appears to be a secondary sill in this region, a structure not seen in other percoids. Additionally, there is usually a thin layer of dermal bone proximal to the ceratobranchials in the same position where supralamellar teeth occur in the Centropomidae.

Relationships of Mioplosus

Cope (1877), who described this genus of western North American Eocene fishes, considered them allied to Labrax and Perca, but he added that with regard to Mioplosus labracoides, "They have much the proportions of the Rock-fish". Although Cope referred to them as perch and believed they probably belonged in the Percidae, they were not formally placed there until Jordan (1923), a decision that was reaffirmed by Grande (1980). Bailey (1938), in a somewhat gradistic analysis, considered Mioplosus as a percid that had undergone convergence toward a centrarchid form, but which might also have been a proto-centrarchid.

An examination of the specimens of Mioplosus in the AMNH revealed that Mioplosus is clearly not a percid, nor is there sufficient evidence to consider it ancestral to the Percidae. Non-alliance with the Percidae was indicated by the following characters:

1. Procurrent spur - Johnson (1975) lists the Percidae as lacking both the procurrent spur and the ventrally foreshortened ray often associated with it. Those specimens in which this region was visible prominently displayed these features (Fig. 14).

2. Supramaxilla - No member of the Percidae possesses the supramaxillary bone (Collette and Banarescu 1977). A large supramaxilla was observed in several specimens of Mioplosus (Fig. 13E).

3. Ceratohyal - The dorsal border of the percid ceratohyal is moderately concave with no evidence of a bony bridge spanning the depression. Mioplosus possessed a distinct oval foramen in that same region.

4. Scale morphology - Percids display a well amputated scalelet pattern in the posterior field of individual scales (by inference from McCully 1962, who noted its similarity of pattern to the scales of Morone and Lateolabrax, described in detail by McCully 1962). A well amputated percid scalelet pattern was confirmed by this study. I found Mioplosus to show a more primitive scale typewith the scalelets unamputated, a pattern displayed in

percichthyids (sensu Johnson 1984), centropomids, and centrarchids, among others.

5. Anal pterygiophore-vertebral column articulation - This study found that the percids, with the exception of the somewhat derived Perca (Collette and Banarescu 1977), possess relatively little articulation between the anterior interhaemals and the haemals. Mioplosus shows considerable bonding between these two sets of elements.

The first four characters listed are primitive in regard to the Percidae, and hence do not rule out, but also do not suggest, an ancestor - descendant relationship for Mioplosus and the percids. Character 5 appears to be more derived in Mioplosus and therefore conflicts with that hypothesis. Moreover, there do not appear to be any clear synapomorphies between the two taxa. Mioplosus was apparently placed in the Percidae because of a basic perch-like physiognomy, and because it possessed only two anal spines. There are many percoid taxa that possess two or less anal spines (Johnson 1984), rendering this a poor indicator of relationship at this taxonomic level.

Bailey (1938) hypothesized Mioplosus as possibly ancestral to the Centrarchidae. While no synapomorphies between these taxa are known to exist, there are far fewer character conflicts between Mioplosus and centrarchids than between Mioplosus and percids. Bailey postulated that the Centrarchidae evolved from marine ancestors which included Mioplosus as an early freshwater derivative of the centrarchid lineage. While the results of this analysis do not prohibit such a scenario, the presence of two anal spines, together with its procurrent spur, a supramaxilla, and an unamputated scalelet pattern all suggest that *Mioplosus* is closely related to the Percichthyidae (sensu Johnson 1984).

Indications of Relationship Suggesting Further Directions of Analysis

Several lines of future research were suggested by the results of this analysis. As McCully (1962) stated, scale morphology indicates a close relationship between percichthyids and centrarchids. An affinity between these two taxa and the Polyprioninae is also suggested based on scale features, and between percichthyids and centropomids based on scale morphology and air bladder and supramaxillary configurations.

Perhaps part of a large monophyletic group derived from some member of the group that includes the more plesiomorphic above-mentioned taxa, scale morphology and ceratohyal type indicates close relationship between lutjanids and their associated families, and sciaenids, moronids, lateolabracids, and percids. Extended epioccipital processes suggest affinity among the latter four taxa. Based on other characters, both Trewavas (1977) and Chao (1978) have discussed the possibility of a close relationship between lutjanids and sciaenids.

-CONCLUSIONS-

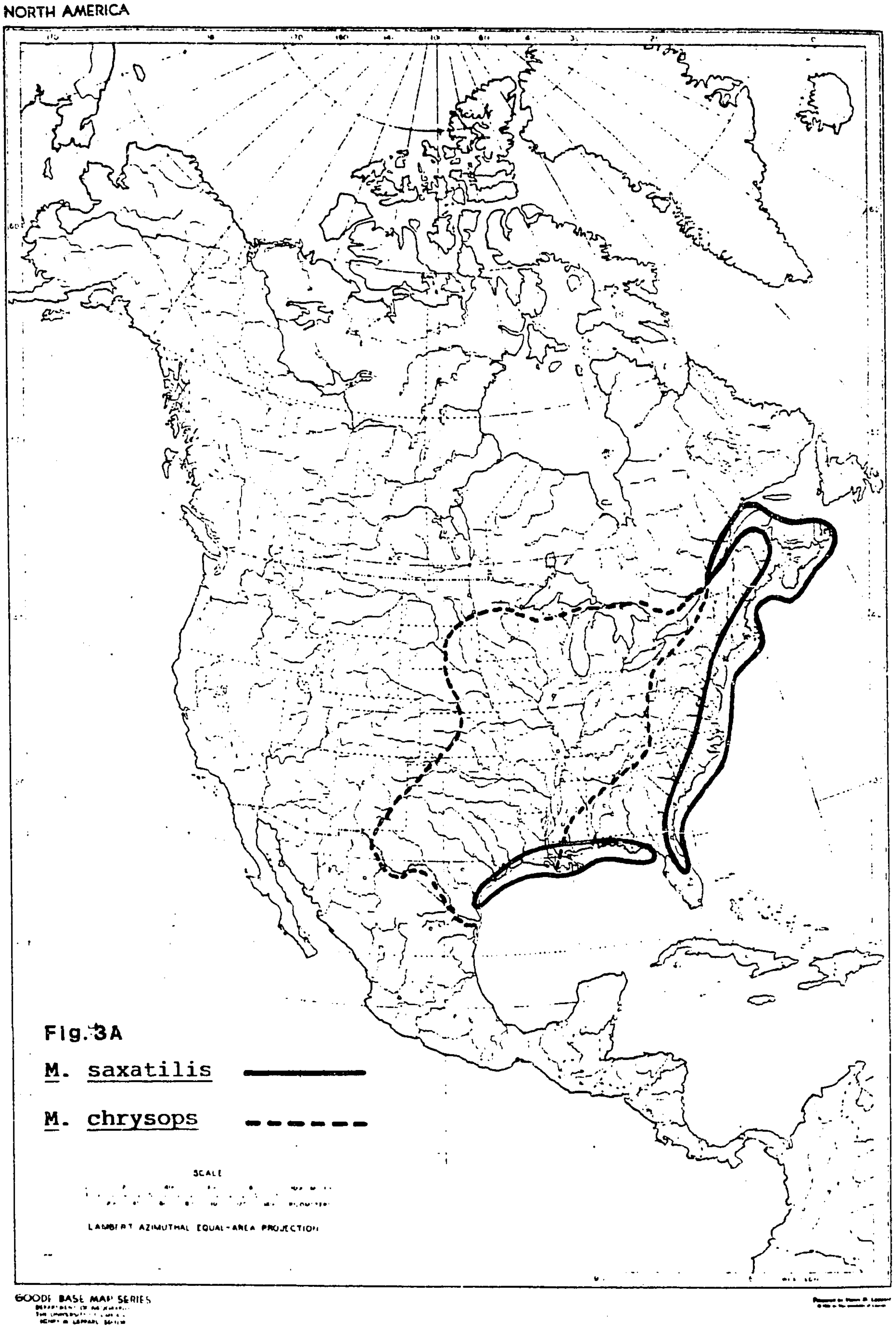
Given the generally good-to-excellent quality of their primary descriptions and prominence as commercially and recreationally important fishes, current comprehension of percoid interrelationships seems poor indeed. Although the genera appear well defined and in most instances the families also, resolution of interfamilial relationships has evaded analytical attempts by systematic ichthyologists.

Johnson (1980), in his discussion of the percoid problem, suggested a need for additional tabular studies of single characters or character complexes across large numbers of taxa. However, he underscored the importance of the alternative approach of investigating a single family or complex of families as steps toward a resolution of percoid interrelationships. I agree with Johnson that such an approach will eventually lead to an understanding of the phylogenetic relationships among these fishes.

