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ABSTRACT

This study examined the intergeneric relationships of North American cyprinid fishes within North America and between certain North American and Eurasian genera. Scale morphology, osteology, meristic and anatomical features were studied. Twenty-eight characters were analysed and used to determine Hennig's coefficients between North American taxa as a measure of phylogenetic relationship. Higher values of Hennig's coefficient, which may vary from 0 to 1, indicated closer relationship. An additional seven characters were utilised in establishing relationships between North American and seven Eurasian genera.

Many relationships between North American genera were difficult to determine by Hennigian methods on the suite of twenty-eight characters used and the analysis separated the genera into five unlinked trees at the final clustering cycle. The relationships suggested by Hennig's coefficients correlated fairly well with the simple matching coefficient of numerical taxonomy. Reservations about the phylogenetic utility of certain characters and their effect on the construction of trees were discussed. However the close relationship of the genera Lepidomeda, Meda and Plagopterus was confirmed although their relationships to other genera could not be determined. The synonymy of Parexoglossum and Exoglossum (see Jenkins and Lachner, 1971 and Gilbert and

Bailey, 1972) was confirmed and the genus Phenacobius was closely allied to them. Semotilus (Margariscus) margarita was considered to be close to and congeneric with other Semotilus species.

Xystrosus Jordan and Snyder 1899 was synonymized with Algansea Girard 1856. Dionda and Hybognathus may also be congeneric.

Yuriria, currently regarded as a subgenus of Hybopsis, assorted with several western genera such as Gila and Orthodon and it was suggested that Yuriria be reinstated as a genus distinct from Hybopsis.

The Eurasian genera studied were Phoxinus, Tribolodon and the Abramidini genera Abramis, Alburnoides, Alburnus, Blicca and Vimba. Phoxinus assorted with Chrosomus with which it shared a derived character in breast tuberculation and was identical in most other characters. The synonymy of Chrosomus with Phoxinus proposed by Banareescu (1964) was confirmed. Notemigonus had its highest Hennig's coefficient with the Abramidini, particularly Alburnus and Alburnoides. Notemigonus was placed in the tribe Abramidini of the Leuciscinae as a distinct genus distinguished from other genera by osteological, tubercle and meristic characters. The relationship of Notemigonus to other North American cyprinids was considered to be remote. The other North American genera formed a fairly homogenous group with two major sub-groupings, a western and an eastern one. They were tentatively placed in the Leuciscinae. The north-east Asian genus Tribolodon has been advanced as a relative of the western North American genus Gila but they

shared a low Hennig's coefficient and Tribolodon assorted instead with other western American genera particularly Mylopharodon, Acrocheilus, Mylocheilus and Ptychocheilus.

RESUME

Cette étude a examiné les relations intergénériques parmi les Cyprinidés d'Amérique du Nord et aussi entre certains Cyprinidés d'Amériques du Nord et d'Eurasie. La morphologie des écailles, l'ostéologie, les traits numériques et anatomiques été étudiés. Comme mesure des relations intergénériques, vingt-huit caractères ont été analysés et utilisés pour déterminer les coefficients d'Hennig entre les taxa d'Amériques du Nord. Les valeurs les plus élevées du coefficient d'Hennig, qui peuvent varier de 0 à 1, ont indiqué une relation étroite. De plus, sept autres caractères ont été utilisés dans l'établissement des relations entre sept genres d'Eurasie et tous ceux d'Amériques du Nord.

A la suite de ces vingt-huit caractères utilisés, plusieurs relations entre les genres d'Amériques du Nord ont été déterminées difficilement par les méthodes d'Hennig; les genres d'Amériques du Nord ont été divisés en cinq arbres phylogénétiques distincts, sans aucun bien, au dernier cycle de regroupement. Les relations proposées par les coefficients d'Hennig s'accordent assez bien avec les coefficients concordants simples de la taxonomie numérique. Certaines restrictions ont été discutées quant à l'utilité phylogénétique de certains caractères et leur effet sur la construction des arbres phylogénétiques. Quoi qu'il en soit la relation étroite entre Lepidomeda, Meda et Plagopterus a

été confirmée, mais leurs relations avec les autres genres n'ont pu être déterminées. La synonymie de Parexoglossum et Exoglossum (voir Jenkins et Lachner, 1971 et Gilbert et Bailey, 1972) a été confirmée et le genre Phenacobius a été relié à ces derniers. Semotilus (Margariscus) margarita a été relié avec les autres espèces Semotilus et n'a pas été considéré comme un genre distinct. Xystrosus Jordan et Snyder 1899 a été considéré comme synonyme de Algansea Girard 1856. Dionda et Hybognathus peuvent être aussi congénériques. Yuriria, anciennement considéré comme sous-genre d'Hybopsis, s'est assorti avec plusieurs genres occidentaux comme Gila et Orthodon et il a été suggéré que Yuriria soit rétabli comme genre distinct d'Hybopsis.

Les genres d'Eurasie étudiés ont été Phoxinus, Tribolodon et les genres d'Abramidini Abramis, Alburnoides, Alburnus, Blicca et Vimba. Phoxinus s'est assorti avec Chrosomus avec lequel il partageait un caractère dérivé dans la tuberculation thoracique et était identique dans la plupart des autres caractères. La synonymie de Chrosomus et Phoxinus tel que proposé par Banarescu (1964) a été confirmée. Notemigonus a eu le plus haut coefficient d'Hennig avec les Abramidini particulièrement avec Alburnus et Alburnoides. Notemigonus a été placé parmi les Abramidini comme genre distinct différencié des autres genres par les caractères ostéologiques, numériques et par les tubercles. La relation de Notemigonus avec les autres genres de Cyprinidés d'Amérique du Nord a été considérée comme reculée.

Les autres genres d'Amériques du Nord ont formé un groupe homogène avec deux sous-groupes, l'un à l'est et l'autre à l'ouest. Ils ont été placés à l'essai parmi les Leuciscinae. Il a été avancé que le genre Tribolodon d'Asie du Nord-Est est apparenté au genre Gila d'Amérique du Nord occidentale mais ils ont eu commun un bas coefficient d'Hennig. Plutôt Tribolodon a eu des rapprochements avec d'autres genres d'Amérique du Nord occidentale particulièrement avec Mylopharodon, Acrocheilus, Mylocheilus et Ptychocheilus.

INTRODUCTION

Fishes belonging to the family Cyprinidae are found in Africa, Eurasia and North America and comprise the largest freshwater family of fishes. Distinguishing characters include possession of a Weberian apparatus, presence of parietal, symplectic and subopercular bones and low numbers of pharyngeal teeth in 1 to 3 rows.

At the generic level three problems confront the North American ichthyologist: 1) determination of which North American taxa are valid at the generic level since many taxa have been treated as both genera and subgenera, 2) the relationships between North American genera, and 3) the validity of proposed relationships between North American and Eurasian genera. This thesis presents new data and summarises published data on scale structures, osteology, meristic and anatomical characters and attempts to interpret and suggest intergeneric relationships on the basis of this information. The work is based principally on the North American cyprinids but also includes some data on Eurasian cyprinids particularly the genera Abramis, Alburnoides, Alburnus, Blicca, Phoxinus, Tribolodon, and Vimba.

Organisation of the thesis

Taxa of North American cyprinids have been allocated to various genera and sub-genera by different authors.

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A detailed review of these changes is not given here but a summary of them is contained in the annotated list of species (Appendix 2). The choice of genera and sub-genera studied for this thesis is discussed in the section on character analysis.

The thesis is divided into 4 sections, each with its own introduction, dealing with scale structures of North American and selected Eurasian genera, osteology of North American genera, character analysis for North American genera and Nearctic - Palaearctic relationships. The latter section also includes osteological data. Appendix 1 lists the material examined and gives some indication of the section it was used in. Appendix 2 is an annotated list of North American cyprinid species. Appendix 3 gives a literature review of the placement of genera in sub-families and Appendix 4 is a note on the nomenclature of the genus Endemichthys. Appendix 5 gives listings of programs used in the character analysis. Appendix 6 lists the genera of North American cyprinids referred to in this thesis with the author and year of publication.

Scale Studies

INTRODUCTION

Scale characters are used with some success in keys for the identification of North American cyprinids, e.g. Moore, 1968; Scott and Crossman, 1973 indicating a consistency of variation in morphology between species and genera. However the use of scales for systematic studies within this family has been largely neglected despite the work of Chu (1935) on Chinese cyprinids which demonstrated marked differences between otherwise similar genera. A general survey of North American cyprinid scale morphology was carried out by Cockerell (1909a, 1909b, 1909c, 1910, 1911a, 1911b, 1914, 1915), Cockerell and Allison (1909), Cockerell and Calloway (1909a, 1909b) and Cockerell and Moore (1910). These studies are of limited value because they were based on only a few scales (Chu, 1935: 72-73) and thus little allowance could be made for variations and abnormalities. The relative importance of other characters and the limits of genera have undergone considerable revision since Cockerell's works and a reassessment of scale morphology in the light of these new considerations is in order.

More recent works on cyprinid classification have found number of scale radii to be a useful criterion for characterising genera and sub-genera (Hubbs and Black, 1947; Jenkins and Lachner, 1971). The importance of scale characters has been acknowledged explicitly in papers by Hubbs and Miller (1972) and Hubbs, Miller and Hubbs (1974) on Great Basin cyprinids.

This study surveys scale structures in 47 genera containing 87 species and over 700 specimens of North American cyprinids and uses this data to indicate generic relationships within North American and between certain North American and Eurasian genera. The close similarity of many North American genera precludes the widespread use of scale data in determining relationships and the characters examined will be assessed with others in a later section.

MATERIALS AND METHODS

Materials

The specimens examined are listed in Appendix I. Wherever possible adult fish were used but in certain species only sub-adult individuals were available.

Procedure

Preserved specimens were probed with a dissecting needle to determine if the scales were caducous or embedded. Scale counts were made on preserved fish except for the smaller scaled species which were stained with alizarin to facilitate accuracy. Scale distribution, lateral line shape, imbrication and overlap count were determined on specimens stained in a 2% potassium hydroxide solution with alizarin. Patches of scales were removed from the areas shown in Figure 1 and examined on slides under a binocular microscope for general shape, radii distribution, focus position, circuli development



Figure 1. Diagram of a cyprinid fish to show areas (X) from which scales were removed for detailed examination.

and mucous tube position on lateral line scales. Morphological descriptions and radii counts were based mainly on non-regenerating scales taken from immediately above the lateral line on the caudal peduncle (Chu, 1935). Photographs were taken of scales mounted on slides with euparal after a brief wash in 95% ethanol. Further explanations of methods used in describing characters is given under "Definitions".

Definitions

Scale studies ("lepidology") have been favoured with a plethora of terms and definitions. A glossary of terms used throughout this study is given below to obviate confusions of meaning. (see also Figure 2).

a) Scale Shape

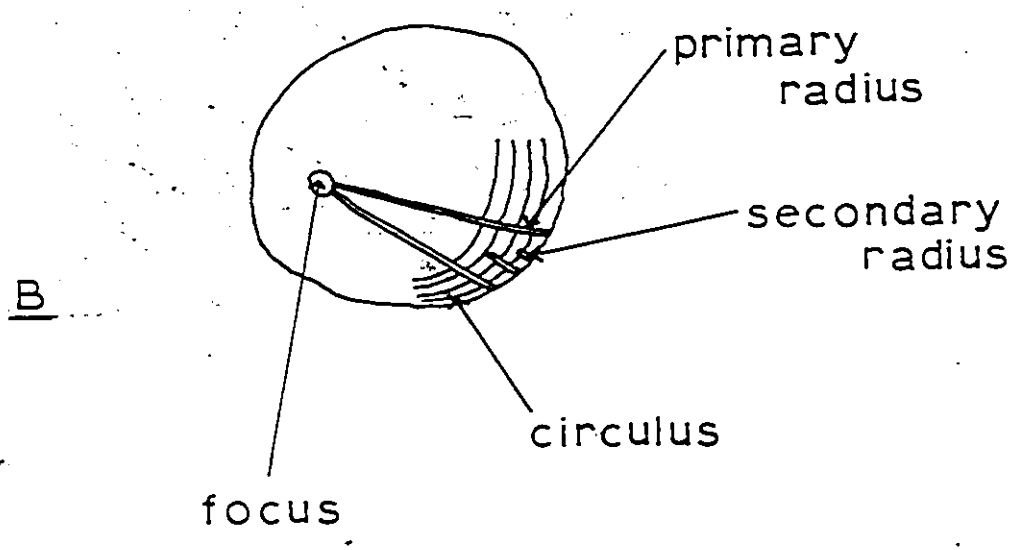
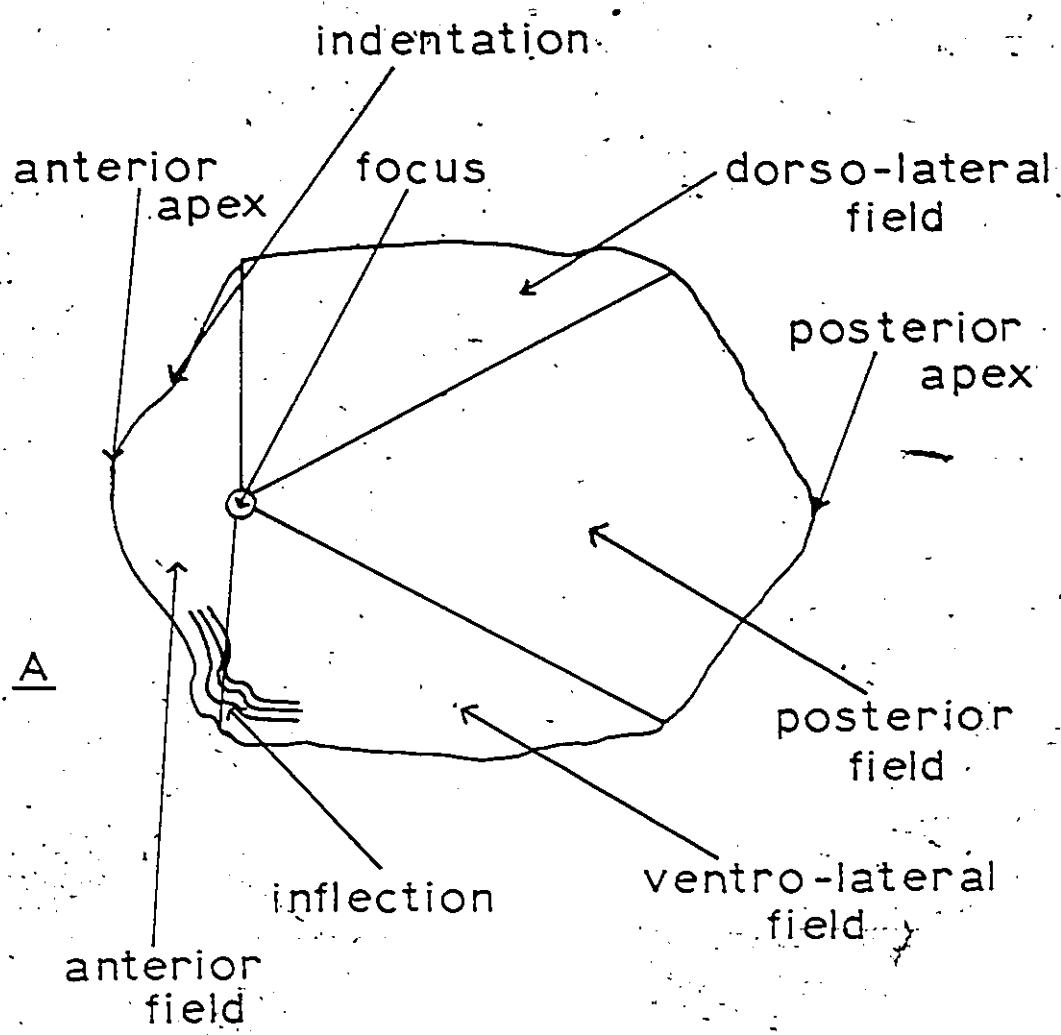
The general shape of scales varies, not only between species but between different parts of the body of an individual specimen. Scales may be approximately hexagonal, oval, circular or triangular.

b) Field

A scale may be divided into 4 distinct areas or fields: the anterior (or basal) field, the dorsal and ventral lateral fields and the posterior (or apical) field (Figure 2). The anterior field is embedded in the dermis and the posterior field is exposed where it overlaps the next posterior scale. The lateral fields are overlapped by adjacent scales. The fields are easily discernible in hexagonal scales but subjective in circular or sub-circular scales. In the hexagonal scale the junction of the anterior and lateral fields is formed by an obvious antero-lateral angle. Postero-lateral



Figure 2. Diagrams of scale structures based on A- Semotilus corporalis caudal peduncle scale 8 mm. in length, and B- Eremichthys acros caudal peduncle scale 0.8 mm. in length.



angles may also be present but are often less marked than antero-lateral angles. The margins of the lateral fields are straight, curved or indented. These edges are parallel or converging posteriorly. The margins of the posterior field are smooth, gently curved and converge to a rounded posterior apex. This apical portion of the scale is more produced than the basal portion. The margins of the anterior field converge to a rounded apex or they form a continuous shallow convex curve. The posterior margins are variably indented, irregular, wavy or smooth. In the oval and circular scales antero- and postero-lateral angles are poorly developed or absent. The margins are usually smooth.

c) Radius

The bony structure of the scale is interrupted by linear grooves known as radii. All North American cyprinids have radii on the posterior field, some have radii on the posterior and lateral fields and others have radii on all fields. A primary radius is one extending from the scale edge half way or more to the focus. Shorter radii extending from the scale edge to a point less than half way to the focus are termed secondary radii. Radii extending from the focus outward were rare and were assigned to primary or secondary status by their length. Primary and secondary radii were counted separately. Short radii lying in mid-field were included in counts of secondary radii and a branched primary or secondary radius was counted as one radius. A maximum of 110 total radii was found in N. American genera.

d) Focus

The focus is the original embryonic scale (Chu, 1935). Its position on the developed scale is variable and is determined by the relative growth of the anterior and posterior fields. The central position is found when the anterior and posterior fields are equal in size and the anterior position when the posterior field is the larger. The posterior or lateral position is not found in North American cyprinids.

e) Circulus

Circuli are bony ridges on the scale surface. These structures are arranged around the focus and are interrupted by the radii. They are variably developed and spaced on the scale fields although the variation is continuous rather than abrupt. Where circuli pass from the lateral fields to a small anterior field the transition may be effected by an antero-lateral inflection. In scales with an anterior focus the posterior circuli are usually fewer and more widely spaced than those on the lateral and anterior fields. This is due to more rapid growth of the posterior field and to loss of circuli in the lateral fields.

f) Scale Counts

Several scale counts are commonly used in identification of cyprinid fishes and are also useful in classification. The lateral line count is the number of pored scales in the lateral line along the flank or the midlateral number of scales along the flank when the lateral line pores are

absent. The count ends at the scale overlying the posterior edge of the hypural tail bones even though there are pored scales posterior to it. The first scale in the series is the first anteriormost pored scale touching the pectoral girdle. No allowance could be made for increase in counts with size (Repa, 1974) but hopefully this was minimal.

Scales above the lateral line are counted from the anterior base of the dorsal fin ventrally and posteriorly to the lateral line but not including the lateral line scale.

Scales below the lateral line are counted in a similar manner from the anterior base of the anal fin dorsally and anteriorly to the lateral line. These two counts follow the natural scale rows and include any small scales at the fin bases including the midventral or mid-dorsal scale where this protrudes lateral to the first fin ray. The predorsal scale count extends from the anterior base of the dorsal fin to the occiput. Scale rows were counted to one side of the dorsal mid-line because mid-line predorsal scales may be small and irregularly arranged in some species. Some literature reports do not state whether predorsal scale rows or predorsal scales along the mid-line were counted. Predorsal counts with a wide range often include individuals or species counted along the mid-line. The caudal peduncle scale count includes all scales around the narrowest part of the caudal peduncle. These five counts were compiled from the available specimens and the literature. Absolute scale size varies with age and the position of the scale on the body.

Scale counts are a more accurate measure of scale size. In addition counts above and below the lateral line may be compared to assess decurvature of the lateral line, e.g. in Notemigonus crysoleucas with a strongly decurved lateral line these counts are 8-11 and 2-4 respectively whereas in Phenacobius mirabilis with an almost straight lateral line, they are 6-7 and 5-6 respectively. It is realised that decurvature may be more readily assessed by using the lateral line to pelvic fin base count but this was not as extensively recorded in the literature as the one used. Two other scale counts were employed, the number of scales per vertebra and the number of scales over- and under-lapping an arbitrarily chosen flank scale. The latter count is described below under imbrication. The number of scales per vertebra is a measure of scale size and is derived from the lateral line scale count and the total number of vertebrae (including 4 Weberian vertebrae and the hypural plate as one vertebra). This relationship, derived in part from the literature, must necessarily be approximate since both scale and vertebral number are subject to clinal or subspecific variation, scales do not exactly overlies vertebrae in a regular ratio and ranges in counts are not strictly comparable. The count was determined by taking the mid-point value for the most extensive range in count of both vertebrae and lateral line scales and dividing mid-point number of scales by mid-point number of vertebrae.

Lateral line counts varied from 30-114, above the lateral

line from 4-33, below the lateral line from 2-21, predorsally from 11-68 and around the caudal peduncle from 10-55. The scale per vertebra count varied from 1.0-2.3.

g) Scale Attachment

Scales may be firmly attached (embedded) or loosely attached (caducous). Various intermediate conditions are difficult to characterise. Strongly caducous scales are usually lost on capture or handling; most scales could be characterised as moderately caducous since embedded scales are comparatively rare.

h) Imbrication

Scales may or may not overlap and underlap each other i.e. imbricate. Scales are characterised as strongly, moderately, minimally or non-imbricate. This character varies with the body region but is usually observed on mid-flank scales below or slightly anterior to the level of the dorsal fin. A partial measure of imbrication may be derived from the number of flank scales over- and under-lapping an arbitrarily chosen scale (The count is termed an overlap count for convenience although both over- and under-lapping scales are included). The count is carried out on the flattest part of the mid-flank region. The count is influenced both by imbrication and by scale shape, strongly imbricate elongate scales having higher counts than weakly imbricate sub-circular ones. The count varied from 7 to 13.

RESULTS

Character Variability

All of the morphological and numerical characters studied were subject to variations and these must be outlined before scale characters can be assessed for systematic significance. Attempts were made to examine most or all of the species within any genus and to include individuals of both sexes, different age groups and different geographical areas. This ideal was not always attained particularly with the more speciose genera and the rarer species. Where good series were available, both of size and origin, due note was taken of those features susceptible to variation.

The variations were found to be governed by several factors: -

a) Life History

Scales grow with the fish and an accompanying increase in number of radii (and circuli) is evident in many species (See Orthodon description, for example). Thus, without extensive samples, too much reliance cannot be placed on radii counts other than to afford a general range for a species which is a more objective character than "many" or "few" radii.

Growth also affects the shape of the scale, and in concert, the focus position. In N. crysoleucas the focus shifts from an anterior position in young fish to a central position in larger fish. Most N. American cyprinids

with an overlapping scale arrangement show greater growth in the free exposed posterior field compared to the embedded anterior field so that the adult focus is anterior. In embedded scales where overlap is minimal growth tends to be equal in all fields.

Older individuals of the larger species often have more irregular scales with ragged edges and scarred surfaces than younger individuals.

Circuli may be alternately close and distinct forming winter lines (or annuli) indicating a reduction in growth during the winter and rapid summer growth. The spawning season may leave a ragged mark on the scale if feeding stops and resorption of the scale margins occurs.

b) Regeneration

Scales are lost because of mechanical injury and regeneration occurs. Regenerated scales are characterised by a large focus devoid of radii or circuli. Injury without scale loss results in an irregular, scarred scale as mentioned above.

c) Geographical Distribution

Hubbs and Black (1947) working on the species of Pimephales s.l. were able to show significant differences in radii number between population samples from different river systems. Some variation was also found in Couesius plumbeus (Table 1) but this was less marked. Geographical variation may be more prevalent in species (such as Pimephales spp.) which have numerous radii and a wide range in radii number.

Table 1

Geographical variation in number of radii for specimens

of Copestus plumbeus, 60-69 mm. S.L.

(n = 50 in all samples)

	Range	Mean	Standard Deviation	Standard Error	
Nova Scotia	Primary Radii	6-10	7.86	0.9899	0.1400
	Secondary Radii	1-9	4.32	1.9107	0.2702
	Total Radii	8-18	12.18	1.8811	0.2660
Saskatchewan	Primary Radii	6-11	8.68	1.2362	0.1748
	Secondary Radii	1-9	3.94	1.5039	0.2127
	Total Radii	10-17	12.62	2.0192	0.2856
Alberta	Primary Radii	6-10	8.84	0.9971	0.1410
	Secondary Radii	1-6	3.22	1.2664	0.1791
	Total Radii	8-15	12.06	1.5960	0.2257
British Columbia	Primary Radii	5-12	7.90	1.4178	0.2005
	Secondary Radii	1-6	2.72	1.1073	0.1566
	Total Radii	6-15	10.62	1.9048	0.2694

Nevertheless this factor should be taken into account. It is suggested that a species or genus may be characterised by a range in radii number where overlap is minimal or non-existent with other species and genera.

d) Body Regions

Some of the greatest variation in scale morphology is found between scales from different regions of the body of an individual fish. It is, therefore, essential to compare scales taken from the same region in all species. Chu (1935) considered caudal peduncle scales from immediately above the lateral line to be least subject to unimportant variations. This study follows Chu's lead to facilitate comparison with his Chinese material although flank scales from below the dorsal fin are also comparatively uniform and have been used in other, more limited studies.

The most regular scales are found along the sides of the body and onto the caudal peduncle. Scale shape becomes more elongate posteriorly and a commensurate alteration in field size and lateral line pore shape ensues. More drastic changes in size and shape occur near the bases of fins and on the belly and predorsally. Scales at fin bases are modified to accommodate the interruption in the body surface caused by the fins. A pelvic axillary scale may be present to aid in streamlining water flow over the appressed pelvic fin. Belly scales are usually sub-circular or oval and much smaller than flank scales. They may also be non-imbricate or lacking over parts or all the belly anterior to the pelvic fins. Predorsal scales

may be as regular as flank scales or they may be smaller, irregular in shape and arrangement, crowded or even absent. Both regularly and irregularly arranged scales may be found in species of the same genus and thus the condition is of little systematic value at the genus level although it is useful in species separation.

The overlap count and degree of imbrication vary with the body region being best developed on the flank. Predorsal scales are often minimally imbricate while belly scales are often non-imbricate.

Numbers of radii and circuli increase with scale size over the body surface and yet even adjacent scales may have quite strong differences in radii count. It is for this reason that five caudal peduncle scales were chosen for radii counts to reduce the chance of choosing an aberrant scale.

The distribution of radii on scale fields is reasonably constant over most of the body scales. Larger scales may have some posterior radii spilling into the lateral fields, a condition not apparent in smaller scales, but more major variation was not found (cf. Chu, 1935: 71).

Variation in focus position on scales from different body regions can be attributed to differing growth axes when, for example, non-imbricate embedded belly scales are contrasted with imbricate, caducous flank scales. Focus size may vary but this was difficult to determine because this region was often fragmented in the detached scale.

Scale descriptions

The following portion of the results describes scale structures of each genus as represented by the available species. Scale counts (Table 2) are based on the available specimens and on literature reports. The latter are cited in the section on character analysis.

Tables 3 and 4 give estimates of lateral line decurvature and number of scales per vertebra respectively. Values obtained in the latter table were usually similar for each species within a genus. Exceptions noted were Gila (range 1.3-2.0, mean 1.7), Erimystax (range 1.0-1.4, mean 1.2), Phenacobius (1.2-1.6, mean 1.4), Semotilus (1.0-1.4, mean 1.2) and Notropis (0.9-1.2, mean 1.0).

Table 5 gives counts of primary, secondary and total radii with the number and size of specimens used.

Comments are given on certain genera in this descriptive section. Assessment of characters generated here is given in the section on character analysis.

GENUS ACROCHEILUS

Monotypic, A. alutaceus, 10 specimens, Figure 3.

Description

Scales over entire body, regularly arranged, small, may be minimally or non-imbricate predorsally and on belly in smaller fish, imbricate laterally, overlap set of 7, caducous. Lateral line moderately decurved, complete and not regular, changing scale row at intervals. Scales on caudal peduncle variable in shape with lateral edges parallel, curved or in-

TABLE 2

Scale counts for cyprinid genera

Genus	Lateral Line	Above Lateral Line	Below Lateral Line	Predorsal	Caudal Peduncle
<i>Actinopterygii</i>	80-108	20-27	13-20	48-67	33-55
<i>Agosia</i>	70-95	13-20	11-18	37-53	41-47
<i>Algansea</i>	52-95	10-23	7-13	23-56	27-55 (approx.)
<i>Campostoma</i> *	41-64	6-9	6-8	15-26	20-22
<i>Chrosomus</i>	63-95	15-22	9-12	35-51	21-41
<i>Clinostomus</i>	48-70	8-10	5-7	22-26	17-20
<i>Coueslus</i>	53-79	10-14	7-9	25-27	22-26
<i>Dianda</i>	31-45	5-7	3-6	11-17	11-20
<i>Eremichthys</i>	64-80	14-19	9-13	38-54	30-43
<i>Ericymba</i>	31-36	4-5	3-4	12-15	12
<i>Erimysfax</i>	32-62	5-7	4-6	15-22	14-16
<i>Evaxxa</i>	74-95	13-17	10-14	38-54	-
<i>Exoglossum</i>	50-59	6-10	5-8	27-34	17-21
<i>Extrarius</i>	31-43	4-7	4-6	14-19	12-16
<i>Gila</i>	40-99	9-29	5-21	22-51	20-54
<i>Hemistremia</i>	37-43	6-7	5-6	17-21	16-18
<i>Hesperoleucis</i>	44-67	10-17	6-12	27-38	21-31
<i>Hybognathus</i>	31-44	4-8	4-6	13-23	11-18
<i>Hybopsis</i>	31-42	4-6	4-5	11-17	10-16
<i>Totichthys</i> †	33-38	-	-	16-20	16-19
<i>Iavania</i>	53-67	12-18	6-11	27-43	23-28
<i>Lepidomeda</i>	77-105	18-23	13-18	37-52	38-49
<i>Macrhybopsis</i>	37-50	4-9	4-8	18-25	16-19
<i>Margariscus</i>	49-79	10-13	7-11	38-48	25-28
<i>Meda</i>			SCALELESS		
<i>Moapa</i>	68-80	17-20	12-15	44-51 (approx.)	35-51
<i>Mylocheilus</i>	65-84	13-15	7-12	28-35	20-24
<i>Mylopharodon</i>	70-80	18-21	12	40-55	32-36
<i>Nocomis</i>	36-48	6-9	4-8	15-21	14-21
<i>Nothemigonus</i>	39-57	8-11	2-4	19-24	14-16
<i>Notropis</i>	30-60	5-11	2-11	11-45	10-20
<i>Opsopocodus</i>	36-41	5-6	3-4	15-24	12-14
<i>Oregonichthys</i>	35-40	5-6	4-5	16-17	12-14
<i>Orthodon</i>	83-114	26-33	14-21	45-66	40-49
<i>Parexoglossum</i>	47-53	8-10	5-7	26-31	15-18
<i>Phenacobius</i>	41-69	6-7	5-6	18-22	13-20
<i>Pimephales</i>	37-55	5-12	4-6	21-30	14-21
<i>Plagopterus</i>			SCALELESS		
<i>Platygobio</i>	42-59	6-8		13-16	16-18
<i>Pogonichthys</i>	57-66	11-14	7-11	22	28
<i>Psychocheilus</i>	63-95	13-29	8-20	36-68	25-27
<i>Relictus</i>	50-70	11-14	10-12	37-41	27-34
<i>Rhinichthys</i>	35-90	7-18	7-15	26-47	22-40
<i>Richardsonius</i>	49-71	10-14	5-9	27-50	18-21
<i>Semotilus</i>	38-70	7-13	5-10	20-40	16-26
<i>Stypodon</i>			NOT AVAILABLE		
<i>Tlagora</i>	65-72	-	-	-	37-46
<i>Xystrosus</i>	60-70	12-18	8-11	22-31	31-37 (approx.)
<i>Yuriria</i>	42-55	8-10	3-6	16-20	18-20

* Moore (1968) cites 62-76 lateral line scales for *Campostoma ornatum* and Alvarez del Villar (1970) cites 35-40 for predorsal scales.

† There are 31-37 scales around the body in front of the dorsal fin.

TABLE 3

Estimates of lateral line decurvature from scale counts

Genus	Scales above lateral line (A)	Scales below lateral line (B)	$\frac{A}{B}$
<i>Acrocheilus</i>	20-27 (23.5)	13-20 (16.5)	1.42
<i>Agosia</i>	13-20 (16.5)	11-18 (14.5)	1.14
<i>Algansea</i>	10-22 (16)	7-13 (10)	1.60
<i>Campostoma</i>	6-9 (7.5)	6-8 (7)	1.07
<i>Chrosomus</i>	15-22 (18.5)	9-12 (10.5)	1.76
<i>Clinosomus</i>	8-10 (9)	5-7 (6)	1.50
<i>Couesius</i>	10-14 (12)	7-9 (8)	1.50
<i>Dionda</i>	5-7 (6)	3-6 (4.5)	1.33
<i>Eremichthys</i>	14-19 (16.5)	9-13 (11)	1.50
<i>Ericymba</i>	4-5 (4.5)	3-4 (3.5)	1.29
<i>Erismysfax</i>	5-7 (6)	4-6 (5)	1.20
<i>Evaxra</i>	13-17 (15)	10-14 (12)	1.25
<i>Exoglossum</i>	6-10 (8)	5-8 (6.5)	1.23
<i>Exocoetis</i>	4-7 (5.5)	4-6 (5)	1.10
<i>Gila</i>	9-29 (19)	5-21 (13)	1.46
<i>Hemitremia</i>	6-7 (6.5)	5-6 (5.5)	1.18
<i>Hesperoleucis</i>	10-17 (13.5)	6-12 (9)	1.50
<i>Hybognathus</i>	4-8 (6)	4-6 (5)	1.20
<i>Hybopsis</i>	4-6 (5)	4-5 (4.5)	1.11
<i>Iotichthys</i>	NOT COUNTABLE		-
<i>Lavinia</i>	12-18 (15)	6-11 (8.5)	1.76
<i>Lepidomeda</i>	18-23 (20.5)	13-18 (15.5)	1.32
<i>Macrhybopsis</i>	4-9 (6.5)	4-8 (6)	1.08
<i>Margariscus</i>	10-13 (11.5)	7-11 (9)	1.28
<i>Meda</i>	SCALELESS		-
<i>Moapa</i>	17-20 (18.5)	12-15 (13.5)	1.37
<i>Mylocheilus</i>	13-15 (14)	7-12 (9.5)	1.47
<i>Mylopharodon</i>	18-21 (19.5)	12 (12)	1.63
<i>Nocomis</i>	6-9 (7.5)	4-8 (6)	1.25
<i>Notemigonus</i>	8-11 (9.5)	2-4 (3)	3.17
<i>Notropis</i>	4-11 (7.5)	2-11 (6.5)	1.15
<i>Opsopocodus</i>	5-6 (5.5)	3-4 (3.5)	1.57
<i>Oregonichthys</i>	5-6 (5.5)	4-5 (4.5)	1.22
<i>Orthodon</i>	26-33 (29.5)	14-21 (17.5)	1.68
<i>Parexoglossum</i>	8-10 (9)	5-7 (6)	1.50
<i>Phenacobius</i>	6-7 (6.5)	5-6 (5.5)	1.18
<i>Pimephales</i>	5-12 (8.5)	4-6 (5)	1.70
<i>Plagopterus</i>	SCALELESS		-
<i>Platygobio</i>	6-8 (7)	5 (5)	1.40
<i>Pogonichthys</i>	11-14 (12.5)	7-11 (9)	1.39
<i>Ptychocheilus</i>	13-29 (21)	8-20 (14)	1.50
<i>Relictus</i>	11-14 (12.5)	10-12 (11)	1.14
<i>Rhinichthys</i>	7-18 (12.5)	7-15 (11)	1.14
<i>Richardsonius</i>	10-14 (12)	5-9 (7)	1.71
<i>Semotilus</i>	7-13 (10)	5-10 (7.5)	1.33
<i>Stypodon</i>	NOT AVAILABLE		-
<i>Tlaxoga</i>	NOT COUNTABLE		-
<i>Xystrosus</i>	12-18 (15)	8-11 (9.5)	1.58
<i>Yuriria</i>	8-10 (9)	3-6 (4.5)	2.00

TABLE 4

Number of lateral line scales expressed in terms of number of vertebrae

Genus	Number of vertebrae	Lateral line scales	Scales/ Vertebrae
<i>Acrocheilus</i>	44-46	80-108	2.0
<i>Agoala</i>	36-39	70-95	2.2
<i>Algansca</i>	33-42	52-95	2.0
<i>Camposoma</i>	40-42	41-76	1.4
<i>Chrosomus</i>	35-40	63-95	2.0
<i>Clinosomus</i>	38-42	48-70	1.5
<i>Couesius</i>	39-44	53-79	1.6
<i>Dionda</i>	33-39	31-45	1.0
<i>Eremichthys</i>	34-36	64-80	2.1
<i>Ericymba</i>	34-36	31-36	1.0
<i>Erismystax</i>	36-43	32-62	1.2
<i>Evarra</i>		NOT AVAILABLE	-
<i>Exoglossum</i>	37-40	50-59	1.4
<i>Extrarius</i>	34-39	31-43	1.0
<i>Gila</i>	35-50	40-99	1.7
<i>Hemitremia</i>	36-38	37-43	1.1
<i>Hesperoleucus</i>	37-41	44-67	1.4
<i>Hybognathus</i>	35-39	31-44	1.0
<i>Hybopsis</i>	35-41	31-42	1.0
<i>Iotichthys</i>	34-35	33-38	1.0
<i>Lavinia</i>	40-44	53-67	1.4
<i>Lepidomeda</i>	41-44	77-105	2.1
<i>Macrhybopsis</i>	39-43	37-50	1.1
<i>Margariscus</i>	37-42	49-79	1.6
<i>Meda</i>		SCALELESS	-
<i>Moapa</i>	36-37	68-80	2.0
<i>Mylocheilus</i>	42-48	65-84	1.7
<i>Mylopharodon</i>	46-47	70-80	1.6
<i>Nocomis</i>	37-44	36-48	1.0
<i>Notemigonus</i>	36-39	39-57	1.2
<i>Notropis</i>	32-44	30-60	1.0*
<i>Opsopocodus</i>	36-39	36-41	1.0
<i>Oregonichthys</i>	35-36	35-40	1.1
<i>Orthodon</i>	42-45	83-114	2.3
<i>Parexoglossum</i>	39-40	47-53	1.3
<i>Phenacobius</i>	38-44	41-69	1.4
<i>Pimephales</i>	35-39	37-55	1.2
<i>Plagopterus</i>		SCALELESS	-
<i>Platygobio</i>	40-47	42-59	1.2
<i>Pogonichthys</i>	41-45	57-66	1.4
<i>Ptychocheilus</i>	40-47	63-95	1.8
<i>Relictus</i>	35-39	50-70	1.6
<i>Rhinichthys</i>	35-44	35-90	1.6
<i>Richardsonius</i>	38-43	49-71	1.5
<i>Semotilus</i>	39-46	38-70	1.2
<i>Stypodon</i>		NOT AVAILABLE	-
<i>Tlaroga</i>	36-40	65-72	1.8
<i>Xystrosus</i>	39-40	60-70	1.7
<i>Yuriria</i>	38-41	42-55	1.2

* Based on counts for individual species rather than total ranges cited here.