It is important, however, that an implicit methodological point in cladistic analysis be emphasized for its application to the percoid problem. In the past, the focus in systematic work on the Percoidei has been on defining families. Characters that define a family are autapomorphic for that family and are hence of no value in interfamilial comparisons. In the future the focus must be directed toward analyzing fully resolved, family-level cladograms to identify which characters are primitive for these groups and yet derived for percoids, and then to search for synapomorphies among them.

Our understanding of relationships among the basal percoids has advanced a small but significant degree in recent years. Johnson

(1984) appears to have defined a more natural Percichthyidae, the taxa left _incertae sedis_ having formed the basis for two hypotheses advanced in this study. Because of the seeming paucity of synapomorphies at this level, such hypotheses may not appear well supported and indeed, there is no doubt that further testing is in order. However, the field of percoid systematics will remain static unless new hypotheses are set forth. As Rosen (1985) declared "... it is a far better thing to have proposed and been rejected on grounds of nonhomology than to never to have proposed at all."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M. saxatilis
M. chrysops
SCALE
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
GOODE BASE MAP SERIES

Fig. 3A

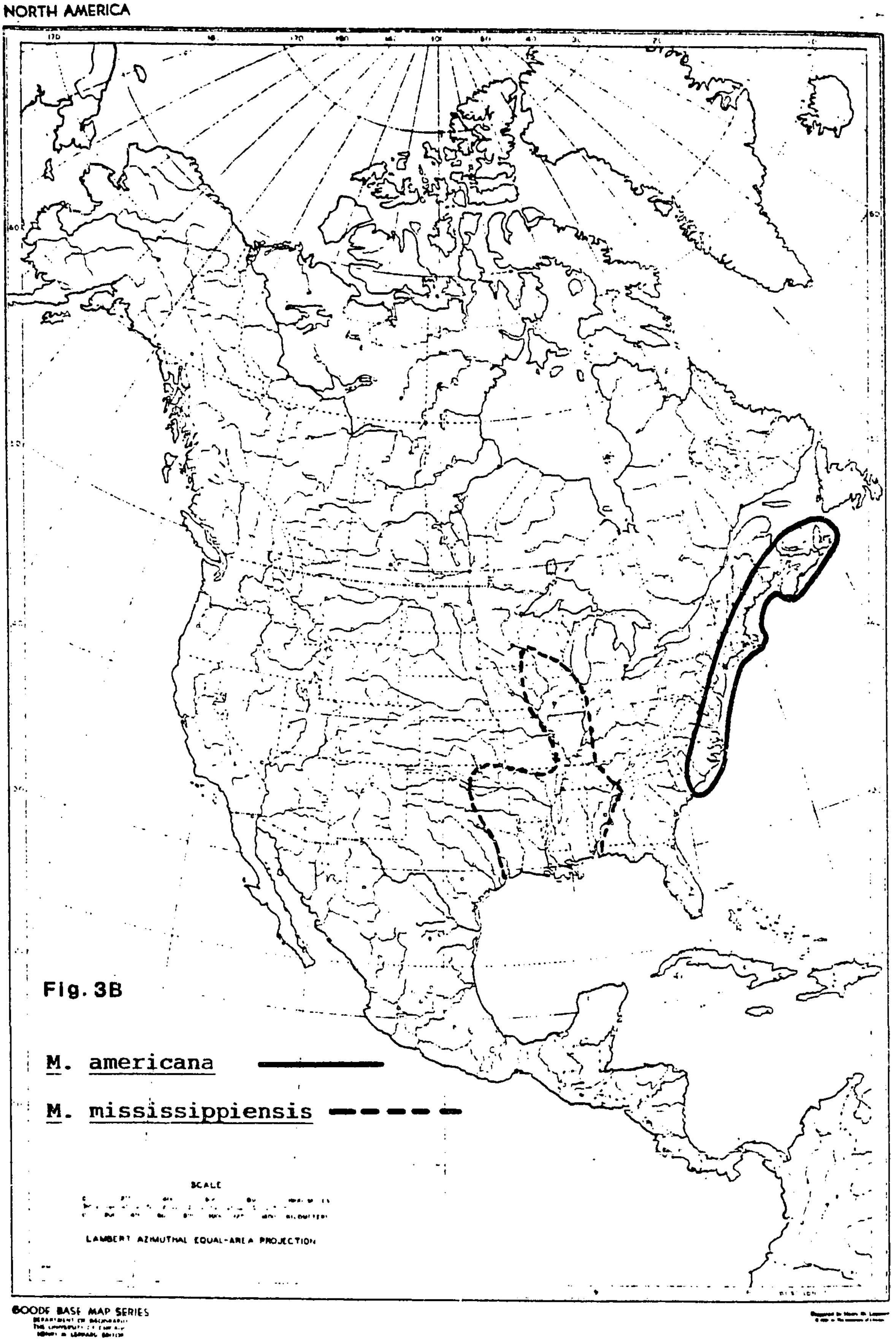

NORTH AMERICA
M. americana
M. mississippiensis
SCALE
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
GOODE BASE MAP SERIES

Fig. 3B

Fig. 3C

Fig. 3D

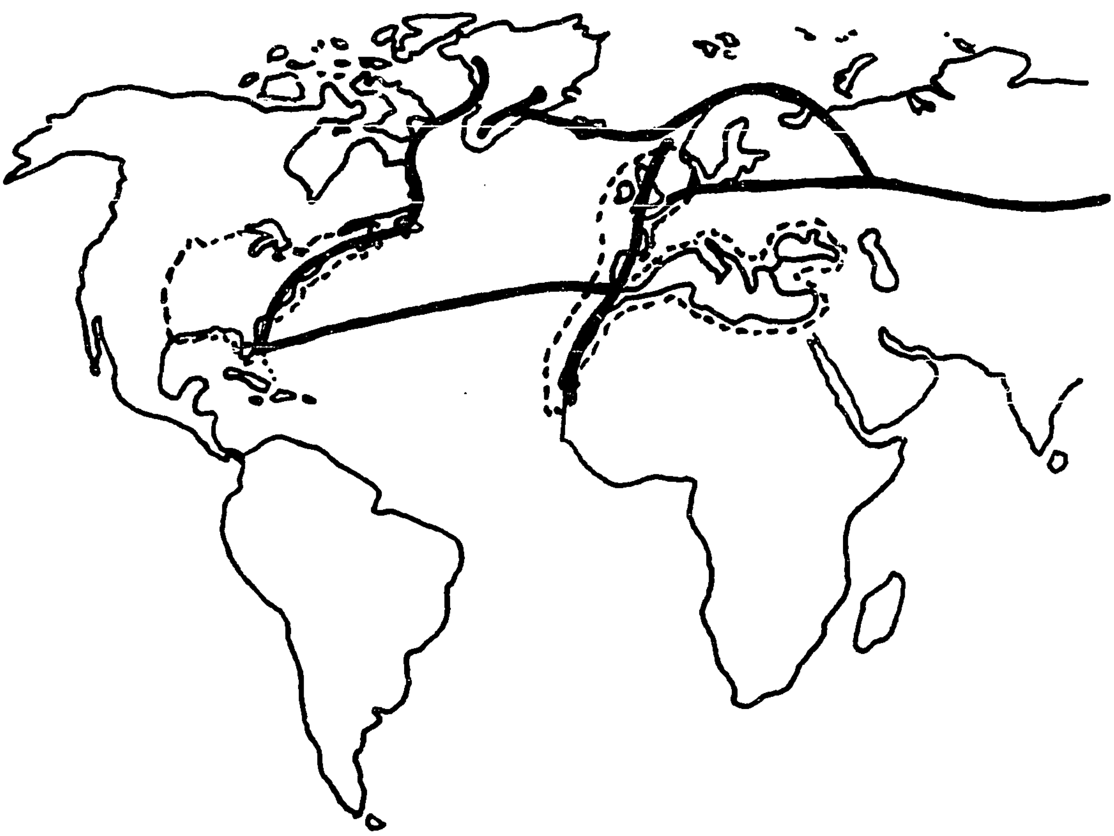


Fig. 4A

Fig. 4B

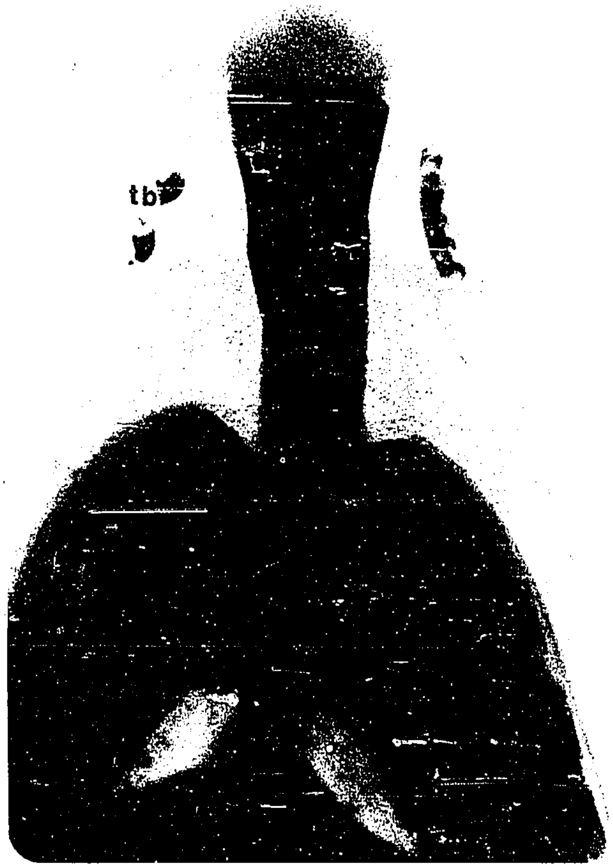
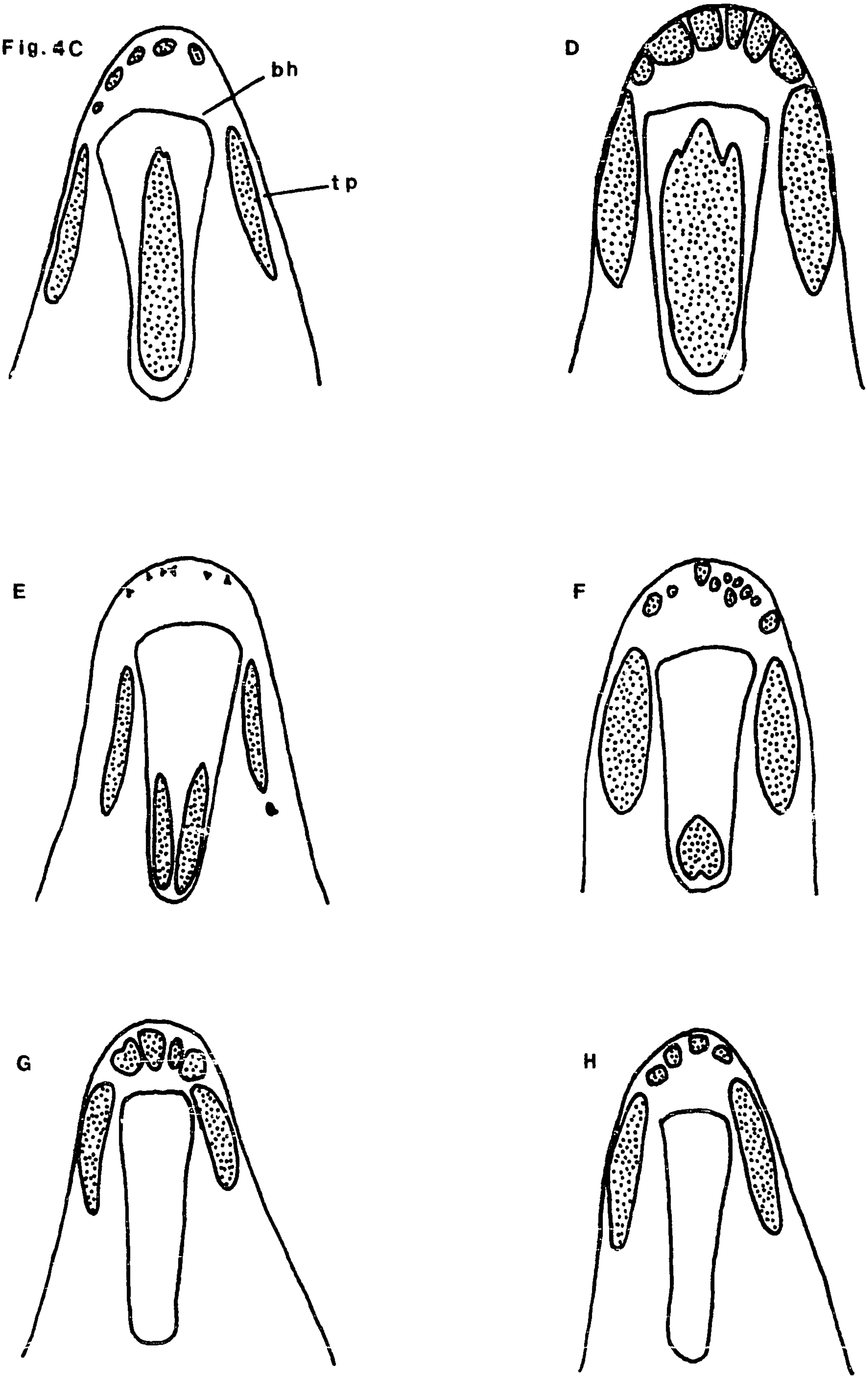