TABLE 5

Number and size of specimens and numbers of scale radii (five caudal peduncle scales were used from each specimen)

Genus	Number	Size (mm S.L.)	Primary radii	Secondary radii	Total radii
<i>Acrocheilus</i> *	8	82-108	4-9	0-14	6-19
<i>Agosia</i>	15	44-67	17-33	3-12	22-40
<i>Algansia</i> *	7	36-58	8-22	0-14	10-26
<i>Camposoma</i>	7	32-64	7-14	0-11	9-25
<i>Chrosomus</i>	30	40-81	12-36	4-28	20-60
<i>Clinosomus</i>	7	55-72	6-13	0-8	8-16
<i>Couesius</i>	42	56-69	5-13	1-13	6-24
<i>Dionda</i>	11	53-81	9-15	2-18	13-32
<i>Eremichthys</i>	20	34-54	21-38	13-38	42-68
<i>Ericymba</i>	16	40-60	7-13	0-12	10-22
<i>Erimystax</i>	15	55-89	6-13	0-9	7-19
<i>Evarra</i>			NOT AVAILABLE		
<i>Exoglossum</i>	8	55-103	10-20	1-10	13-29
<i>Extrarius</i>	20	32-60	10-17	4-14	15-30
<i>Gila</i> *	40	40-232	4-33	0-14	5-40
<i>Hemistremia</i>	5	35-41	9-13	2-7	12-19
<i>Hesperoleucus</i> *	14	52-97	9-28	0-24	12-48
<i>Hybognathus</i>	19	46-82	7-14	0-14	8-25
<i>Hybopsis</i>	21	37-61	6-12	1-10	8-21
<i>Isichthys</i>	5	26-35	14-19	7-14	21-32
<i>Lavinia</i>	4	153-233	9-17	2-14	12-30
<i>Lepidomeda</i> *	21	52-85	5-18	1-13	7-22
<i>Macrhybopsis</i>	10	31-59	3-9	1-12	8-18
<i>Margariscus</i>	14	85-105	7-15	1-19	10-36
<i>Meda</i>			SCALELESS		
<i>Moapa</i>	4	47-70	10-27	2-10	15-35
<i>Mylocheilus</i>	4	189-219	12-18	3-9	17-25
<i>Mylopharodon</i>	3	93-121	7-17	3-12	13-23
<i>Nocomis</i>	22	87-162	13-27	2-15	13-35
<i>Nothemigonus</i>	27	72-130	4-10	1-4	4-11
<i>Notropis</i>	85	36-135	4-34	0-37	5-71
<i>Opsopocodus</i>	6	34-37	5-9	1-4	8-12
<i>Oregonichthys</i>	8	41-44	7-12	0-8	10-16
<i>Orthodon</i>	3	128-228	21-33	2-9	26-42
<i>Parexoglossum</i>	5	32-35	6-10	0-3	8-12
<i>Phenacobius</i>	8	42-91	6-13	0-10	6-19
<i>Plimphales</i>	19	40-71	6-22	1-20	7-41
<i>Plagopterus</i>			SCALELESS		
<i>Platygobio</i>	4	110-170	9-19	1-15	10-29
<i>Pogonichthys</i>	1	105	12-16	1-4	16-18
<i>Psychocheilus</i> *	5	285-375	21-48	16-65	40-110
<i>Relictus</i>	8	44-66	16-31	4-20	23-47
<i>Rhinichthys</i> *	50	40-103	6-38	0-24	9-56
<i>Richardsonius</i>	5	45-65	5-8	0-7	7-15
<i>Semotilus</i>	27	81-236	14-30	1-33	16-58
<i>Stypodon</i>			NOT AVAILABLE		
<i>Tiaroga</i>	8	37-51	10-30	2-15	14-35
<i>Xystrosus</i> *	14	104-116	4-16	0-8	4-23
<i>Yuriria</i>	8	38-52	5-7	0-4	7-11

* Includes anterior radii when present

dented curving posteriorly to a rounded posterior apex, without evident postero-lateral corners. Antero-lateral corners are usually evident and the anterior edge indents immediately on each side of a pronounced anterior apex. Flank scales are sub-circular in shape. Focus anterior but anterior field is well developed. Circuli thicker and more widely spaced posteriorly becoming finer and closer together laterally and anteriorly. Radii principally on the posterior and lateral fields but on some scales the anterior fields have small radii. Occasional radii lying in mid-field. Anterior radii may be absent from small specimens.

Comments

The pronounced anterior apex is characteristic of certain Gila species. Cockerell (1909a) includes Acrocheilus and Orthodon of N. America with the European Chondrostoma in a sub-family, the Chondrostominae. Chondrostoma has scale characters of typical European Leuciscinae with a central focus, radii on anterior and posterior fields, numerous, fine concentric circuli and much larger scales (52-66 in lateral line, Berg, 1949; Wheeler, 1969).

GENUS AGOSIA

Monotypic, A. chrysogaster (but see Miller, 1956), 15 specimens, Figure 3.

Description

Scales over entire body but some individuals lack scales around pectoral, pelvic and anal fin bases and bare patches are often found on the belly and close to the isthmus.

Scales small, particularly on belly, minimally imbricate, overlap set of 7, embedded. Lateral line complete, mid-lateral, wobbly, not completely to end of scales in some fish. Scales on caudal peduncle vary from a horizontal oval to a sub-hexagonal shape. Predorsal and belly scales are sub-circular and flank scales are sub-circular to vertically oval grading into the horizontally oval caudal peduncle scales. The focus is anterior and may be well set-off or close to the anterior edge. Circuli are at their thickest and widest posteriorly where they may be slightly broken up and wavy. Laterally and basally the circuli become thinner and more crowded. Radii are found on all the fields and occasionally they may be branched, interrupted or extend from the focus to mid-field.

GENUS ALGANSEA

Several species currently under revision (see Appendix 2), this description based on A. monticola and A. tincella, 7 specimens, Figure 3.

Description

Scales regularly arranged but may be minimally imbricate on the breast.

There is considerable variation in lateral line counts between species (R.R. Miller, pers. comm., 1975).

Scales moderate to very small in size, strongly imbricate, overlap set of 7-9, weakly caducous. Caudal peduncle scales an elongate rectangle or oval with evident posterior corners or a rounded, smooth, transition to a rounded posterior apex. Anterior corners evident or not

and anterior edge a gentle curve not produced as an apex. Focus anterior with a very small anterior field. Circuli widest spaced and thickest posteriorly and may form elongate lozenges between radii. Radii on posterior and lateral fields and usually on anterior field too but may be absent or faint in some specimens of A. lacustris and A. tincella.

Comments

R.R. Miller (pers. comm.; 1975) suggests that Algansea and Xystrosus are congeneric and derived from a Gila-like ancestor. Scale characters provide no conclusive evidence of this but neither do they offer proof against such relationships.

GENUS CAMPOSTOMA

Two species, C. anomalum, and C. ornatum. Description based on C. anomalum, 7 specimens, Figure 4.

Description

Scales regularly arranged over body and moderate in size, imbricate except on belly where little or non-imbricate, overlap set of 11, not very caducous. Lateral line complete, little decurved almost straight in some fish (decurvature estimate from scale counts is 1.00). Scales on caudal peduncle sub-hexagonal with long parallel lateral edges passing through poorly developed postero-lateral corners to a rounded posterior apex. Antero-lateral corners are more evident and the shallow anterior scale edge is wobbly, indented, and the anterior apex may be present or absent. The focus is anterior, compressing the anterior field. Circuli are coarser and more

widely spaced on the posterior field compared to the lateral and anterior fields. An inflection may be present at the antero-lateral field junctions. Many circuli are "lost" at the edge of the lateral field. Radii are found on the posterior field spreading laterally.

GENUS CHROSOMUS

Four species, C. eos, C. erythrogaster, C. neogaeus and C. oreas were examined, 30 specimens, Figures 4, 5 and 6.

Description

Scales over whole body but in some specimens may be non-imbricate particularly predorsally and on the belly but also on the flanks.

Scales small, non- or minimally imbricate, overlap set of 7, embedded but slightly caducous. Lateral line pores may be absent, extending to level of dorsal fin or complete. Quite strongly decurved in latter case, may be interrupted, and rises sharply below dorsal fin. Scales on caudal peduncle generally sub-circular, may be horizontally or vertically oval and occasionally approaching a sub-hexagonal shape. The belly behind the operculum bears rows of imbricate scales, larger and with a distinct morphology from the other non-imbricate belly scales. These scales may be squarish, rectangular or more rounded with a well developed posterior field. The posterior radii on these scales are long, wide and often parallel such that much of the posterior circuli is obscured. Eocus position is variable from central to sub-central anterior. Circuli are more developed and widely spaced posteriorly than

anteriorly and laterally even in some flank scales where the anterior and posterior fields are of the same size.

Radii are numerous and found on all fields.

Comments

Development of radii on all fields is characteristic of Chrosomus and of certain other N. American genera in particular Agosia, Eremichthys, Moapa, Relictus, Rhinichthys and Tiaroga and variably in Acrocheilus, Orthodon, some Algansea and Gila species and in some Lepidomeda, Ptychocheilus and Xystrosus specimens. Hubbs, Miller and Hubbs (1974)

Suggest that the development of anterior radii is correlated with deep embedding of scales and is of limited value in determining relationships because of independent derivation in several western genera. The similarity of Eurasian Phoxinus and Moroco scales to Chrosomus scales in this respect may also be due to convergence but the weight of other evidence (see p.337) suggests a relationship.

A brief summary of Phoxinus (including Moroco) scale characters follows. Scales are small, 62-118 in the lateral line or lateral series, embedded, overlap set of 0 (P. cze-kanowskii, P. issykkulensis), 7 (P. phoxinus, P. lagowskii, Moroco percnurus) or 7-13 (Moroco steindachneri jouyi, P. percnurus), decurvature values range from 1.44-1.83 and scales per vertebra range from 1.9-2.3. As shown by the overlap values scales are non-imbricate over much of the body in some species, except on the mid-flank posteriorly and the caudal peduncle. Scales are also minimally imbricate

or non-imbricate predorsally and on the belly and around paired fin bases. Belly and paired fin base scales may be absent. Scale arrangement is irregular in many areas of the body. The lateral line is moderately decurved and may be complete or interrupted or absent. It may also stop and recommence up to three scale rows higher on the flank. Scale shape on the caudal peduncle varies from sub-hexagonal to oval to sub-circular. Anterior flank scales are usually close to circular in shape. Caudal peduncle scales have weakly expressed corners, sometimes quite evident, and the posterior rounded apex is more developed than the anterior apex. The anterior edge may be produced a little and rounded or be almost straight. The focus is sub-central anterior or rarely central. Anterior scales have a focus centrally placed or close to it. Circuli are finest and most closely spaced anteriorly and laterally and an antero-lateral inflection is not present. Radii are found on all fields, some originating at the focus and terminating in mid-field, or branching. Radii number 9-35 primary, 1-22 secondary and 16-51 total and variation may be quite marked between scales from the same specimen.

GENUS CLINOSTOMUS

Two species, C. elongatus and C. funduloides. Description based on C. funduloides, 7 specimens, Figure 6.

Description

Scales regularly arranged over body and non- or minimally imbricate on belly from pectorals anteriorly.

Scales of moderate size, imbricate, overlap set of 10, caducous. Lateral line complete, slightly decurved. Scales on caudal peduncle sub-hexagonal with parallel or slightly rounded sides, rounded postero-lateral corners and a rounded apex. Antero-lateral corners well-developed, anterior edge may be almost straight or slightly indented on each side of a rounded apex. Focus anterior, compressing anterior field. Circuli thickest and most widely spaced posteriorly, anteriorly much compressed and with a strong antero-lateral inflection. Radii on posterior field, edging slightly into lateral fields.

GENUS COUESIUS

Monotypic, C. plumbeus, 42 specimens, Figure 6.

Description

Scales regularly arranged over whole body, moderate in size, strongly imbricate, overlap set of 7 but very close to higher counts, caducous. Lateral line moderately decurved, complete. Scales sub-hexagonal or sub-oval with parallel sides passing via rounded, almost absent postero-lateral corners to a rounded apex. The anterior margin is wavy or indented and the anterior apex is not well developed being rounded, notched or indiscernible. Predorsal scales are regularly arranged and are only minimally imbricate. Belly scales are minimally or non-imbricate. Focus anterior, slightly compressing the anterior field. Circuli are best developed on the posterior field becoming thinner and closer laterally and anteriorly. There is an antero-lateral inflection.

Radii restricted to the posterior field. Geographical variation in radii numbers is minimal (Table 1)'.

Comments

Jenkins and Lachner (1971) give a range in total radii of 15-22, mean 18.5 for scales taken from below the dorsal fin. Cockerell and Allison (1909) have noted strongly angulate posterior circuli at the scale median in Couesius, Semotilus, Phenacobius and Nocomis but this was not seen in the present study except in a few scales of Semotilus. Couesius and Margariscus are very similar in all scale characters except predorsal scale count.

GENUS DIONDA

Five species, D. diaboli, D. episcopa, D. erimyzonops, D. nubila and D. rasconis. Description based on D. episcopa, 11 specimens, Figure 6.

Description

Scales arranged regularly but minimally imbricate on belly and predorsally. Scales lacking from isthmus region in some species.

Scales large, imbricate, overlap set of 7-9, caducous. Lateral line little decurved or almost straight, usually complete, may follow an irregular, wobbly path. Scales on caudal peduncle somewhat irregular in shape being sub-triangular because postero-lateral corners hardly evident. Anterior sides parallel and antero-lateral corners well developed. Anterior edge a shallow curve, wavy and indented. All margins subject to indentations and ragged appearance.

Focus anterior, anterior field large. Circuli thickest and most widely spaced posteriorly with a slight or strong antero-lateral inflection. Radii on posterior field, edging laterally, with a tendency to fan out widely from the focus.

GENUS EREMICHTHYS

Monotypic, E. acros, 20 specimens, Figure 7.

Description

Scales over whole body, crowded predorsally. Arrangement irregular in places.

Scales small, imbricate, overlap set of 7 but variable because scale arrangement is often irregular, slightly embedded. Lateral line moderately decurved anteriorly, wobbly, sometimes incomplete or interrupted or complete. Interruption usually below dorsal fin and lateral line may be displaced upward 1-3 scale rows. Scales on caudal peduncle sub-circular, oval or squarish; on belly and nape sub-circular or oval, sometimes a rounded triangle on belly; on flank of large fish squarish without a posterior point but with a rounded anterior point and with rounded corners; on flank of smaller fish sub-circular or oval (size range 64-75 mm S.L.). Focus anterior but not close to anterior edge. Focus not fragmented or empty but a meeting place of radii. Circuli not strongly developed, more crowded basally and laterally. Posterior circuli somewhat irregularly placed, not forming perfect rings. Radii on all fields converging to a point focus; radii often branched and fragmented.

GENUS ERICYMBA

Monotypic, E. buccata, 16 specimens, Figure 7.

Description

Scales arranged regularly on body, absent only from anteriormost part of belly.

Scales large, moderately imbricate, overlap set of 7, caducous. Lateral line slightly decurved and usually complete but may be absent on a few scales. Scales sub-hexagonal with parallel or slightly rounded lateral edges and rounded lateral corners. There is a rounded posterior apex and a less evident rounded anterior apex which may have indentations dorsally and ventrally. Focus anterior, compressing anterior field. Circuli largest and most widely spaced posteriorly. There is a mild lateral inflection where the circuli pass from the lateral to the anterior fields. Radii are present on the posterior field only and converge broadly onto the focus.

GENUS ERIMYSTAX

Six species, this description based on E. dissimilis and E. x-punctata, 15 specimens, Figure 7.

Description

Scales regularly distributed except variably absent on anterior part of belly.

Scales large to moderate, variably imbricate, overlap set of 7, 11 or 13, caducous. Lateral line straight or slightly decurved. Scales on caudal peduncle sub-hexagonal with parallel or slightly rounded sides passing through rounded postero-

lateral corners to a rounded apex. Antero-lateral corners are well developed and the anterior edge bears a blunt apex with indentations dorsally and ventrally. This edge may approach a flat, vertical shape. Focus anterior, usually compressing the anterior field. Circuli thickest and most widely spaced posteriorly and with an antero-lateral inflection. Radii on the posterior field encroaching laterally. Some radii with expanded spaces along their length.

Comments

Jenkins and Lachner (1971) give a range in total radii of 5-26 with means varying from 5.7 to 18.5 depending on the species. They took scales from below the dorsal fin on the flank.