Fig. 4C



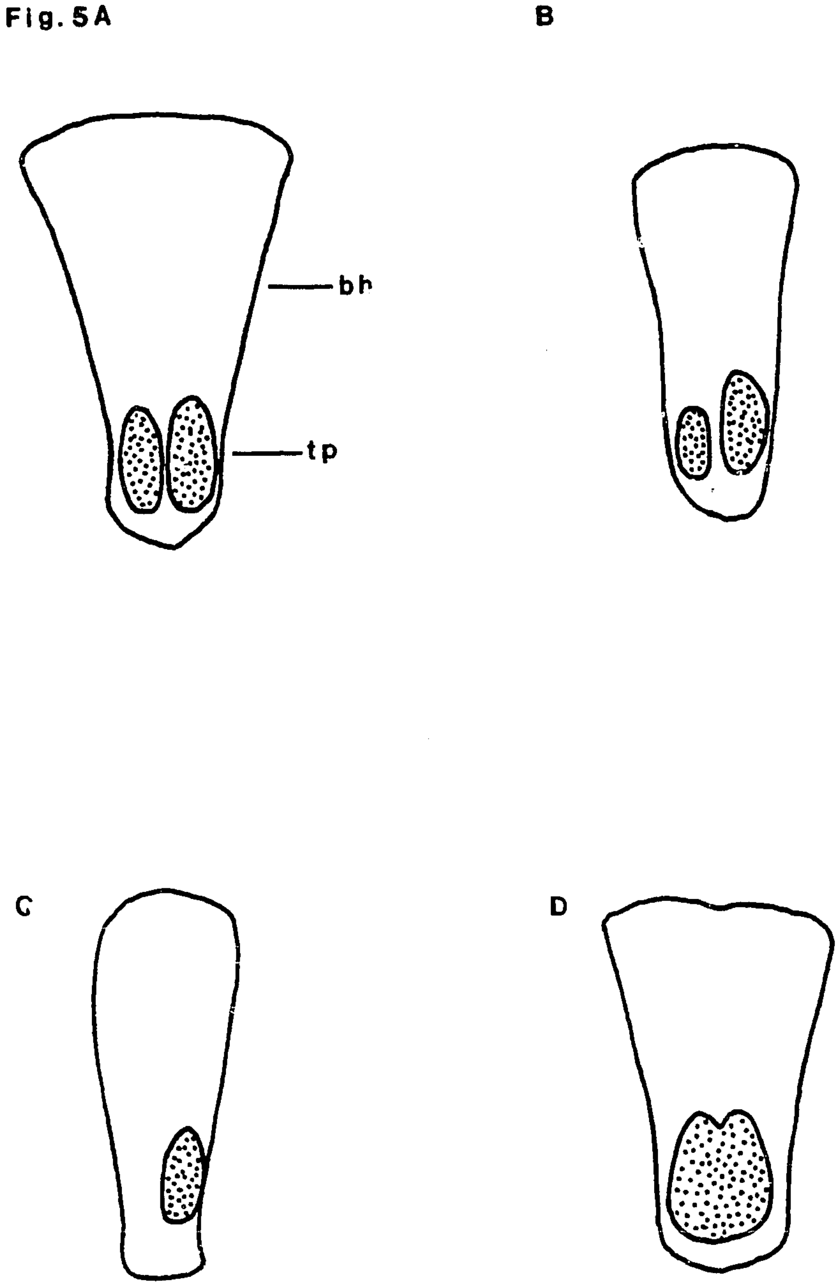


Fig. 5A

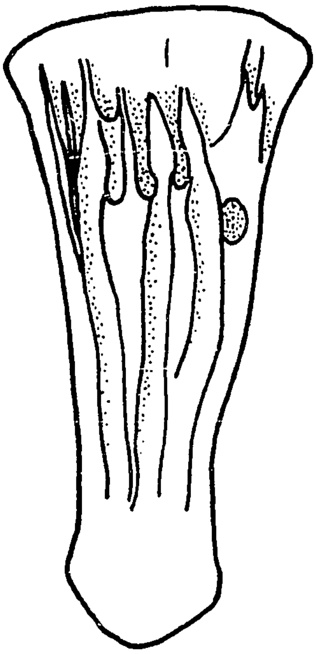
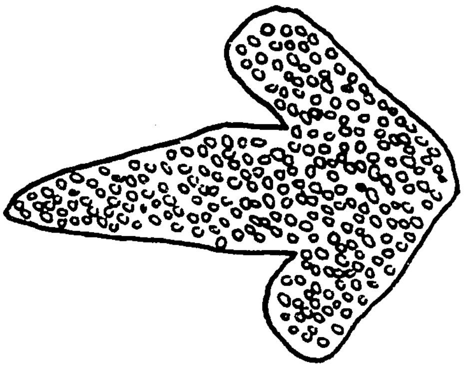
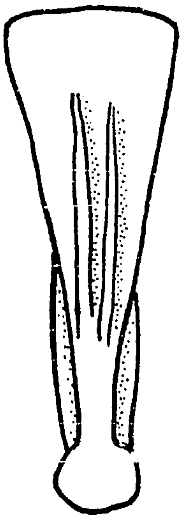


Fig. 6A

Fig. 7A





6B

7B

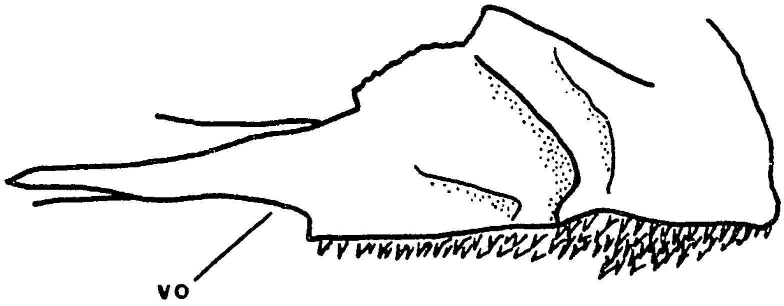
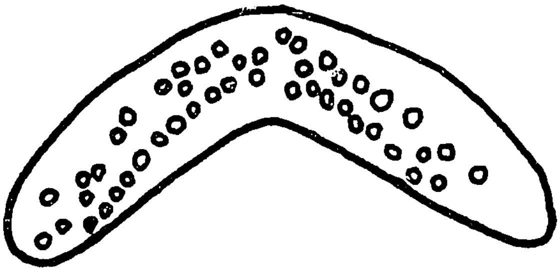


Fig. 7C



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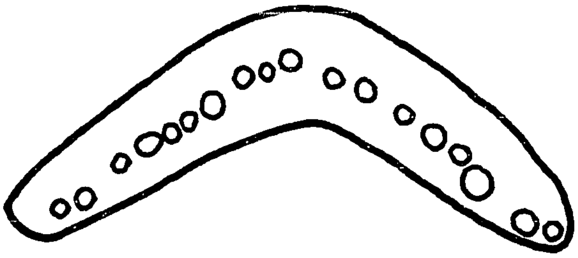

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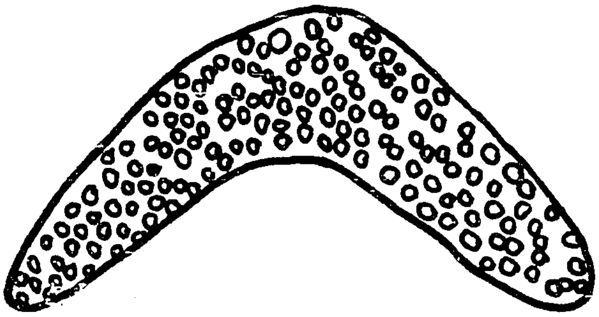
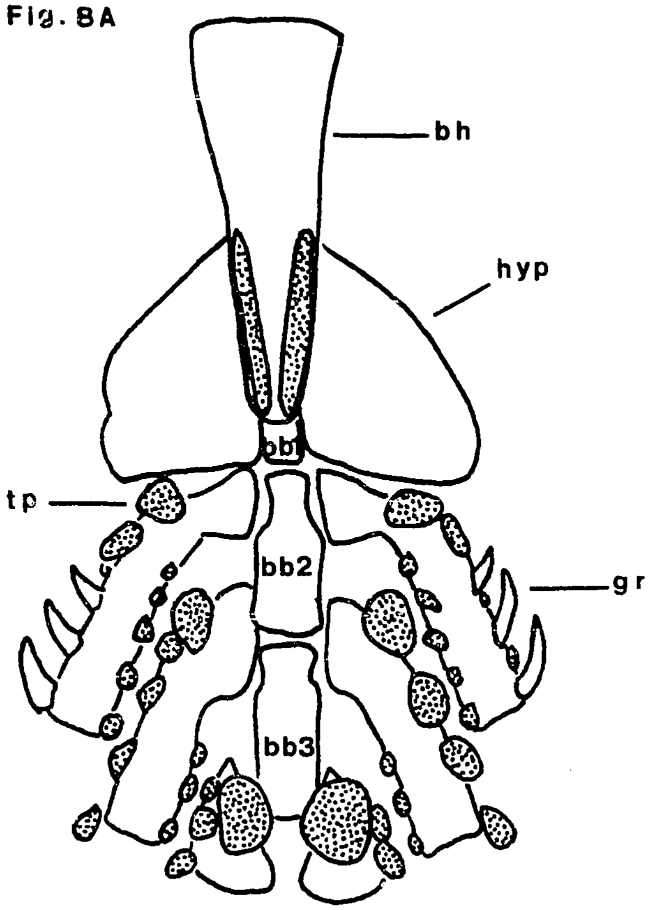


Fig. 8A



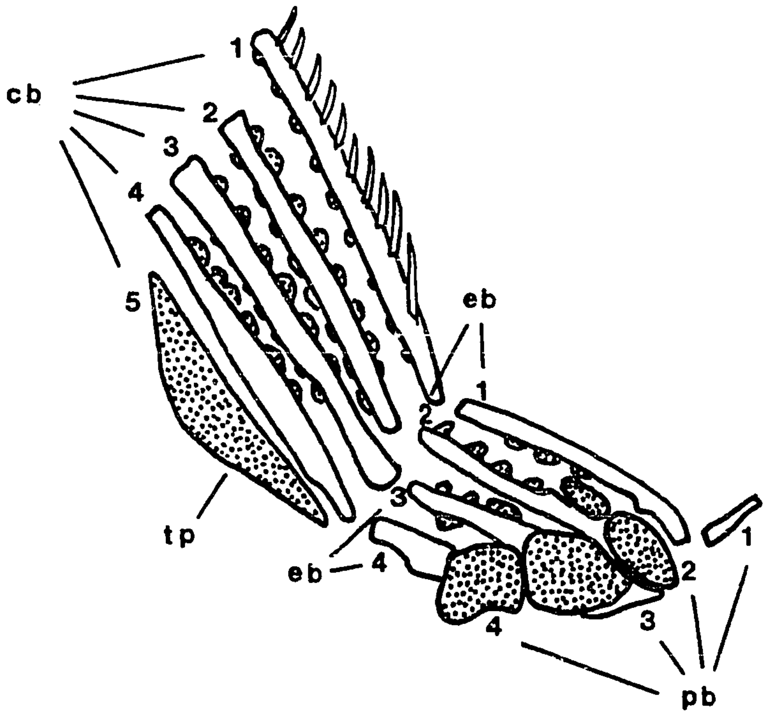
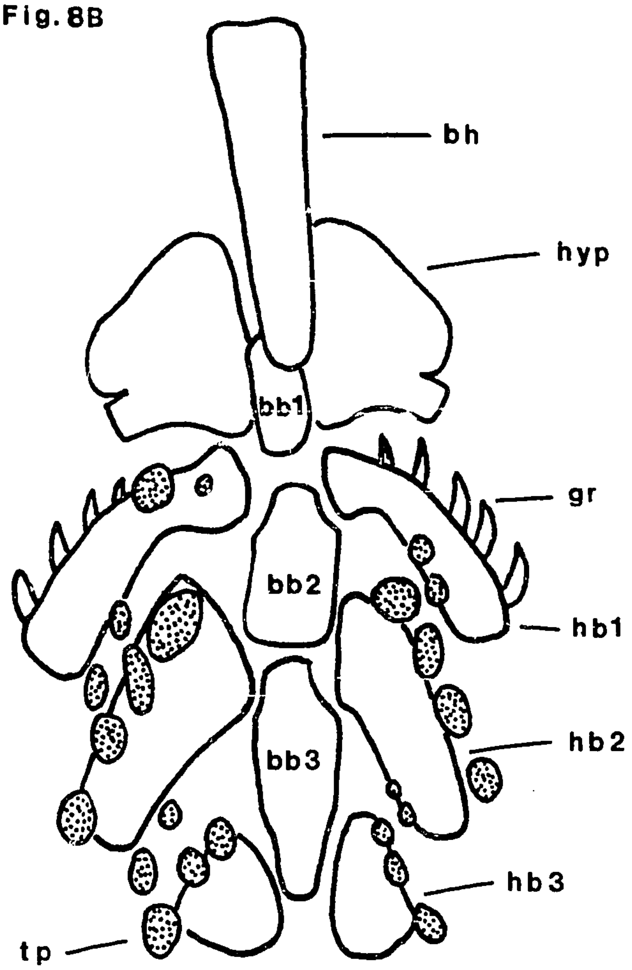


Fig. 8B



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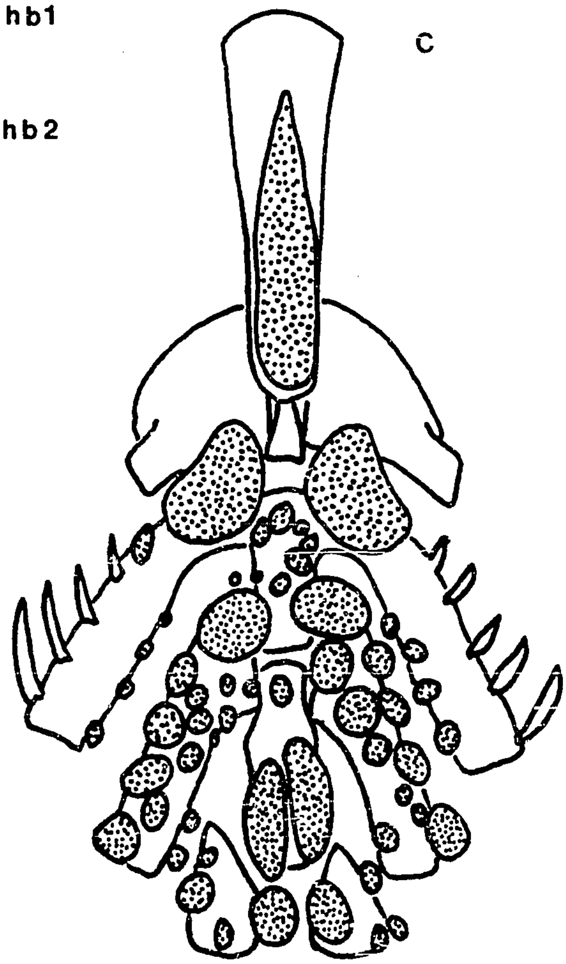
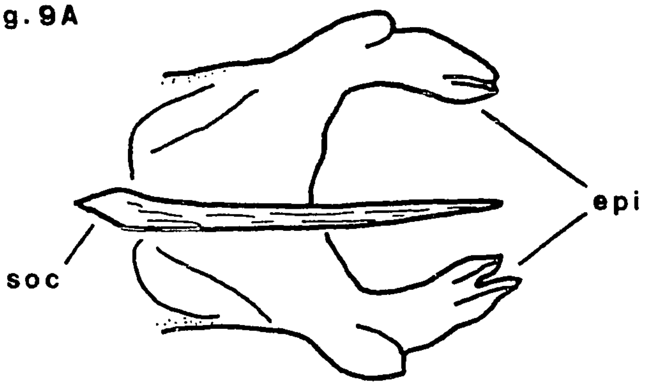


Fig. 9A



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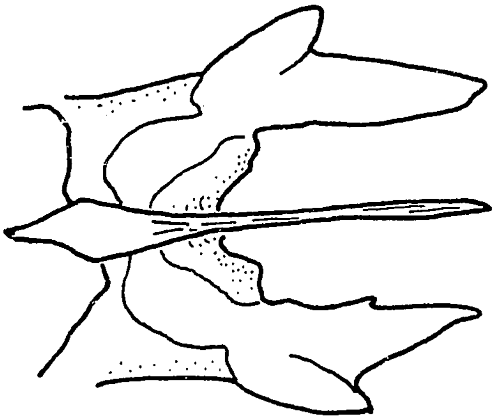

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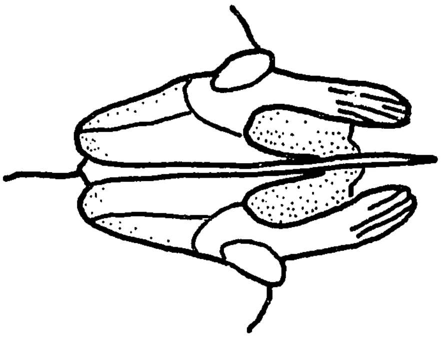
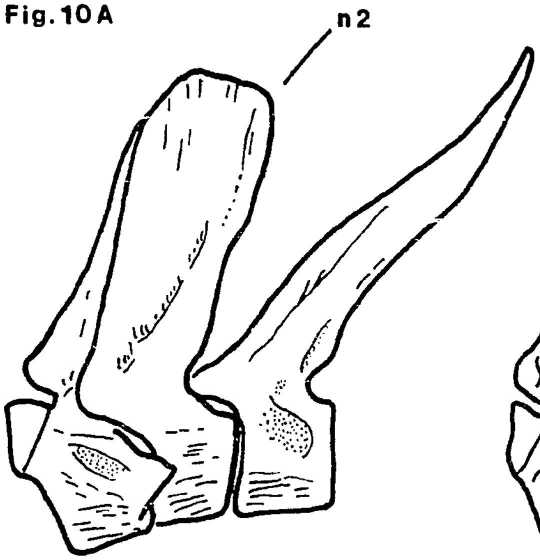