GENUS EVARRA

Three species, poorly represented in museum collections, none available for study. Woolman (1895), Jordan and Evermann (1896), Meek (1902), Navarro (1955), Alvarez and Navarro (1957) and Alvarez del Villar (1970) give scale characters of this genus as follows: -

Scales very small, over whole body, those on belly and predorsal area minute, lateral line complete, straight except anteriorly where decurved above the pectoral fins.

GENUS EXOGLOSSUM

Monotypic, E. maxilllingua, 8 specimens, Figure 8.

Description

Scales regularly arranged except predorsally in parts and becoming non-imbricate on anterior part of belly.

Scales moderate in size, imbricate, overlap set of 7 caducous. Lateral line complete, slightly decurved. Scales on caudal peduncle with short parallel sides passing through rounded postero-lateral corners to a rounded produced apex. Antero-lateral corners are sharper and lead to an anterior edge with a variable shape but usually having a rounded apex with an indentation on each side. The focus is anterior, compressing the anterior field. Circuli are thickest and most widely spaced posteriorly and there is an antero-lateral inflection. Radii are limited to the posterior field sometimes spreading extensively into the lateral fields.

GENUS EXTRARIUS

Monotypic, E. aestivalis, 20 specimens, Figure 8.

Description

Scales regularly arranged but absent from pelvic fins, anteriorly on belly and non-imbricate predorsally and on upper anterior flanks.

Scales large, moderately imbricate, overlap set of 7, caducous. Lateral line complete, almost perfectly straight. Caudal peduncle scales sub-triangular since postero-lateral corners merge into curve of sides to a rounded posterior apex. Antero-lateral corners rounded and anterior edge varying from a shallow curve to a small, very rounded apex with small indentations dorsally and ventrally. Focus anterior compressing anterior field. Circuli thickest and most widely spaced posteriorly and sometimes with an antero-lateral inflection. Radii on posterior field encroaching laterally.

Comments

Jenkins and Lachner (1971) give a range in total radii of 4-12, mean 6.9 for scales from below the dorsal fin. These specimens were probably smaller than the ones used for the present study since a range of 13-21 was found for 20 anterior flank scales from three specimens (53-57 mm S.L.) examined here. This is, however, a geographically variable species.

GENUS GILA

About 14 species, this description based on G. alvordensis, G. atraria, G. bicolor, G. orcutti, G. robusta, 40 specimens, Figures 8 and 9.

Description

Scales may be regularly distributed over the whole body or practically non-imbricate on the belly and minimally imbricate predorsally. The degree of imbrication in these regions is probably related to size, smaller fish being least imbricate. In some fish the belly and back may be naked and in some Colorado River populations scales may be virtually absent (Moore, 1968). Predorsal scales may or may not be crowded and irregular.

Scales small to moderate to large in size, in G. copei giving a "leathery" appearance. Scales strongly imbricate, overlap set of 7 but close to 13 in many instances, embedded. Lateral line complete or incomplete, moderately decurved, may break off and recommence a row higher, pore may be off-centre on scales. Scales on caudal peduncle an elongate oval

or sub-hexagonal shape with sides parallel or rounded passing through rounded postero-lateral corners to a rounded apex. Antero-lateral corners usually more abrupt passing to an anterior edge which may be wavy and indented or gently rounded or possessing a markedly produced and rounded anterior apex. The focus is anterior and may be well set-off from the anterior scale edge or compressing it. Circuli are thickest and most widely spaced posteriorly. There may be an antero-lateral inflection. In large G. bicolor some posterior circuli are broad and forked. Radii may be restricted to the posterior field, encroach laterally or be found on all fields. Radii distribution is also intra-specifically variable. Hubbs, Miller and Hubbs (1974) characterise Gila as "basal radii usually lacking".

Variation in radii counts between species is quite marked and may reflect, in part, variations in size of adults of different species:-

		Primary Radii	Secondary Radii	Total Radii
<u>G. alvordensis</u>	49-75 mm S.L., adults	13-33	2-14	19-40
<u>G. atraria</u>	46-79 mm S.L., young	5-9	1-6	7-13
<u>G. bicolor</u>	95-232 mm S.L., adults	4-17	3-14	9-23
<u>G. orcutti</u>	40-55 mm S.L., sub-adult	6-12	0-6	8-17
<u>G. robusta</u>	52-103 mm SL.. young- sub-adult	4-12	0-11	5-22

Miller (1945a) cites a count of 33-51 radii for G. ditaenia, presumably flank scales from below the dorsal fin. This is a small species of Gila and specimens were probably less than

100 mm S.L. Counts are also given by Cockerell and Allison (1909) on several species.

Comments

Tribolodon, a northeastern Asian genus of cyprinids has been suggested to be a relative of Gila and the scale characters of one species, T. hakonensis, are described here for comparison.

Scales are small, 61-98 in the lateral line, strongly imbricate, overlap set of 13 and with 1.7 scales per vertebra. The lateral line is complete and moderately decurved (estimate of decurvature 1.50). Scales on the caudal peduncle are elongate with parallel or slightly curved sides, rounded postero-lateral corners and posterior apex and rounded but more evident antero-lateral corners. The anterior edge has a pronounced rounded apex. The focus is anterior with a well developed anterior field. Circuli are fine and numerous in large fish and thickest and most widely spaced posteriorly. An antero-lateral inflection is weak or absent because of the large anterior field which facilitates the curvature of circuli into it from the lateral fields. Radii are restricted to the posterior field, encroaching laterally, and number 12-20 primary radii, 5-16 secondary radii and 17-36 total radii.

All these characters fall within the range of characters shown by Gila species.

GENUS HEMITREMIA

Monotypic, H. flammea, 5 specimens, Figure 10.

Description

Scales regularly arranged over body, large, moderately imbricate, overlap set of 7 but very close to 13, caducous. Lateral line moderately decurved terminating below or anterior to the dorsal fin. Scales on caudal peduncle with parallel or rounded sides passing to a rounded posterior apex via rounded postero-lateral corners. Anterior edge irregular or indented on either side of a small rounded apex. Focus anterior compressing anterior field. Circuli thickest and most widely spaced on posterior field and also a little fragmented, compressed anteriorly and with an antero-lateral inflection. Radii restricted to the posterior field, occasionally tightly sinuous rather than straight.

GENUS HESPEROLEUCUS

Four species have been recognised but these may be only subspecifically distinct (Moore, 1968). Here treated as monotypic, H. symmetricus, for convenience (specimens were H. symmetricus symmetricus (12) and H. symmetricus navarroensis (2), Figure 10.

Description

Scales regularly arranged, moderate in size, imbricate, overlap set of 13, caducous. Lateral line moderately to strongly decurved, complete. Scales on caudal peduncle an elongate, almost perfect hexagon with round postero- and antero-lateral corners, the latter being sharpest. The anterior edge may be slightly wavy or indented but forms an anterior rounded apex. Small specimens have sub-circular or

• oval scales on the caudal peduncle. Focus anterior, compressing anterior field. Circuli are thickest and most widely spaced posteriorly where they may fragment and become lozenge-like. There is often an antero-lateral inflection and in larger scales the anterior circuli may be almost obscured by the focus. Radii are variably present on the anterior field but always present posteriorly and laterally.

GENUS HYBOGNATHUS

Four species, H. hankinsoni, H. hayi, H. nuchalis and H. placitus. Description based on all four species, 19 specimens, Figure 10.

Description

Scales regularly distributed over body, large, moderately imbricate, overlap set of 7-13 (higher values in larger fish) caducous. Lateral line slightly decurved, complete. Scales on caudal peduncle sub-hexagonal with parallel or slightly rounded sides, rounded postero-lateral corners and a rounded posterior apex. The antero-lateral corners are sharp and the anterior edge usually comes to a blunt apex though this is little produced and the anterior edge is almost vertical in some scales. Focus anterior, may be compressing anterior field or well set-off from anterior edge. Circuli are thickest and most widely spaced posteriorly and there is a strong antero-lateral inflection. Radii are found principally on the posterior field but also encroach laterally in some individuals and species.

GENUS HYBOPSIS

Seven species, this description based on H. amblops and H. labrosa, 21 specimens, Figure 10.

Description

Scales regularly distributed except belly between pectorals may be naked, scaled or partially scaled.

Scales large, moderately imbricate, overlap set of 7, caducous. Lateral line almost straight or slightly decurved, complete. Scales on caudal peduncle sub-triangular with short parallel or rounded sides passing to a rounded posterior apex without much evidence of postero-lateral corners. Antero-lateral corners more evident and the anterior edge is indented on either side of a rounded apex. Occasionally this edge may be irregular in outline. Focus anterior, compressing the anterior field. Circuli are thickest and most widely spaced posteriorly and there is an antero-lateral inflection. Radii are found on the posterior field, encroaching laterally.

Comments

Jenkins and Lachner (1971) give a range in total number of radii in scales from below the dorsal fin of 5-25, mean values varying from 7.0 to 19.2 depending on the species.

GENUS IOTICHTHYS

Monotypic, I. phlegethontis, 5 specimens, Figure 11.

Description

Scales regularly arranged over the whole body, quite large, imbricate, caducous. Lateral line absent or on up to 4 scales. Scales on caudal peduncle sub-

circular but are deeper than broad. Their basal edge may be gently rounded or almost straight. Predorsal and belly scales may approach a tear-drop shape with a rounded posterior point. The focus is anterior but clearly distinct from the anterior edge. Circular are few and widely spaced, slightly wavy and occasionally fragmented. They are thickest posteriorly and most compressed laterally and anteriorly. Radii are found on the posterior and lateral fields converging broadly onto a large focus. Some scales have many secondary radii and branched and fragmented radii.

GENUS LAVINIA

Monotypic, L. exilicauda, 9 specimens, Figure 11.

Description

Scales regularly arranged over body, small on belly. Scales moderate in size, imbricate, not very caducous, overlap set of 7. Lateral line moderately decurved, complete. Scales on caudal peduncle sub-hexagonal with parallel or slightly rounded sides. The antero- and postero-lateral corners may be quite sharp but the anterior apex is more rounded and may bear indentations dorsally and ventrally. Large fish tend to have irregular margins. Focus anterior but well set-off from anterior margin of scale. Circuli are thickest and most widely spaced on the posterior field and there is an antero-lateral inflection. Radii are found on the posterior field encroaching laterally. For specimens 53-60 mm S.L. primary radii numbered 5-9, secondary radii 0-6, total radii 7-11; for specimens 153-233 mm S.L. primary

radii numbered 9-17, secondary radii 2-14, total radii 12-30. Only the latter samples are adult specimens.

GENUS LEPIDOMEDA

Four species, L. albivallis, L. altivelis, L. mollispinis and L. vittata. This description based on L. vittata and L. mollispinis, 21 specimens, Figure 11.

Description

Scales regularly arranged over body but may not be imbricate beneath paired fins and may be lacking around anus.

Scales small, moderately imbricate, overlap set of about 9, embedded. Lateral line slightly decurved, complete or almost complete, slightly wobbly i.e. not in a regular line but switching vertically one or two scales. Scales on caudal peduncle a rounded sub-hexagonal or sub-circular, with, in some scales, an indented anterior edge on either side of a produced apex. Scale sides parallel or slightly rounded and posterior and anterior apices evident and rounded or in sub-circular scales merging into curvature of scale edge. Focus anterior, close to anterior edge of scale. Circuli are thickest and most widely spaced on posterior field where they may be irregular and sinuous between radii. Anteriorly and laterally finer and more crowded with an antero-lateral inflection. Radii on posterior and lateral fields with occasional radii extending from focus to mid-field. In some scales there are weak but definite anterior radii.

Comments

The produced anterior apex and traces of anterior radii

are similar to Gila. Scale characters add weight to the opinion of Miller and ~~Hubbs~~ (1960) that the Plagopterini (Lepidomeda, Meda and Plagopterus) are derived from a Gila - like ancestor.

GENUS MACRHYBOPSIS

Two species H. gelida and M. meeki, 14 specimens, Figure 12.

Description

Scales regularly arranged but absent around pectoral fin bases and in some absent on belly from head to anus, others with scales scattered from pelvic fins to anus. Predorsal and anterior upper flank scales may be non-imbricate.

Scales large, minimally imbricate, overlap set of 7, caducous. The fleshy keels on scales of M. gelida are not related to any underlying bony scale structure. Lateral line complete, hardly decurved or mid-lateral. Caudal peduncle scales with short sides which often curve directly into the rounded posterior apex. The anterior edge has a rounded apex with indentations and there are evident antero-lateral corners. The basic scale shape is oval or sub-triangular. Focus anterior compressing the anterior field. Circuli are thickest and most widely spaced posteriorly and there is an antero-lateral inflection. Radii are restricted to posterior field.

Comments

Jenkins and Lachner (1971) gave a range in total radii of 7-20 and mean values of 10.0 (meeki) and 13.7 (gelida) for scales taken from below the dorsal fin.

GENUS MARGARISCUS

Monotypic, M. margarita, 14 specimens, Figure 12.

Description

Scales regularly arranged but minimally imbricate predorsally and minimally to non-imbricate on belly. Flank scales may be irregularly arranged so accurate overlap counts are difficult.

Scales moderate to small in size, imbricate, overlap set of 9, 11 or 13, caducous. Lateral line slightly to moderately decurved, may be irregular and wavy or even doubled for a short distance. Caudal peduncle scales with parallel straight or slightly rounded sides, postero-lateral corners rounded but evident leading to a rounded posterior apex which is not greatly produced. Antero-lateral corners sharp or very rounded, anterior edge indented on each side of a rounded apex. Focus anterior, compressing anterior field. Circuli thickest and most widely spaced posteriorly and with an antero-lateral inflection. Radii are present on the posterior field extending into the lateral fields.

Comments

Comparison of these scales with those of Semotilus atromaculatus (76-92 mm S.L.) showed them to be very similar except the latter were ~~larger~~ larger and less rounded and certain scales bore sharply angled circuli in the mid-line of the posterior field. Larger scales from adult Semotilus spp. are much more distinct from Margariscus but this is a consequence of the disparity in size.

Jenkins and Lachner (1971) cite a moderate number of total radii (15-21) for scales from below the dorsal fin.

GENUS MEDA

Monotypic, M. fulgida, 15 specimens.

Description

"Scales" as minute bony remnants are confined to the lateral line and range in number from 46-75. The higher counts are of almost complete lateral lines; lower counts lack "scales" posteriorly. The lateral line may be almost complete or interrupted. It is slightly decurved below the dorsal fin and in this region may be very wobbly. The "scales" are much reduced being the tube sides decreasing to bone fragments posteriorly (44-51 mm S.L. - adult specimens).

GENUS MOAPA

Monotypic, M. coriacea, 20 specimens, Figure 12.

Description

Scales are absent from parts of the belly and predorsally. Little imbricate over much of the body except around the lateral line.

Scales small, overlap set of 7, embedded. Lateral line complete, little decurved except anteriorly and above anal fin where bends up to mid-line of caudal peduncle. Caudal peduncle scales sub-circular or oval with antero-lateral rounded corners evident on some scales. The anterior edge may be a curve from these corners or in larger fish it may be indented. Focus anterior sometimes obscuring anterior field. Circuli are obscured on the anterior field by the

focus in small fish and sometimes in large fish. When present anterior circuli are few and crowded. Posterior and lateral circuli are equally developed. Radii are present on all fields and may be branched or fragmented.

GENUS MYLOCHEILUS

Monotypic, M. caurinus, 4 specimens, Figure 12.

Description

Scales regularly arranged over whole body, particularly small on belly.

Scales small, imbricate, overlap set of 7 varying to 9 or 11 in some specimens, caducous. Lateral line complete, almost mid-lateral but slightly decurved anteriorly. Scales on caudal peduncle sub-hexagonal with parallel sides or sides sloping, i.e., converging, slightly posteriorly. Postero-lateral corners rounded and posterior apex quite evident but also rounded. Antero-lateral corners rounded but more obvious than postero-lateral ones. Anterior edge indented on either side of a rounded apex or wavy. Focus anterior compressing anterior field which is nevertheless distinct. Circuli widest and thickest posteriorly and with an antero-lateral inflection. Radii are restricted to the posterior field, encroaching a little laterally.

GENUS MYLOPHARODON

Monotypic, M. conocephalus, 5 specimens, Figure 13.

Description

Scales small, distributed over whole body, imbricate, overlap set not determined, caducous.

Lateral line complete, slightly decurved. Scales on caudal peduncle elongate, sub-circular with a rounded posterior apex. Antero-lateral corners evident and anterior edge indented on each side of apex. Focus anterior but anterior field distinct. Circuli are thickest and most widely spaced posteriorly and some scales have an antero-lateral inflection. Radii are found on the posterior field, encroaching laterally.

GENUS NOCOMIS

Seven species, this description based on N. asper, N. biguttatus, N. effusus, N. leptocephalus, N. micropogon and N. platyrhynchus, 22 specimens, Figure 13.

Description

Scales regularly arranged over body except breast which may be completely scaled to naked. Lachner and Jenkins (1971) discuss breast squamation in detail. Occasionally predorsal scales are slightly crowded.

Scales large, imbricate, overlap set 13 sometimes 11 latter count seen in younger fish, caducous. Lateral line complete and slightly to moderately decurved. Scales on caudal peduncle sub-hexagonal with parallel sides or with sides curving slightly posteriorly and merging into rounded postero-lateral corners and rounded apex. Occasionally there is a slight slope anteriorly, i.e. convergence, of sides.

Antero-lateral corners rounded but sharper than postero-lateral corners. Anterior edge wavy or almost straight or indented on either side of a rounded apex. Apex itself may

have a little notch. The focus is anterior and often compresses the anterior field. Circuli are widest spaced and thickest posteriorly although this is not as marked as in species with fewer circuli. There is an antero-lateral inflection. Radii are found principally on the posterior field but encroach laterally and in some specimens of N. bi-guttatus almost extend to the anterior corners of the scale.

Comments

Jenkins and Lachner (1971) give higher total radii counts 23-54, for scales from below the dorsal fin. These authors did not give sizes of specimens they examined and differences in counts here and in Yuriria and Extrarius may be accounted for by size discrepancies and body position from which scales were taken.

GENUS NOTEMIGONUS

Monotypic, N. crysoleucas, 27 specimens, Figures 13, 14, 15.

Description

Scales regularly arranged over entire body except on belly where a narrow, naked, fleshy keel extends from the pelvic fins posteriorly to the anus. The keel may be almost obscured by scales but not overlapped.

Scales large, strongly imbricate, overlap set of 13, caducous. Lateral line strongly decurved, complete. Scales on caudal peduncle sub-hexagonal with straight or slightly rounded lateral edges, rounded postero-lateral corners and a rounded or wavy but shallow posterior apex. Antero-lateral corners well developed, anterior edge variable from almost

	Lateral line shape	Naked ventral keel	Adult focus position	Circuli	Radii number and position	Overlap Count	Scales/Vertebra
<u>Notemigonus crysoleucas</u>	very strongly decurved †(3.2)	present	central	fine, concentric	4-11, posterior	13	1.2
<u>Abramis ballerus</u>	moderately decurved (1.6)	present	central	fine, concentric	4-10, posterior	13	1.5
<u>Abramis brama</u>	moderately decurved (1.8)	present	central	fine, concentric	16-40, posterior, anterior, a few laterally	7-9 (specimens small)	1.4
<u>Abramis sapa</u>	moderately decurved (1.3)	present	central	fine, concentric	9-19, *posterior, anterior, a few laterally	9-11	1.1
<u>Alburnoides bipunctatus</u>	strongly decurved (2.4)	present	sub-central anterior	fine anteriorly, coarser posteriorly, eccentric	8-17, posterior, a few laterally	7	1.2
<u>Alburnus alburnus</u>	strongly decurved (2.3)	present	slightly sub-central anterior	fine, concentric	17-47, posterior, anterior, a few laterally	7	1.2
<u>Blicca bjoerkna</u>	moderately decurved (1.7)	present	slightly sub-central anterior	fine, concentric	11-28, posterior, anterior, a few laterally	11 (specimens small)	1.2
<u>Vimba vimba</u>	moderately decurved (1.8)	present	slightly sub-central anterior	fine, concentric	16-38, posterior, anterior, often laterally	11 variable	1.2

† Figures in parentheses are estimates of lateral line decurvature from scale counts.

* Two samples were examined here and the Rumanian specimens had radii restricted to the posterior field. These specimens were counted for radii but the smaller Russian specimens with radii on all fields were not.

straight to wavy to marked indentations with an apex.
 Focus central or slightly sub-central anterior or posterior.
 On small fish focus markedly sub-central anterior. Circuli
 regular, fine, concentric about focus, almost equally devel-
 oped on all fields but posterior ones slightly more evident,
 much more evident on smaller fish up to about 85 mm S.L.
 Radii few restricted to posterior field, primary radii 4-10,
 infrequently 1-4 secondary radii, total radii 4-11 (72-130 mm
 S.L. - adult to sub-adult specimens).

Comments

Cockerell (1909b) described juvenile scale characters and on this basis considered Notemigonus unrelated to Eurasian Abramidini. This was later amended (Cockerell, 1914). The combination of a naked keel, strongly decurved lateral line, central focus, fine concentric circuli and few posterior radii make this species unique within North America. In these characters it most closely resembles the Eurasian Abramidini (page 50). The Eurasian Cultrinae also share some of these characters (see p. 69) but differ in several other important respects (see p. 480) which exclude them from a possible relationship with Notemigonus.

GENUS NOTROPIS

Polytypic, in excess of 117 species, descriptions here based on N. atherinoides, N. atrocaudalis, N. bifrenatus, N. blennius, N. cornutus, N. hudsonius, N. lutrensis, N. procne, N. proserpinus, N. texanus, N. umbratilis, N. venustus and N. volucellus with numerous published accounts, 85 specimens, Figures 16.

Description

Scales regularly arranged but in certain species absent on the nape, predorsally crowded or regular, breast naked or scaled. Mean values of lateral line counts are distributed as follows: - 30-34 (10%), 35-39 (60%), 40-44 (23%), 45-49 (3%), 50-54 (2%) and 55-60 (1%); in the range 30-44 (94%) (based on published accounts and personal observations for a total of 96 species). Predorsal scale counts include many mid-line counts as well as scale row counts.

Scales large, imbricate, overlap set of 7, often very caducous. Lateral line usually complete and slightly decurved but in some species incomplete and occasionally quite strongly decurved. Scales on caudal peduncle are sub-hexagonal or sub-triangular, the latter shape being approached in scales where the postero-lateral corners are poorly developed. The sides are parallel, convex or sloping slightly to the anterior. A posterior rounded apex is evident. The antero-lateral corners are much sharper than the postero-lateral ones. The anterior edge may be a shallow curve, almost vertically straight, or it may be indented on each side of a rounded, small apex. Focus anterior, variably well set-off from anterior edge or compressing it. Circuli are most widely spaced and thickest posteriorly and an antero-lateral inflection is present. The posterior field may be broken up and irregular in some larger fish. Radii are restricted to the posterior field, encroaching laterally in some species.

Radii numbers vary, some larger species having many

radii and smaller species relatively few, e.g. in Notropis cornutus, (75-135 mm S.L.), primary radii number 10-34, secondary radii 2-37, total radii 16-71; in N. venustus (49-61 mm S.L.), primary radii number 5-7, secondary radii 0-2, total radii 6-8; in N. umbratilis (36-47 mm S.L.), primary radii number 4-9, secondary radii 0-8, total radii 5-15.

There are however specific and sub-generic differences (Cockerell and Calloway, 1909b; Jenkins and Lachner, 1971).

Comments

Many eastern N. American genera share several scale characters with Notropis species. Other genera may be distinguished on the basis of certain characters, e.g. scale radii counts are higher in Nocomis than in Hybopsis s.l. and Notropis (Jenkins and Lachner, 1971).

GENUS OPSOPOEODUS

Monotypic, O. emiliae, 6 specimens, Figure 17.

Description

Scales regularly distributed except crowded predorsally and absent on anterior part of belly.

Scales large, moderately imbricate, overlap set of 7, caducous. Lateral line complete usually but may be interrupted or terminate above anal fin, slightly decurved. Scales on caudal peduncle have rounded sides which curve to a rounded posterior apex. The antero-lateral corners are evident and there is a shallow rounded anterior apex. Focus anterior, compressing the anterior field. Circuli thickest and most widely spaced posteriorly and an antero-lateral inflection is present. Radii are restricted to the posterior field.

GENUS OREGONICHTHYS

Monotypic, O. crameri, 8 specimens, Figure 17.

Description

Scales regularly distributed on body except on belly where absent anteriorly and non-imbricate immediately posterior.

Scales large, moderately imbricate, overlap set of 7, caducous. Lateral line complete, little decurved. Scales on caudal peduncle with short rounded sides sloping to a rounded posterior apex with the postero-lateral corners hardly evident. The anterior scale edge is a gentle curve with a trace of an apex and dorsal and ventral indentations in some scales. Focus anterior compressing the anterior field. Circuli thickest and most widely spaced posteriorly and with an antero-lateral inflection. Radii are restricted to the posterior field.

Comments

Jenkins and Lachner (1971) gave a range in total radii of 7-13, mean 10.8 for scales taken from below the dorsal fin.

GENUS ORTHODON

Monotypic, O. microlepidotus, 18 specimens, Figure 17.

Description

Scale arranged somewhat irregularly over whole body, small, weakly imbricate, overlap set of 7, embedded. Lateral line descending steeply from head then slightly decurved on mid-line, wobbly, occasionally interrupted, ending a few

scales before caudal fin. Caudal peduncle scales usually sub-hexagonal, with parallel sides and rounded corners, the anterior and posterior apices varying from blunt to absent because merged into curved scale edge. Focus anterior, anterior field evident. Circuli are widely spaced posteriorly and take the form of elongate lozenges between the radii. Anteriorly and laterally circuli are fine and crowded. Radii are found on all fields except in small fish where they may be restricted to the posterior field. Some radii commence at the focus and extend to mid-field, others may be in mid-field. Cockerell (1909a) seems to have examined a juvenile specimen since the species was characterised as having few apical radii. Smaller specimens 72-90 mm S.L. have primary radii numbering 4-11, secondary radii 0-10, and total radii 4-17.

GENUS PAREXOGLOSSUM

Monotypic, P. laurae; 5 specimens. Hubbs (1931) figures an anterior flank scale. See Figure 18 also.

Description

Scales regularly arranged over body except immediately behind head predorsally where small and irregularly arranged and on breast where absent anteriorly and non-imbricate posteriorly. In larger specimens breast completely covered (Hubbs, 1931).

Scales moderate in size, imbricate, overlap set of 7, caducous. Lateral line complete, only a little decurved, sometimes wavy. Scales on caudal peduncle with short,

parallel sides passing through evident posterior corners to a rounded posterior apex. Anterior corners sharp and anterior edge indented on each side of a rounded apex. Edge may be wavy or a smooth curve. Focus anterior close to anterior edge. Circuli largest and most widely spaced posteriorly and with an antero-lateral inflection. Radii restricted to the posterior field.

GENUS PHENACOBIOUS

Five species, this description based on P. mirabilis and P. uranops, 8 specimens, Figure 18.

Description

Scales distributed regularly over body, except variably naked on belly anterior to pectoral fin bases and sometimes non-imbricate posteriorly on belly.

Scales large to moderate, imbricate, overlap set of 7-13, caducous. Lateral line complete, almost perfectly horizontal on flank and caudal peduncle. Scales on caudal peduncle with parallel or rounded sides leading via well-marked postero-lateral corners to a rounded posterior apex. Antero-lateral corners more sharp, anterior edge a shallow curve, irregular or indented with an anterior apex. Focus anterior, distinct from or close to anterior edge. Circuli thickest and most widely spaced posteriorly and with an antero-lateral inflection. Radii are found on the posterior field, sometimes encroaching laterally.

Comments

Jenkins and Lachner (1971) cite a range of about 8-15 total radii for scales taken from below the dorsal fin.

GENUS PIMEPHALES

Four species, P. notatus, P. promelas, P. tenellus and P. vigilax, description based on P. notatus, P. promelas and P. vigilax, 19 specimens, Figure 18.

Distribution

Scales over whole body, usually crowded predorsally, belly naked from pectoral fin bases anteriorly.

Scales large, imbricate, overlap set of 7, caducous. Lateral line little decurved, complete or incomplete variably within and between species. Scales on caudal peduncle with a short horizontal axis, sides rounded or parallel but short passing through rounded, pronounced or non-evident postero-lateral corners to a compressed rounded apex. The antero-lateral corners may also be non-evident or sharp and the anterior edge is compressed without a marked apex and often irregular. Anterior flank scales are a vertical oval. Focus anterior, well set-off or compressing anterior field. Circuli are thickest and most widely spaced posteriorly and there is a slight to strong antero-lateral inflection. Radii are found on the posterior field, encroaching laterally.

Comments

Hubbs and Black (1947) described geographical variation in total radii of scales from below the dorsal origin of P. vigilax and give ranges and means of counts for six 10 mm size classes of the Pimephales species.

GENUS PLAGOPTERUS

Monotypic, P. argentissimus, 10 specimens.

Description

True scales absent, rudimentary slivers of bone without radii or circuli found along lateral line, in several irregular rows above lateral line extending on to the back before the dorsal fin, few or none on flank beneath dorsal fin and up to three rows on the back at the caudal peduncle. Patches also found occasionally below the lateral line near the operculum and on the breast below the pectoral fin (4-9 in number usually in two rows). A single row of "scales" is found on the ventral edges of the caudal peduncle between the anal and caudal fins. Along the lateral line bone remnants number 16-65, above the lateral line 8-10 and predorsally 15-24.

"Scales" are strongly embedded and outside the lateral line non-imbricate. "Scale" shape varies from vase-like to oblong. The lateral line is mid-lateral and the scales are contiguous near the operculum becoming non-imbricate posteriorly. "Scales" in the lateral line may extend almost to the tail or end abruptly anterior to the dorsal fin. The lateral line may be wobbly. Lateral line scales consist of a bony tube with dorsal and ventral flanges decreasing in size posteriorly.

GENUS PLATYGOBIO

Monotypic, P. gracilis, 10 specimens, Figure 19.

Description

Scales regularly arranged over whole body, small to moderate in size, imbricate, overlap set of 13 (11 in some

small specimens), caducous. Lateral line complete, slightly to moderately decurved. Scales on caudal peduncle sub-hexagonal with parallel sides and rounded postero-lateral corners leading to a rounded apex. Antero-lateral corners sharp with the anterior edge wavy or indented on each side of a rounded apex. Focus anterior with a large anterior field. Focal area large and lacking radii and circuli in these specimens. Circuli are thickest and most widely spaced posteriorly and there is an antero-lateral inflection. Circuli are numerous in these large specimens. Radii are restricted to the posterior field but sometimes encroach laterally.

Comments

Jenkins and Lachner (1971) gave a range in total radii of 13-18, mean 14.8 for scales from below the dorsal fin.

GENUS POGONICHTHYS

Monotypic, P. macrolepidotus, 1 specimen, Figure 19.

Description

Scales over whole body, those on belly irregular in shape and of varying sizes.

Scales moderate in size, imbricate, overlap set not determined, caducous. Lateral line complete, slightly decurved anteriorly. Scales on caudal peduncle sub-triangular with rounded sides and a rounded posterior apex. The antero-lateral corners are sharp and the anterior edge is variously a shallow curve, wavy or indented on each side of a rounded apex. Focus anterior, but anterior field large. Circuli

thickest and most widely spaced posteriorly and with an antero-lateral inflection. Radii on posterior field encroaching laterally. Cockerell (1914) cites 35 apical radii.

GENUS PTYCHOCHEILUS

Four species, this description based on P. oregonensis, 8 specimens, Figure 19.

Description

Scales regularly arranged but small predorsally and even smaller on the belly.

Scales small, imbricate, overlap set 7 but may be 11 in places, caducous. Lateral line complete, slightly to moderately decurved. Scales on caudal peduncle sub-hexagonal with parallel sides though edge may be wavy, rounded corners and equally developed apices. The anterior edge may be wavy or irregular but is often a smooth or indented curve to a rounded apex. Some scales have a produced anterior apex like Gila. Focus anterior with a large anterior field. Circuli are thickest and most widely spaced posteriorly and there is an antero-lateral inflection. Circuli are numerous in these large specimens. Radii are present on all fields but often sparse to absent on the anterior field. Lateral radii may be few or numerous and both lateral and anterior radii may be broken, branching or lie in mid-field.

GENUS RELICTUS

Monotypic, R. solitarius, 8 specimens, Figure 20.

Description

Scales somewhat irregularly arranged but distributed over whole body.

Scales small, minimally imbricate, overlap set of 7-9, (exact arrangement hard to determine because of irregular scale arrangement), embedded. Lateral line interrupted and usually ending before the level of the dorsal fin. Pores number 3-29 (Hubbs, Miller and Hubbs, 1974). Scales on caudal peduncle sub-circular to sub-hexagonal with sides converging slightly to the anterior. All corners rounded and edges smooth except anterior edge may be wrinkled. Focus anterior, anterior field large. Circuli thickest and most widely spaced posteriorly and there are numerous fine circuli on the anterior field. Radii are found on all fields but are most abundant and crowded posteriorly. Branched radii, radii lying in mid-field and radii extending from focus to mid-field were common.

GENUS RHINICHTHYS

Five species namely Rhinichthys atratulus, R. cataractae, R. evermanni, R. falcatus and R. osculus. Description based on specimens of all these species, 50 specimens, Figure 20.

Description

Scales regularly arranged over body with the exception of the predorsal region in some specimens where scales may be crowded and on the isthmus where they may be absent. Scales are also absent from the fleshy pectoral and pelvic axillary processes.

Scales moderate to small in size, strongly imbricate, overlap set of 7-13, caducous. Lateral line is usually complete and little decurved but in R. osculus in particular

it may be irregular in its path along the flank, interrupted and terminating before the caudal peduncle. Scales on caudal peduncle are an elongate sub-hexagonal usually with parallel sides, rounded postero-lateral corners (may be merged into a curve to the posterior apex such that the scale is sub-triangular), a rounded posterior apex and evident antero-lateral corners. The anterior scale margin may be rounded, wavy or form an apex. Focus anterior and close to anterior edge obscuring circuli in some scales but clearly set off in others. Circuli are thickest and most widely spaced posteriorly but close to the focus they become fragmented or absent. There may be an antero-lateral inflection. Radii are usually present on all fields though they may be absent laterally and anteriorly in some scales of R. atratulus and R. falcatus. Branching may be common. Wide range in radii numbers between fish of similar size.

GENUS RICHARDSONIUS

Two species, R. balteatus and R. egregius, this description based on R. balteatus, 5 specimens, Figure 21.

Description

Scales are distributed over the whole body in a regular fashion but slightly crowded predorsally and very small on the belly.

Scales moderate in size, imbricate, overlap set of 7, caducous. Lateral line moderately to strongly decurved, occasionally interrupted. Scales on caudal peduncle sub-circular or oval with little evidence of corners and a wavy, rounded or indented anterior edge. Focus anterior compressing

anterior field a little. Circuli thickest and most widely spaced posteriorly and with a slight antero-lateral inflection in some scales. Radii are found on the posterior field, encroaching laterally.

Comments

The genus Clinostomus has been synonymised with Richardsonius by Uyeno (1961). Scale characters are comparable differing principally in scale counts above the lateral line, the overlap set and scale shape.

GENUS SEMOTILUS

Two species, S. atromaculatus and S. corporalis; 27 specimens, Figure 21

Description

Scales regularly arranged except on belly where may be absent anteriorly, irregularly arranged and minimally imbricate especially in young.

Scales of large to moderate size, moderately to strongly imbricate, overlap variable 7, 11 or 13, caducous. Lateral line complete, slightly to moderately decurved. Scales on caudal peduncle sub-hexagonal with parallel or slightly convex sides, evident, rounded postero-lateral corners and rounded posterior apex. Antero-lateral corners sharp. Anterior edge variable in form, from a smooth shallow curve through a wavy irregular edge to a rounded apex with dorsal and ventral indentations. Focus anterior with evident anterior field. Circuli are finest and most closely spaced anteriorly and laterally. Posterior field circuli may

develop hollow spaces or become irregular and wavy between radii. In certain, but not all, scales posterior circuli may pass through a sharp to moderate angle in the mid-line (see Cockerell and Allison, 1909). Radii are restricted principally to the posterior field although they may encroach laterally.

Comments

Jenkins and Lachner (1971) cite about 25-40 as a range in total radii for scales from below the dorsal fin. These authors also consider scale morphology of Semotilus and Nocomis to be similar and this agrees with the present data.

GENUS STYPODON

Monotypic, S. signifer, and probably extinct. No specimens were available for study. Garman (1881) gives the following scale characters. Scales moderately large, easily detached, broadly rounded on the posterior margin, lateral line complete, below the middle of the side of the tail, lateral line scales 35, in transverse series $6 + 1 + 2$.

GENUS TIAROGA

Monotypic, T. cobitis, 8 specimens, Figure 21.

Description

Scales restricted anteriorly to lateral line and 1-3 rows above and below it. Posteriorly the number of rows increases so that the caudal peduncle is almost completely scaled. The belly is naked with some scattered scales between the pelvic fins. The back in front of the dorsal fin may be naked or there may be some scales immediately anterior to the fin.

but not on the nape. The bases of the dorsal and anal fins also lack scales.