Fig. 10A



10B

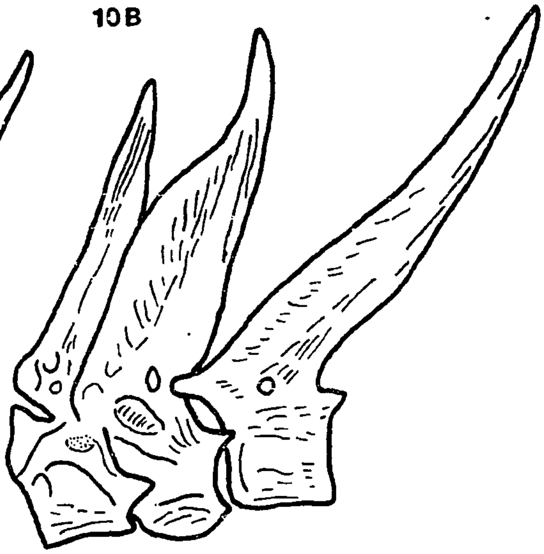


Fig. 11

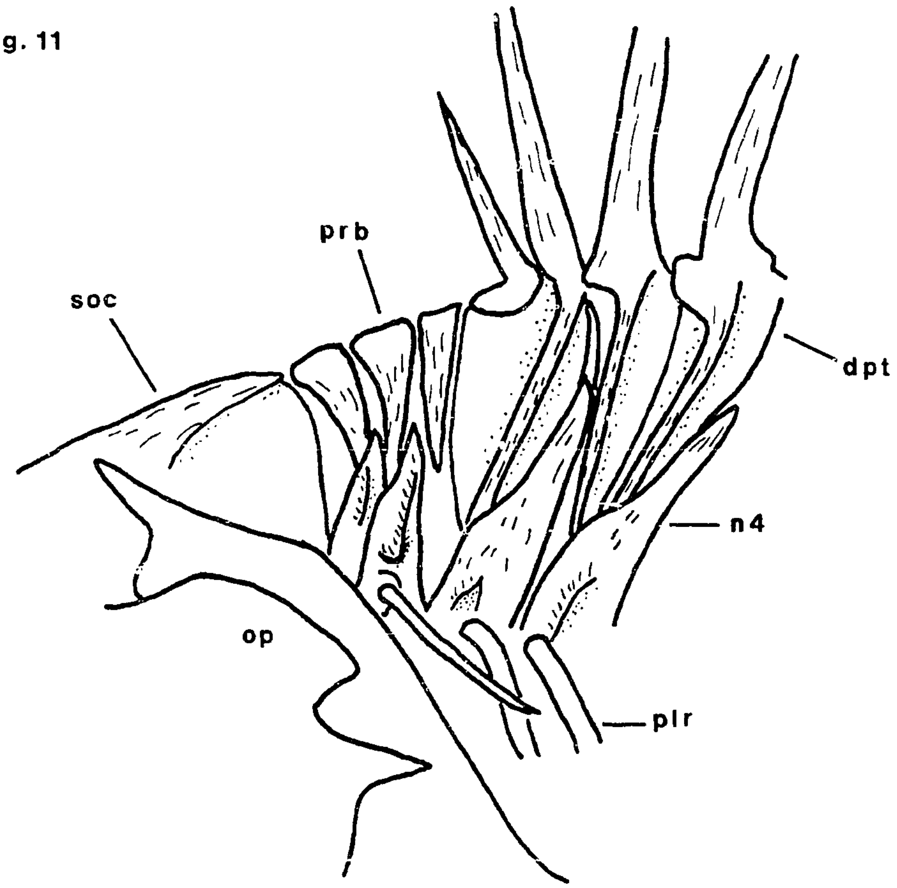
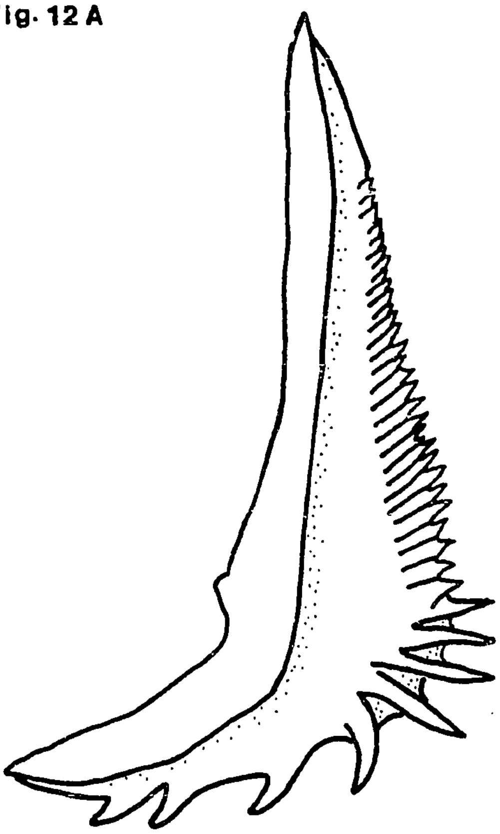


Fig. 12 A



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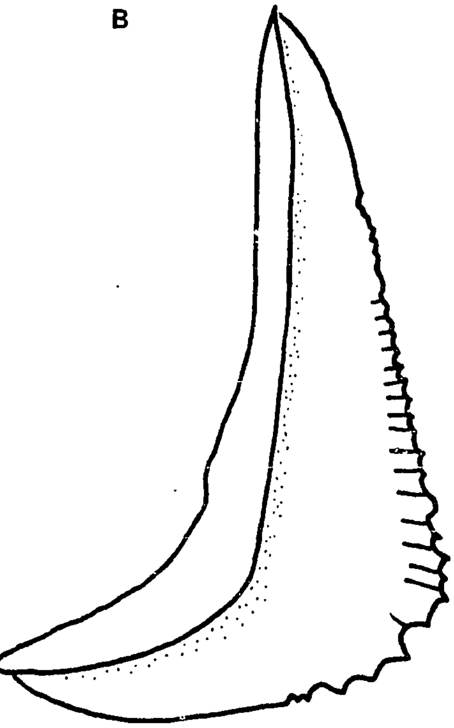
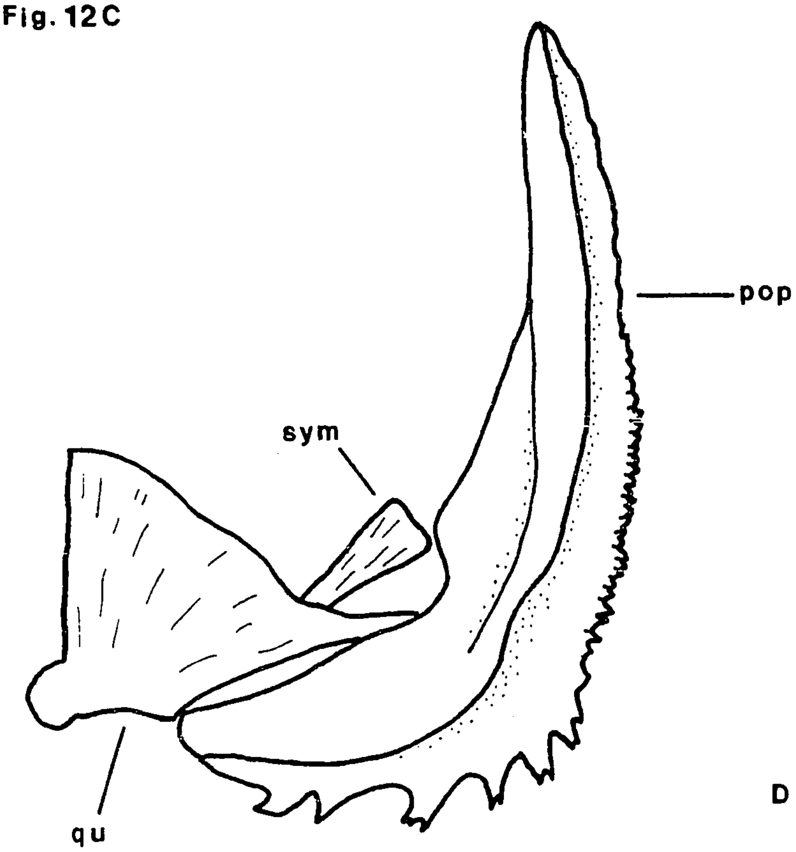


Fig. 12C



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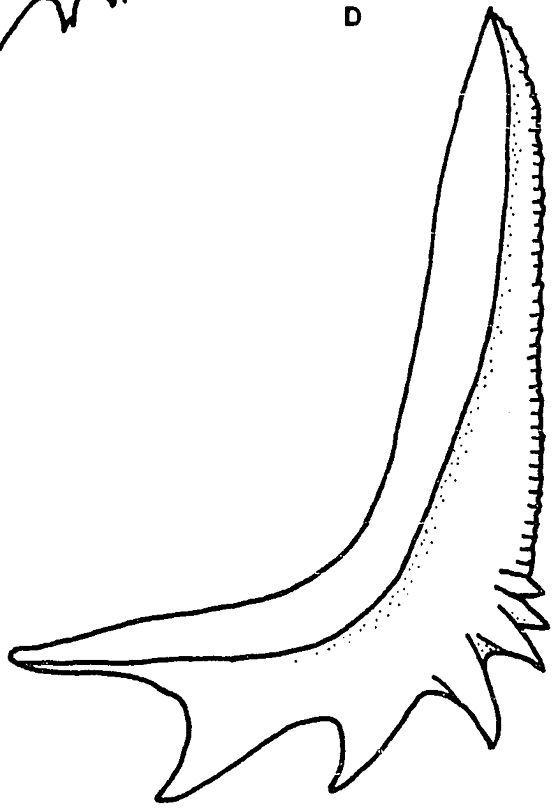
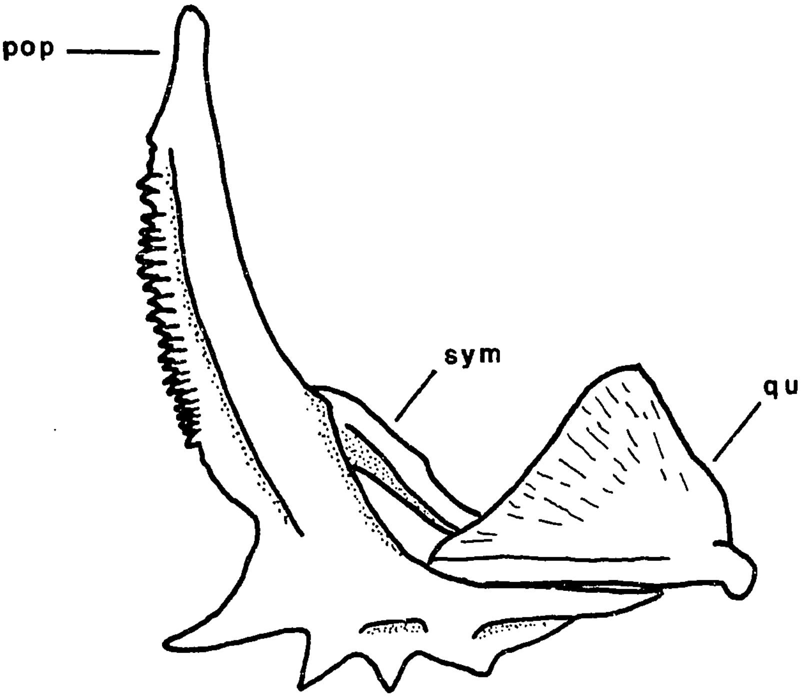