Scales small, non-imbricate except in and about lateral line, embedded, overlap count 7. Lateral line complete and almost horizontal. General shape oval or circular without evident corners or apices. Focus sub-central anterior or rarely almost central. Circuli thicker and more widely spaced posteriorly while thinner and more crowded anteriorly. On scales with a central focus circuli are equally developed on all fields. Radii on all fields, equally developed, with some branching and radii extending from focus to mid-field.

Genus Xystrosus

Monotypic, X. popoche, 4 specimens, Figure 22.

Description

Scales regularly distributed over whole body, small to moderate in size, strongly imbricate, overlap set of 13. Lateral line complete, moderately decurved and occasionally wavy. Scales on caudal peduncle with sides slightly rounded and slightly diverging posteriorly. General shape a rounded, elongate rectangle with evident posterior apex and an anterior edge with a rounded apex, irregular or a rounded curve. Posterior corners may be rounded or quite evident while anterior corners follow a general curve into the anterior edge. Focus anterior, anterior field distinct but small. Circuli thickest and most widely spaced posteriorly with a slight antero-lateral inflection. Circuli in the mid-line of the posterior field are sharply angled in some scales, more rounded in others.

There is some indication that sharply angled circuli predominate in scales with radii restricted to the posterior and lateral fields. Radii may be restricted to the posterior and lateral fields or they may be found on all fields. Even adjacent scales show a marked difference in counts of radii.

Genus Yuriria

Monotypic, Y. alta, 8 specimens, Figure 22.

Description

Scales regularly arranged over body, smallest on anterior belly.

Scales moderate in size, imbricate, overlap set of 7, caducous. Lateral line complete, moderately decurved. Sides of caudal peduncle scales parallel only anteriorly and may be rounded. The sides pass to a rounded posterior apex without obvious postero-lateral corners. Antero-lateral corners sharp, anterior edge rounded or a rounded apex with dorsal and ventral indentations. Focus anterior, well separated from anterior edge. Circuli are thickest and most widely spaced posteriorly where they are wavy and in some instances fragmented. There is an antero-lateral inflection. Radii are restricted to the posterior field, encroaching laterally.

Comments

Jenkins and Lachner (1971) gave a range in total radii of 16-21, mean 17.7 based on scales taken from below the dorsal fin. The discrepancy in counts is probably due to differences in size of specimens and possibly body position from which scales were taken.

Scale characters of cyprinid sub-families

This section attempts to summarise the scale characters of Old World cyprinids in order to facilitate comparison with New World cyprinids. It is based on the available specimens listed in brief here and in more detail in Appendix 1 and on the works of Cockerell (1910), Cockerell (1911a), Cockerell (1911b), Cockerell (1914), Cockerell (1915), Cockerell and Moore (1910), Chu (1935), Haque (1955), Galkin (1958), Kobayashi (1958), Kobayashi and Hayasi (1958), Das (1962) and Berry and Low (1970). The genera examined in these works are listed here; some are probably synonymous, and allocation of some to sub-family is disputed (see Appendix 3).

Sub-family Acheilognathinae

Specimens of Rhodeus and published descriptions of this genus and of Acanthorhodeus, Acheilognathus, Paracheilognathus, Pseudoperilampus.

Scales small to moderate in size with 33-55 in a complete or incomplete and slightly decurved lateral line. Moderately imbricate, overlap set of 7, caducous. Anterior flank scales are a vertical oval but those on the caudal peduncle are a short sub-hexagonal or sub-ovate shape. The sides are parallel or slope posteriorly. There is a posterior apex and a slight anterior apex. The focus is central or sub-central anterior with a large anterior field (but central on anterior scales). The posterior circuli may be finer than those elsewhere or they may form "bubbles" or degenerate.

Radii are restricted to the posterior field and number about 13-30. They are often degenerate or wavy.

Sub-family Barbinae

Specimens of Barbus and published descriptions of this genus and of Catla, Capoeta, Cirrhinus, Cyclocheilichthys, Garra, Labeo, Lissocheilus, Onychostoma, Osteocheilus, Periocypis, Procypis, Pseudogyrinocheilus, Ptychidio, Puntius, Semilabeo, Sinibarbus, Sinilabeo, Spinibarbus, Spinibarbichthys, Tor and Varicorhinus.

Scales small to large with 17-103 in the lateral line which is complete and moderately decurved. Variably imbricate, overlap set 7-13, caducous. Caudal peduncle scales sub-hexagonal with parallel, slightly rounded or slightly converging anteriorly sides. Postero- and antero-lateral corners usually well developed occasionally curving to the posterior apex. The antero-lateral corners are most distinct and the anterior edge is formed into a marked apex, or is wavy, irregular or curved and nearly vertical. The focus is sub-central anterior but the anterior field is always very well developed. In some species the focus is almost central. Circuli are finest and most closely spaced anteriorly. Posteriorly they may degenerate and "bubbles" are commonly found between the radii distally while basally close to the focus there are fine reticulations. Radii are usually present on all fields and are often numerous up to more than 100 in some species,

much less in others. Chu (1935) included Barbinae in Cyprininae (i.e. Cyprinus and Carassius). The latter have few radii but are otherwise similar to Barbinae in scale characters for certain species. Note that Hague (1955) shows scales of Barbus (Puntius) species with regenerating nuclei or focal areas similar to Cyprinus and Carassius.

Sub-family Cultrinae

Specimens of Pelecus cultratus and published descriptions of this genus and of Anabarilius, Chanodichthys, Chela, Culter, Cultriculus, Erythroculter, Hemiculter, Hemiculturella, Megalobrama, Metzia, Parabramis, Parapelecus, Pseudolaubuca, Rohanus, and Toxabramis.

Scales small to large in size, caducous, numbering about 32-105 in the slightly or greatly decurved and sometimes wavy lateral line. A naked keel extends, at its maximum, from the anus to the throat, in some only from the pelvic fin bases to the anus. Scales on caudal peduncle are ovate or sub-hexagonal with parallel or rounded sides passing through rounded postero-lateral corners to a posterior apex. The antero-lateral corners are usually quite evident and the anterior edge forms a shallow apex or may be rounded. The focus is usually sub-central anterior but it is occasionally central. The posterior circuli may be degenerate, partially modified into tubercular prominences, reticulations and granulations or regular. Regular circuli are often acutely angled in the mid-line of the posterior field. Radii are

restricted to the posterior field, rarely there may be a few incomplete anterior radii. Radii number 4-21.

Sub-family Cyprininae

Specimens of Carassius and Cyprinus and published descriptions of these genera.

Scales large numbering about 28-41 in the almost straight, complete lateral line. Scales are caducous and imbricate with an overlap set of 10-13. Caudal peduncle scales are sub-hexagonal but this may vary. Sides parallel, slightly curved, or indented. Posterior apex not always developed, edge then being curved. The anterior edge is wavy or irregular and variably indented. Focus sub-central anterior or posterior, or central. A regenerated focal area is characterised by a network of lines. Circuli are most widely spaced posteriorly but are fine, numerous and concentric overall. The posterior circuli can form bubbles or bead-like swellings. Radii are found on all fields but tend to be sparser laterally. Total radii number about 8-20 in Carassius spp., more in Cyprinus carpio.

Sub-family Danioninae

Specimens of Brachydanio, Danio and Rasbora and published descriptions of these and Aphyocypris, Atrilinea, Barilius, Ochetobius, Opsariichthys, Phoxinus, Squaliobarbus, Tanichthys, and Zacco.

Scales large to small, numbering about 27-102 in a complete

or incomplete lateral line. One genus lacks scales (Swamba). Scales are caducous or embedded, overlap set 7-13. Caudal peduncle scales shape varies from sub-hexagonal to oval. Focus sub-central anterior varying from close to anterior edge to close to scale centre. Circuli are thickest and most widely spaced posteriorly where they may be regular or degenerate or form granular, bubble-like structures with fine reticulations close to the focus. Radii numerous on all fields, or on all fields but poorly developed laterally, or absent anteriorly. Radii numbers may be few e.g. up to 16 on all fields, or numerous e.g. up to 40 on posterior field only.

Sub-family Gobioninae

Specimens of Gobio and Pseudorasbora and published descriptions of this genus and of Abbotina, Belligobio, Biwia, Chilogobio, Coreius, Coreoleuciscus, Gnathopogon, Hemibarbus, Paracanthobrama, Paraleucogobio, Pseudogobio, Pungtungia, Rhinogobio, Sarcocheilichthys, Saurogobio and Sinigobio.

Scales large to moderate in size numbering about 33-58 in a complete, little decurved lateral line. Scales are caducous, overlap count is 7-13 and belly scales are often absent. Caudal peduncle scales are sub-hexagonal with parallel or slightly curved sides and a rounded elongate posterior apex, or sub-triangular narrowing posteriorly. The anterior edge may be wavy or irregular. Focus sub-central anterior, often markedly. Circuli are finest laterally and anteriorly with an antero-lateral inflection. Posteriorly circuli dege-

nerate or are modified into tubercular or bubble-like structures. Radii are restricted to the posterior field and number about 8-30.

Sub-family Hypophthalmichthyinae

Published descriptions of Aristichthys and Hypophthalmichthys.

Scales very small, embedded, 96-120 in moderately de-curved lateral line. A naked keel extends from the throat to the anus. Caudal peduncle scales are sub-circular to sub-hexagonal, deepest posteriorly, corners poorly developed. Focus central or slightly sub-central posterior. Circuli concentric, more widely spaced posteriorly. Radii on posterior field varying from 0 (anterior flank scales) to a maximum of about 10 (on caudal peduncle scales).

Sub-family Leuciscinae

Specimens of Abramis, Alburnoides, Alburnus, Aspius, Blicca, Chondrostoma, Leuciscus, Rutilus, Scardinius, Tribolodon and Vimba and published descriptions of these and Ctenopharyngodon, Capoetobrama, Chalcalburnus, Danioides, Hemigrammocypripis, Ischikauia, Leucaspius, Luciosoma, Nicholsicypris, Oreoleuciscus, Elopichthys, Luciobrama, Mylopharyngodon, Pseudaspius and Tinca.

Scales large to very small numbering 55-155 in complete or, rarely, incomplete lateral line. Some species (Abramidini) with a naked keel from pelvic fins to anus. Scales usually caducous, overlap set of 7-15. Caudal peduncle scale shape

is usually sub-hexagonal, oval or occasionally sub-triangular. Focus sub-central anterior or central, rarely sub-central posterior. The regenerating focal area in some species forms a network of lines as in Cyprininae (e.g. Leuciscus idus, L. borysthenicus, L. cephalus, Rutilus rutilus and probably others). Circuli in the posterior field may be fine and concentric, or thicker and more widely spaced than in other fields or degenerate and forming bubbles. Usually circuli are fine and concentric in all fields. Posterior radii are almost invariably present, anterior radii are present or absent and lateral radii usually absent but sometimes present. Total radii number up to about 40 but may be few.

Sub-family Schizothoracinae

Published descriptions of Chuanchia, Diptychus, Gymnocypris, Gymnodiptychus, Herzensteinia, Paratylognathus, Platypharodon, Ptychobarbus, Schizopyge, Schizopygopsis, and Schizothorax.

Scales small except in region of anus, anal fin base and lateral line where relatively enlarged. In some genera (Schizopygopsis, Gymnocypris and Gymnodiptychus) scales have been lost except along the lateral line, behind the operculum, around the anus and anal fin, and sometimes around the ventral fins. The circuli and radii are not evident or absent on these scales. Scales minimally imbricate in almost straight lateral line and numbering 73-118. Caudal peduncle scales rounded or ovate. Focus sub-central

anterior. Circuli thickest and most widely spaced posteriorly where may be irregular. Radii on all fields numbering about 20-50.

Sub-family Xenocyprininae

Published descriptions of Distoechodon, Plagiognathops, Pseudobrama, and Xenocypris.

Scales small to moderate, numbering 40-84 in almost mid-lateral line. There is a post-pelvic fin keel. Caudal peduncle scales are sub-hexagonal or ovate with parallel or rounded sides leading to a posterior apex. Antero-lateral corners more evident than postero-lateral corners which may merge into sides and posterior apex. Anterior edge forming an apex or irregular and wavy. Focus sub-central anterior or almost central. Circuli are concentric and widest spaced posteriorly where they may degenerate or be modified into tubercular prominences. Radii restricted to posterior field, numbering up to about 20.

DISCUSSION

All cyprinid sub-families are not readily separable by scale characters alone, at least as presently recognised. Certain sub-families possess unique scale characters, e.g. Schizothoracinae and Hypophthalmichthyinae, which distinguish them from other sub-families and exclude them from common ancestry with the N. American cyprinids. Other sub-families may be excluded on the basis of other characters (see Appendix 3 for more detailed discussion). The N. American cyprinids cannot be placed in an Eurasian sub-family solely on the basis of apomorphic scale characters, with the exception of Notemigonus. Similarities in scale characters were noted between Chrosomus and Phoxinus and between Gila and Tribolodon. This reflects a common ancestry for Chrosomus and Phoxinus when considered with other characters but the relationship of Gila and Tribolodon is obscured by differences in other characters (see p.357).

Many of the scale characters examined in N. American cyprinids were very similar and indicate the close relationship of these genera. Certain characters have been assessed and are used in the character analysis.

Figure 3. Caudal peduncle scales[†] of Acrocheilus alutaceus, 96 mm. S. L., scale length 1.4 mm; Agosia chrysogaster*, 67 mm. S. L., scale length 0.8 mm; Algansea monticola, 40 mm. S. L., scale length 1.1 mm; Algansea tincella, 54 mm. S. L., scale length 1.3 mm.

[†] All scales are orientated with the anterior apex at the bottom except those with an * after the species name where the anterior apex is at the left. Scales are listed upper left, upper right, lower left, lower right. Scale length is measured from the tip of the anterior apex to the tip of the posterior apex.

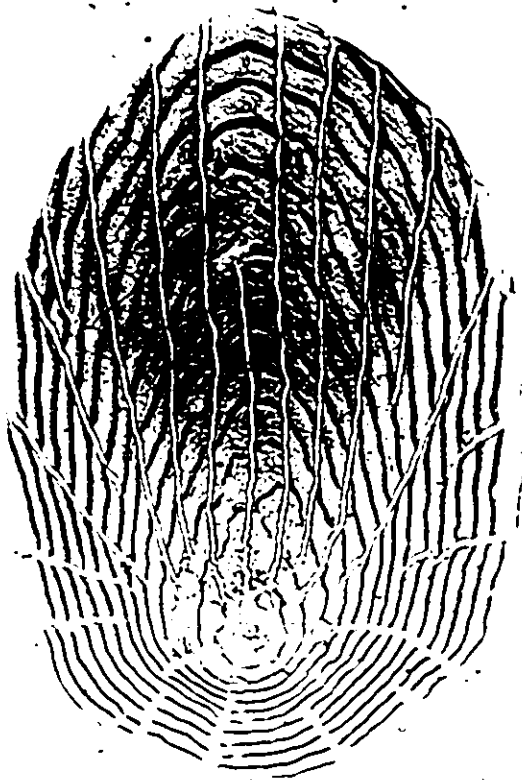
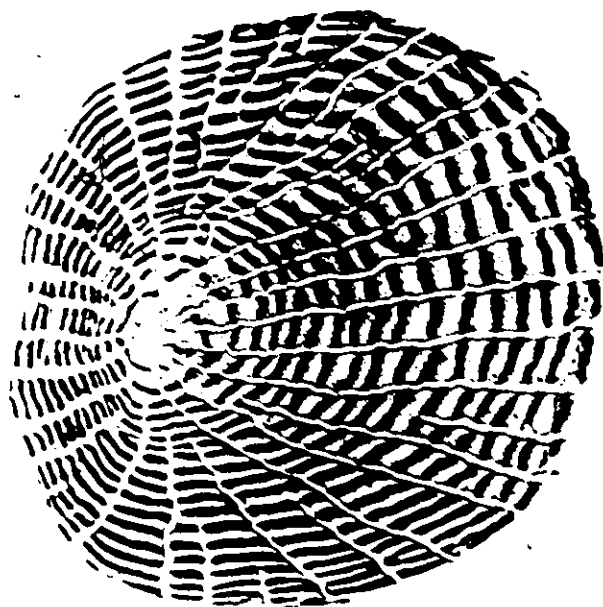
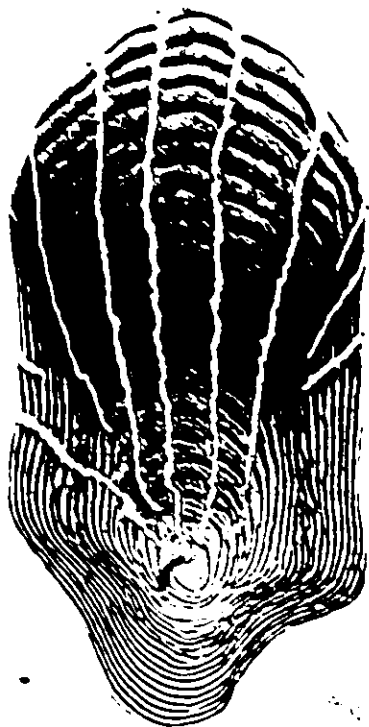
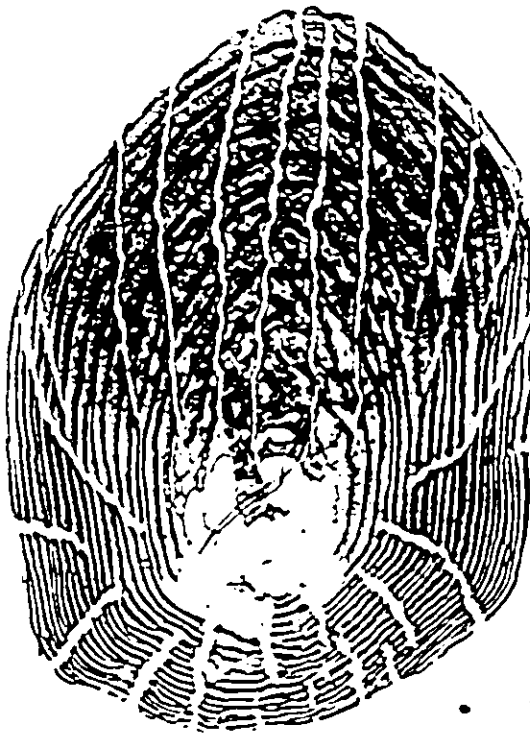
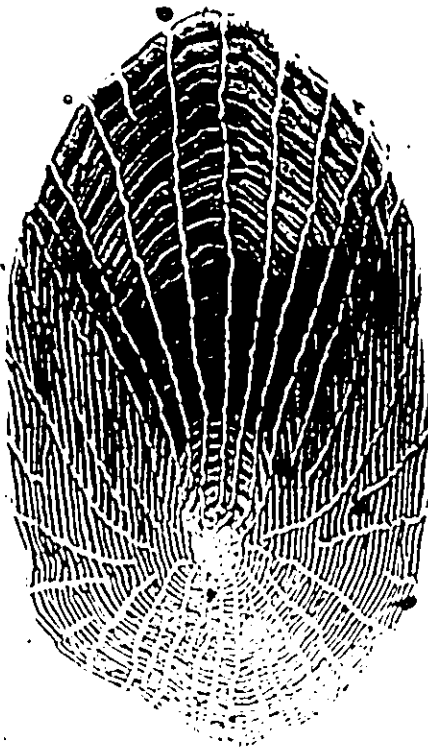
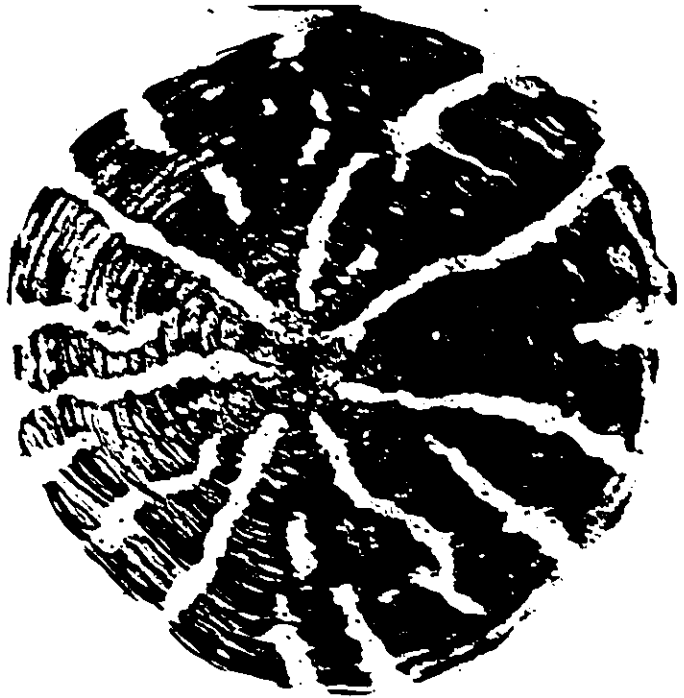


Figure 4. Caudal peduncle scales of Campostoma anomalum, 64 mm. S. L., scale length 1.0 mm; Chrosomus erythrogaster, 58 mm. S. L., scale length 0.7 mm; Chrosomus neogaeus,* 81 mm. S. L., scale length 0.9 mm; Chrosomus oreas, 55 mm. S. L., scale length 0.9 mm.



Figure 5. Caudal peduncle scales of Phoxinus czekanowskii, 56 mm. S. L., scale length 0.8 mm; Phoxinus issykkulensis*, 49 mm. S. L., scale length 0.3 mm; Phoxinus lagowskii, 110 mm. S. L., scale length 1.8 mm; Phoxinus percnurus, 53 mm. S. L., scale length 1.0 mm.



WILSON, J. L. 1954. The Great Lakes
Fishes. Michigan Department of Natural Resources
Bulletin 100. Lansing, Michigan.



Figure 6. Caudal peduncle scales of Phoxinus phoxinus, 64 mm. S. L., scale length 1.0 mm; Clinostomus funduloides, 72 mm. S. L., scale length 1.8 mm; Couesius plumbeus, 51 mm. S. L., scale length 1.4 mm; Dionda episcopa, 66 mm. S. L., scale length 2.7 mm.

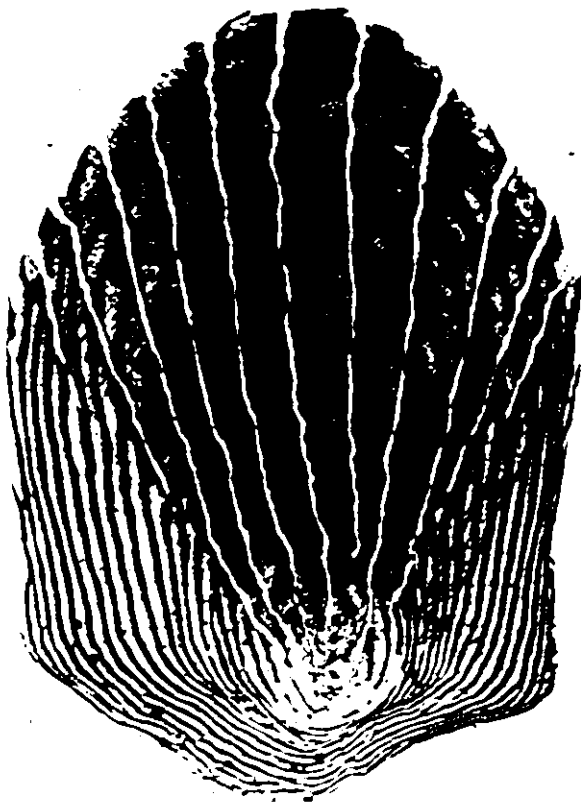


Figure 7. Caudal peduncle scales of Eremichthys acros, 52 mm. S. L., scale length 0.9 mm; Ericymba buccata*, 49 mm. S. L., scale length 2.0 mm; Hybopsis (Erimystax) dis-similis, 89 mm. S. L., scale length 2.8 mm; Hybopsis (Erimystax) x-punctata, 55 mm. S. L., scale length 1.9 mm.

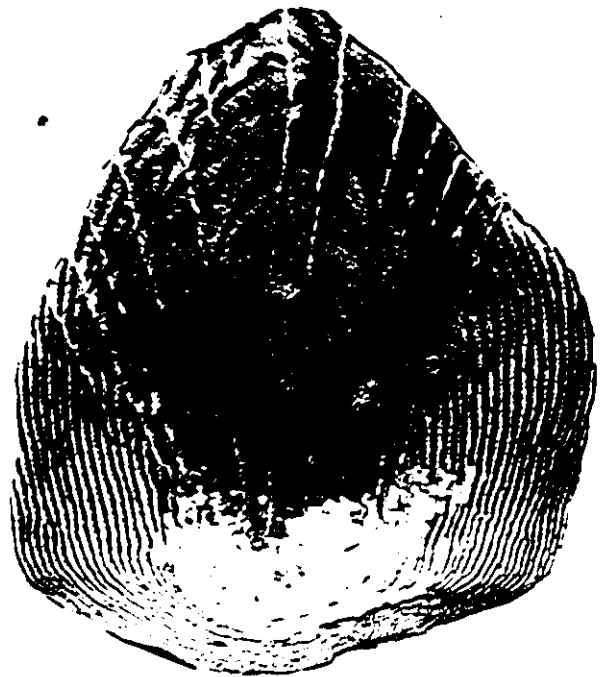
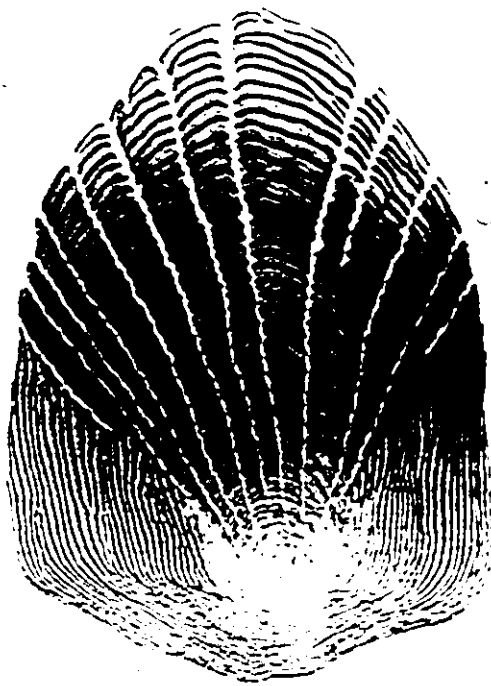
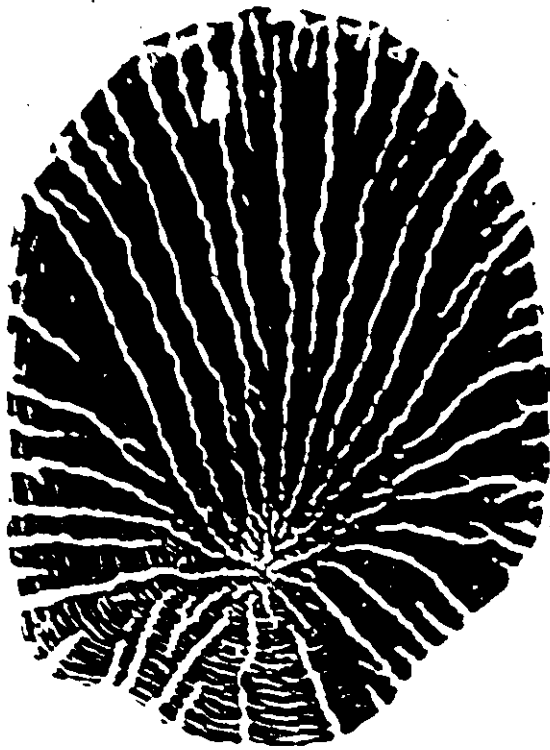


Figure 8. Caudal peduncle scales of Exoglossum maxilllingua, 103 mm. S. L., scale length 3.5 mm; Hybopsis (Extrarius) aestivalis, 47 mm. S. L., scale length 2.5 mm; Gila alvordensis, 53 mm. S. L., scale length 0.9 mm; Gila atraria, 67 mm. S. L., scale length 2.1 mm.

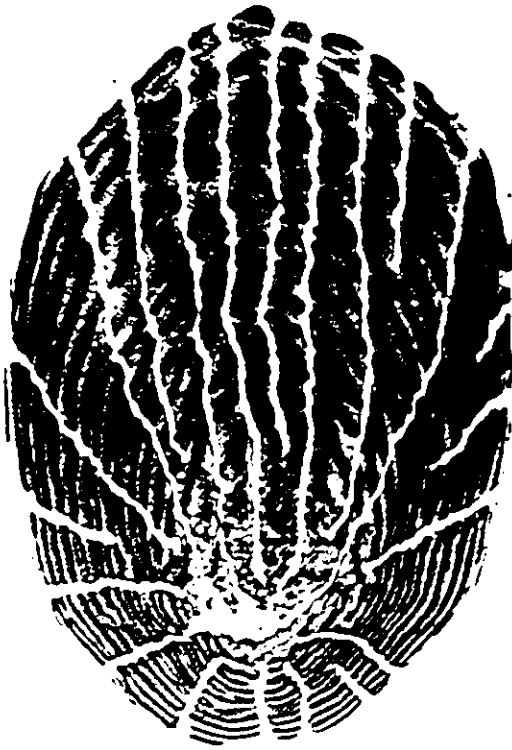
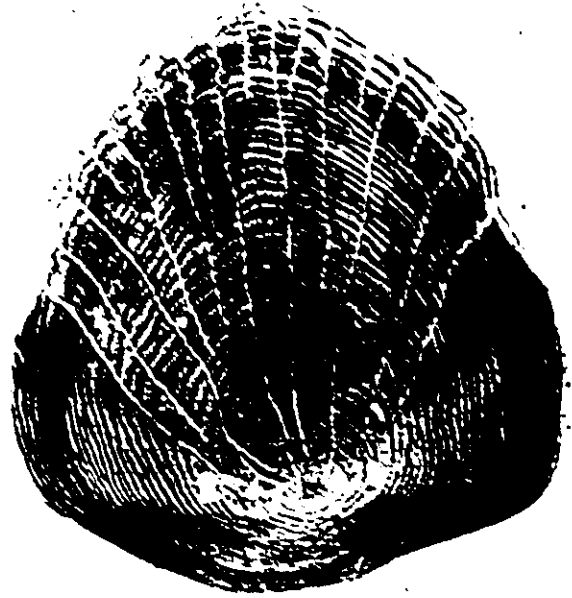


Figure 9. Caudal peduncle scales of Gila orcutti, 55 mm. S. L., scale length 1.7 mm; Gila robusta, 103 mm. S. L., scale length 1.6mm; Tribolodon hakonensis, 220 mm. S. L., scale length 7.7 mm; Tribolodon hakonensis, 170 mm. S. L., scale length 3.8 mm.

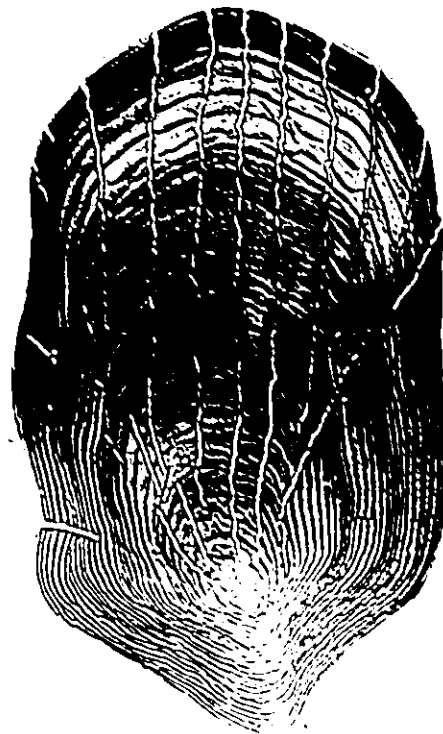
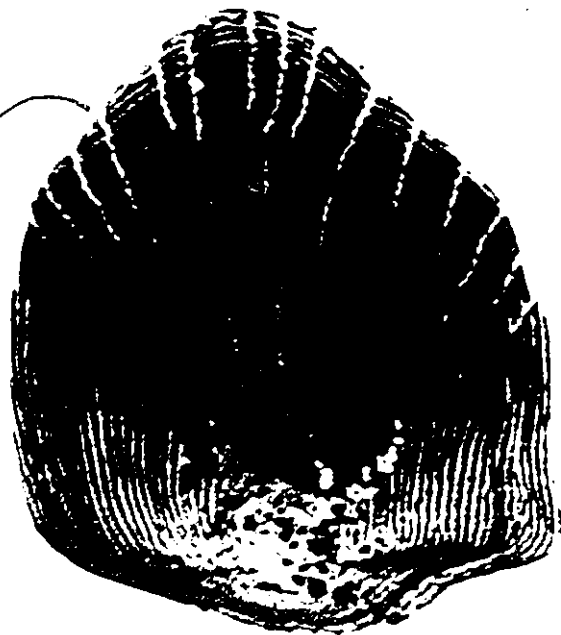
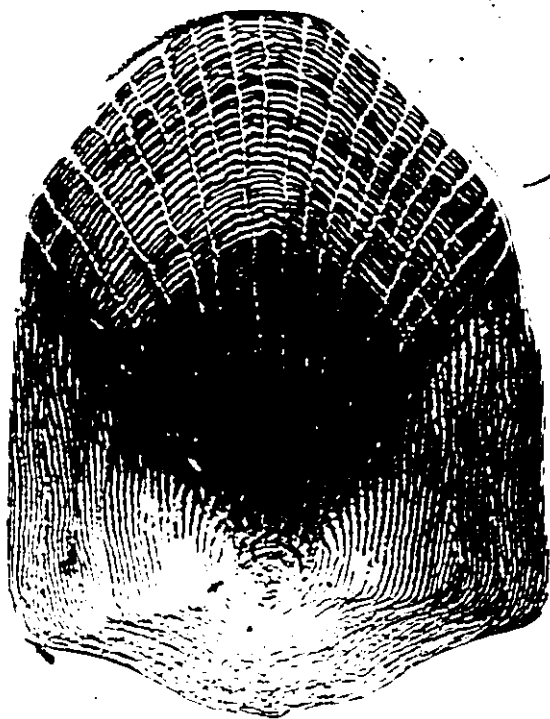
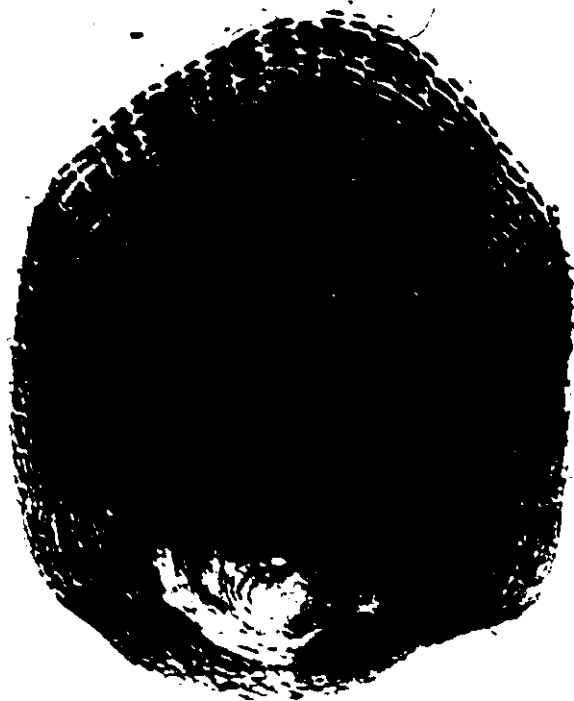
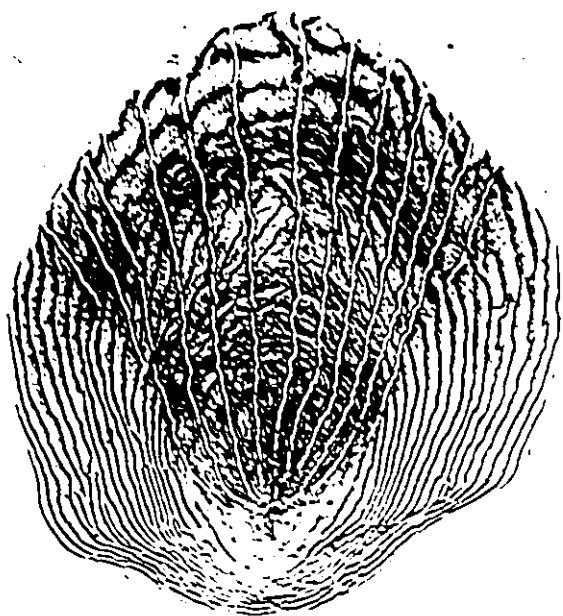


Figure 10. Caudal peduncle scales of Hemitremia flammea, 40 mm. S. L., scale length 1.4 mm; Hesperoleucus symmetricus, 97 mm. S. L., scale length 3.0 mm; Hybognathus placitus, 79 mm S. L., scale length 3.1 mm; Hybopsis (Hybopsis) amblops, 55 mm. S. L., scale length 2.6 mm.