Fig.12E



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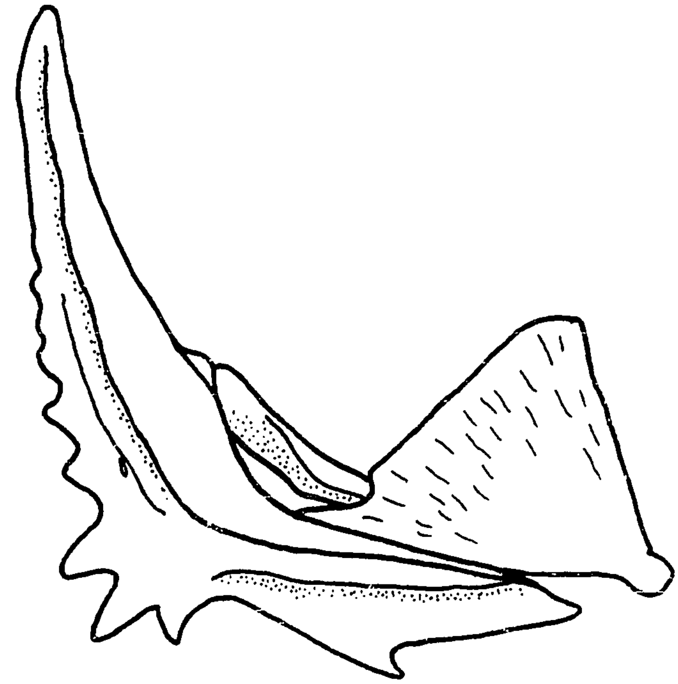


Fig. 13

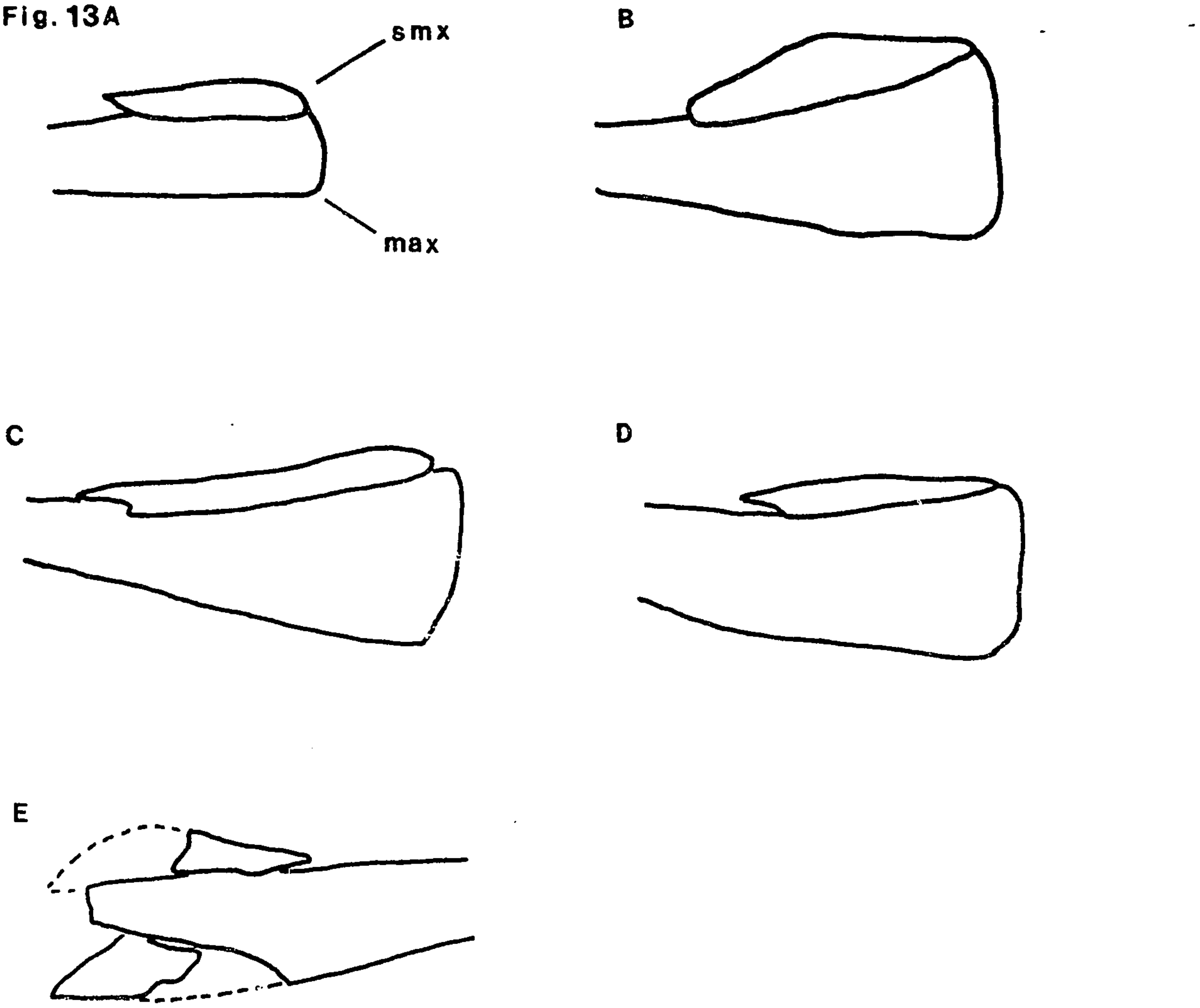


Fig.14

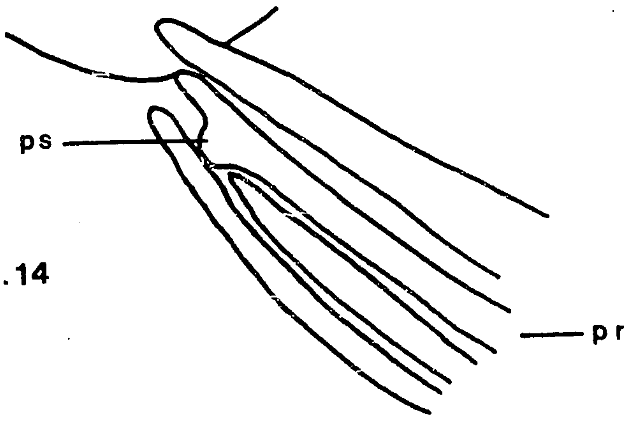
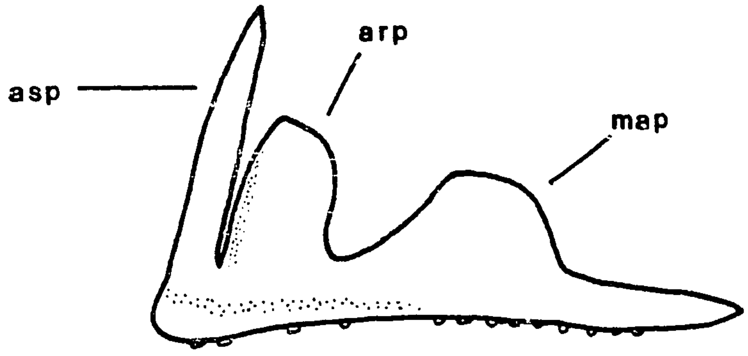
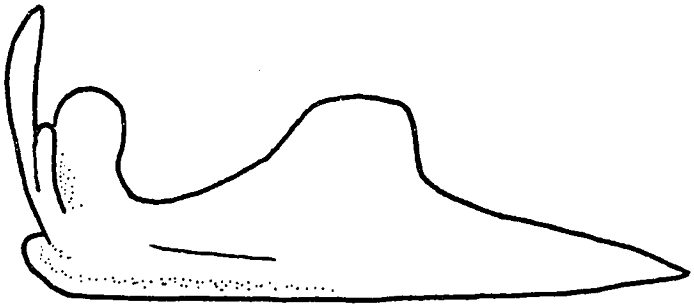


Fig.15A



B



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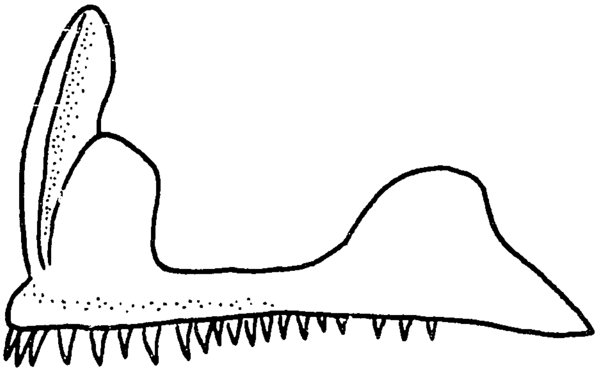


Fig.16A

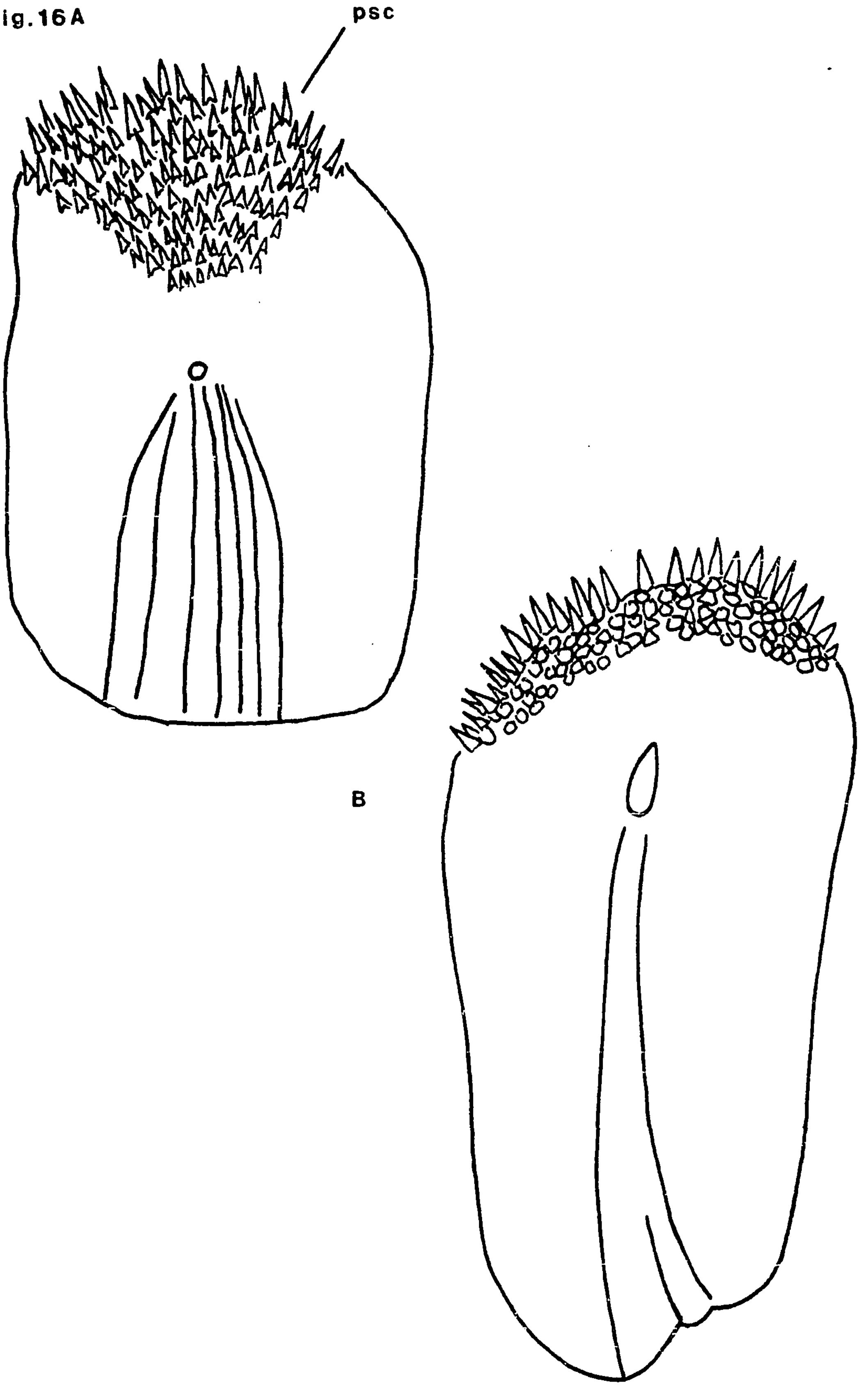


Fig. 16C

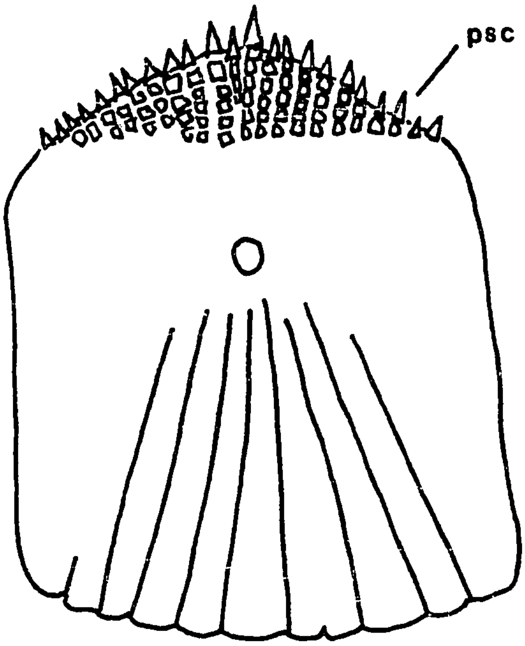
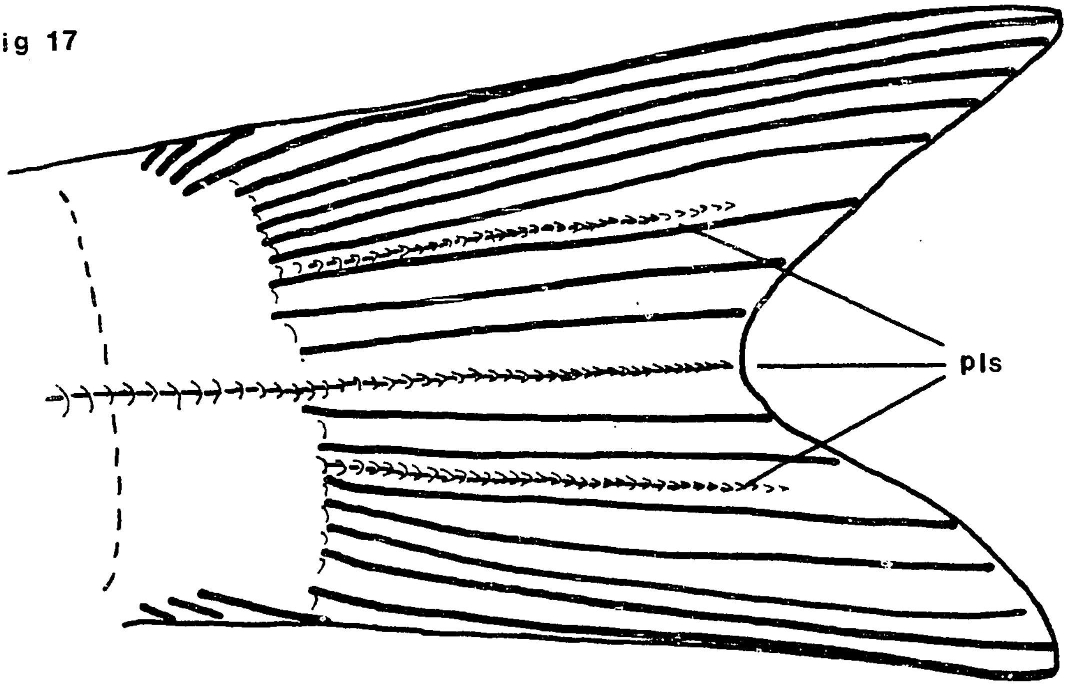


Fig 17



LIST OF ABBREVIATIONS USED IN FIGURES

arp - articular premaxillary process
asp - ascending premaxillary process
bb_{1-3} - basibranchial
bh - basihyal
cb_{1-5} - ceratobranchial
dpt - dorsal pterygiophore
eb_{1-4} - epibranchial
epi - epioccipital process
gr - gill raker
hb_{1-3} - hypobranchial
hyp - hypohyal
map - maxillary process
max - maxilla
n_{1-4} - neural spine
op - opercle
pb_{1-4} - pharyngobranchial
plr - pleural rib
pls - pored lateral line scales
pop - preopercle
pr - procurrent ray
prb - predorsal bone
ps - procurrent spur
psc - posterior scalelets
qu - quadrate
soc - supraoccipital
smx - supramaxilla
sym - symplectic
tb - tooth bud
tp - tooth patch
vo - vomer

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