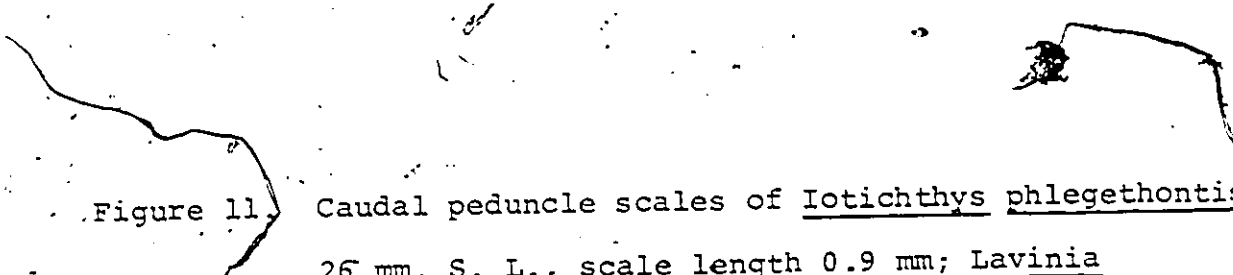


Figure 11. Caudal peduncle scales of Iotichthys phlegethontis,⁺ 26 mm. S. L., scale length 0.9 mm; Lavinia exilicauda, 75 mm. S. L., scale length 1.8 mm; Lavinia^A exilicauda, 233 mm. S. L., scale length 5.4 mm; Lepidomeda vittata, 81 mm. S. L., scale length 1.6 mm.

⁺ Anterior flank scale

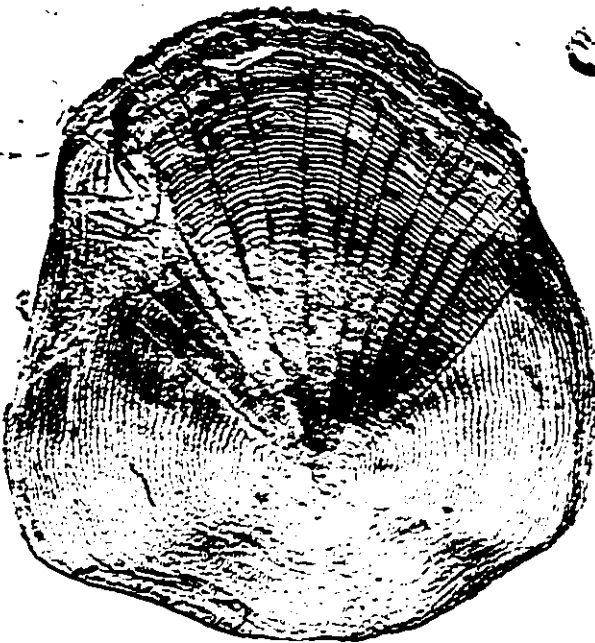
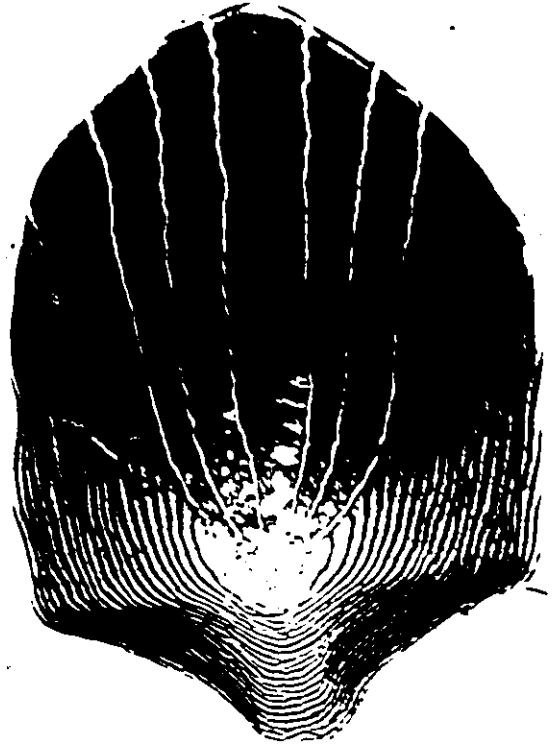


Figure 12. Caudal peduncle scales of Hybopsis (Macrhybopsis) gelida, 35 mm. S. L., scale length 1.1 mm; Semotilus (Margariscus) margarita, 87 mm. S. L., scale length 1.6 mm; Moapa coriacea, 45 mm. S. L., scale length 0.5 mm; Mylocheilus caurinus, 146 mm. S. L., scale length 2.4 mm.

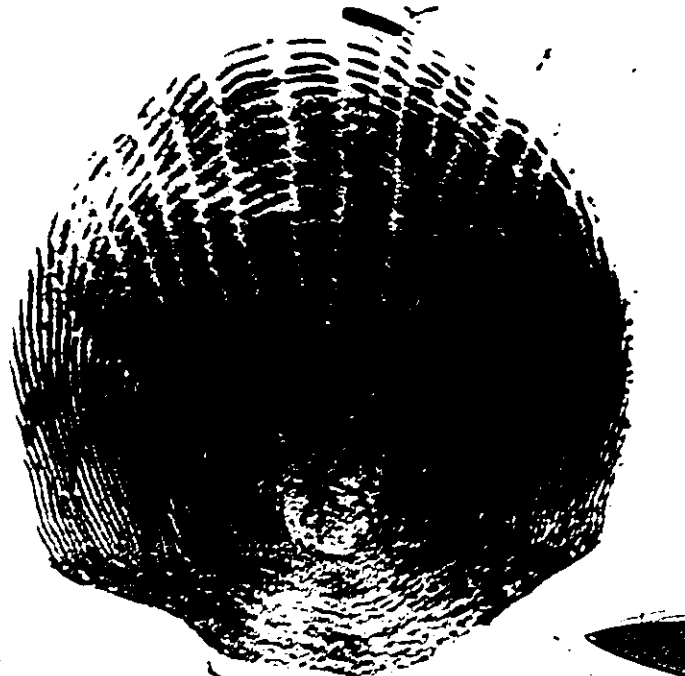
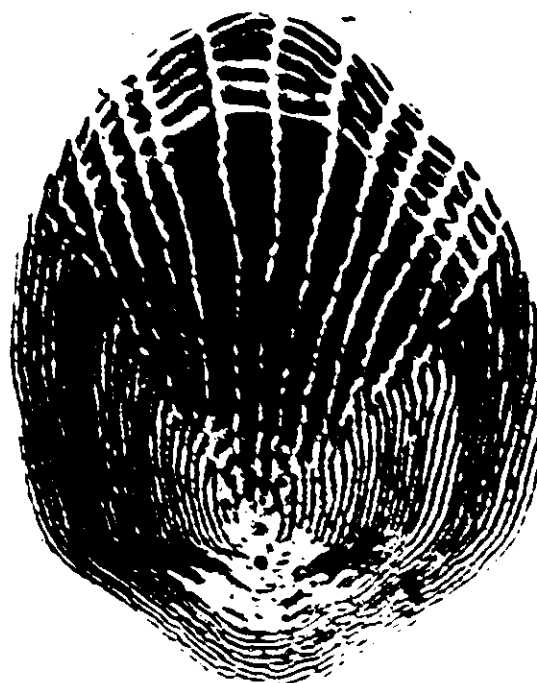
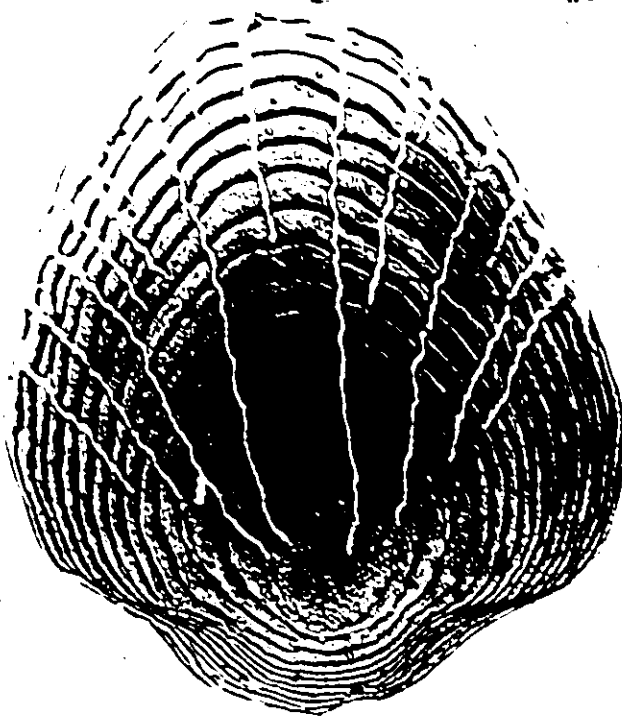




Figure 13. Caudal peduncle scales of Mylopharodon conocephalus, 111 mm. S. L., scale length 2.4 mm; Nocomis asper, 97 mm. S. L., scale length 3.0 mm; Nocomis micropogon, 88 mm. S. L., scale length 3.5 mm; Notemigonus crysoleucas[†], 109 mm. S. L., scale length 4.4 mm.

[†] Anterior apex at upper left corner

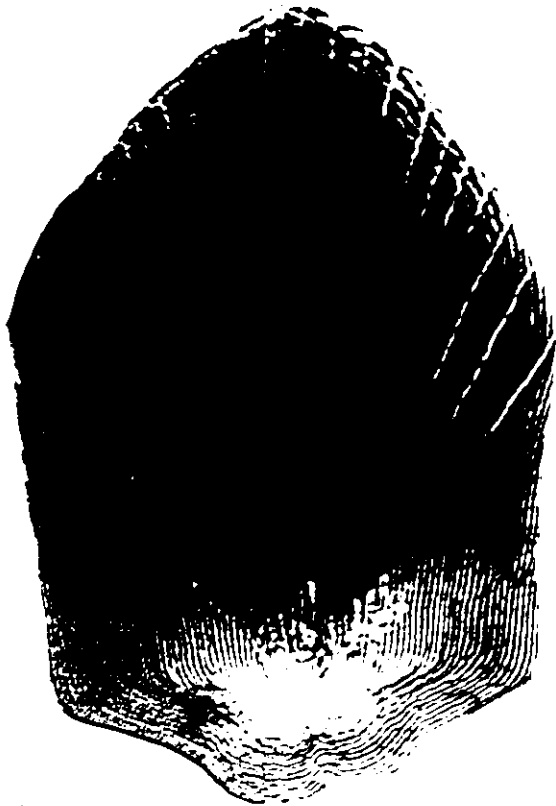


Figure 14. Caudal peduncle scales of Abramis ballerus, 201 mm.

S. L., scale length 3.9 mm; Abramis brama, 220 mm.

S. L., scale length 7.1 mm; Abramis brama^{*}, 56 mm.

S. L., scale length 1.6 mm; Abramis sapa[†], 52 mm.

S. L., scale length 2.4 mm.

† Anterior apex at upper left corner

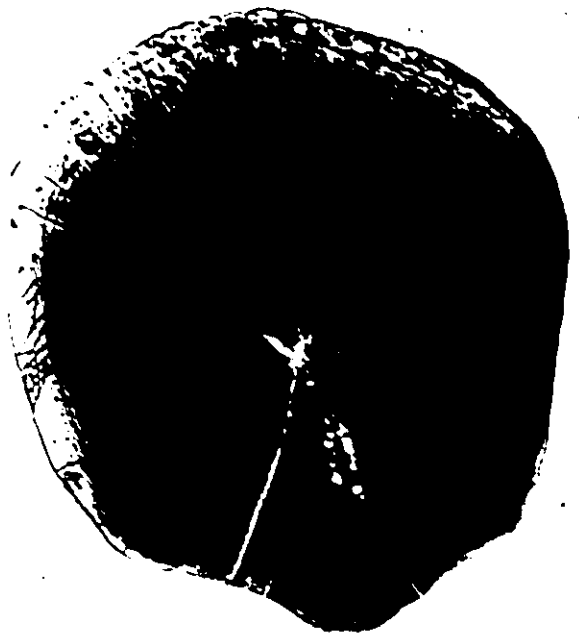
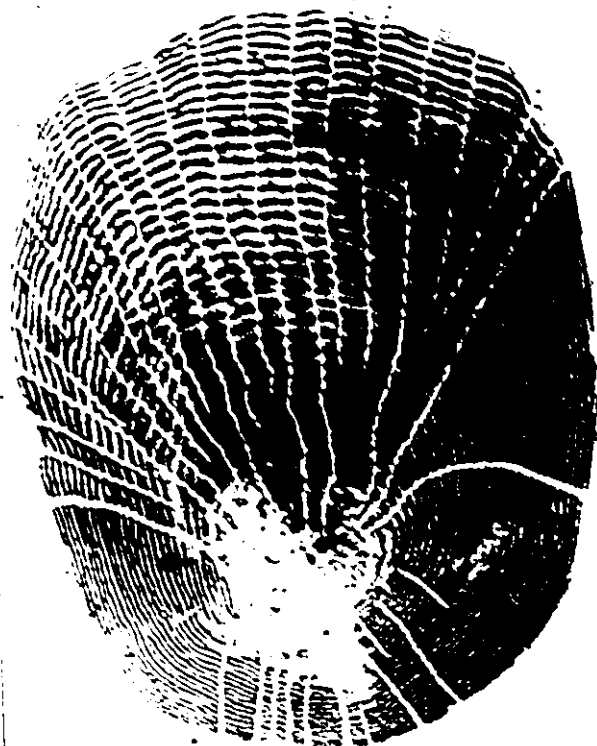


Figure 15. Caudal peduncle scales of Alburnoides bipunctatus, 80 mm. S. L., scale length 3.1 mm; Alburnus alburnus, 114 mm. S. L., scale length 2.9 mm; Blicca bjoerkna*, 64 mm. S. L., scale length 3.1 mm; Vimba vimba, 97 mm. S. L., scale length 3.1 mm.



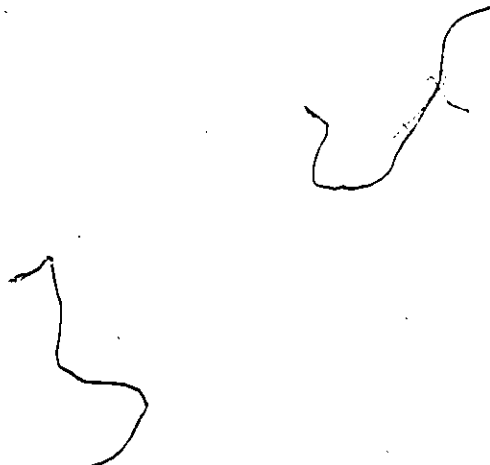


Figure 16. Caudal peduncle scales of Notropis bifrenatus, 33 mm. S. L., scale length 1.3 mm; Notropis lutrensis, 44 mm. S. L., scale length 1.6 mm; Notropis proserpinus, 42 mm. S. L., scale length 1.4 mm; Notropis umbratilis*, 43 mm. S. L., scale length 1.2 mm.

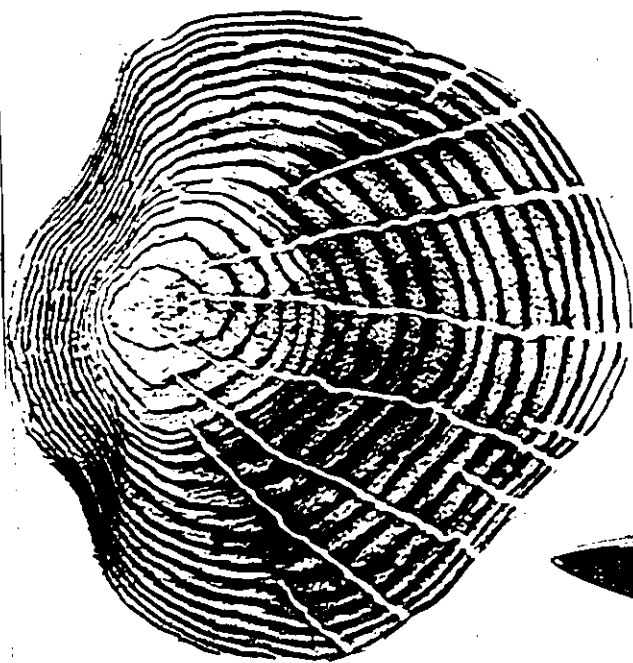
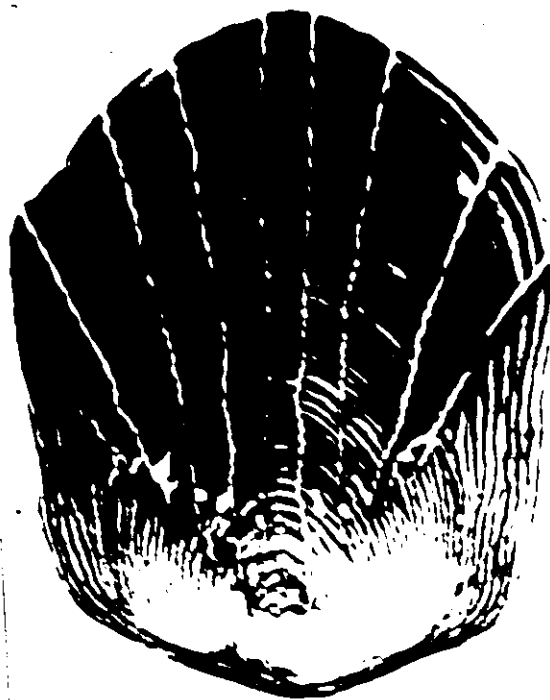


Figure 17. Caudal peduncle scales of Opsopoeodus emiliae*,
37 mm. S. L., scale length 1.1 mm; Hybopsis
(Oregonichthys) crameri*, 41 mm. S. L., scale
length 1.4 mm; Orthodon microlepidotus, 228 mm.
S. L., scale length 3.0 mm; Orthodon microlepidotus,
88 mm. S. L., scale length 1.0 mm.



Figure 18. Caudal peduncle scales of Parexoglossum laurae, 33 mm. S. L., scale length 1.1 mm; Phenacobius uranops, 87 mm. S. L., scale length 2.7 mm; Pimephales promelas*, 61 mm. S. L., scale length 1.6 mm; Pimephales vigilax*, 52 mm. S. L., scale length 1.8 mm.

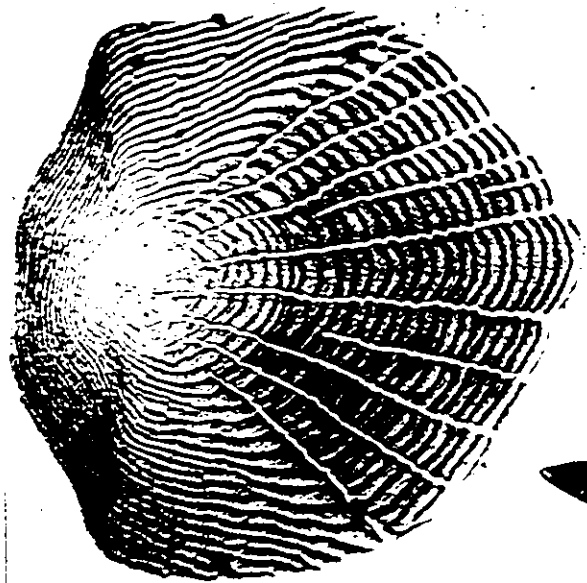
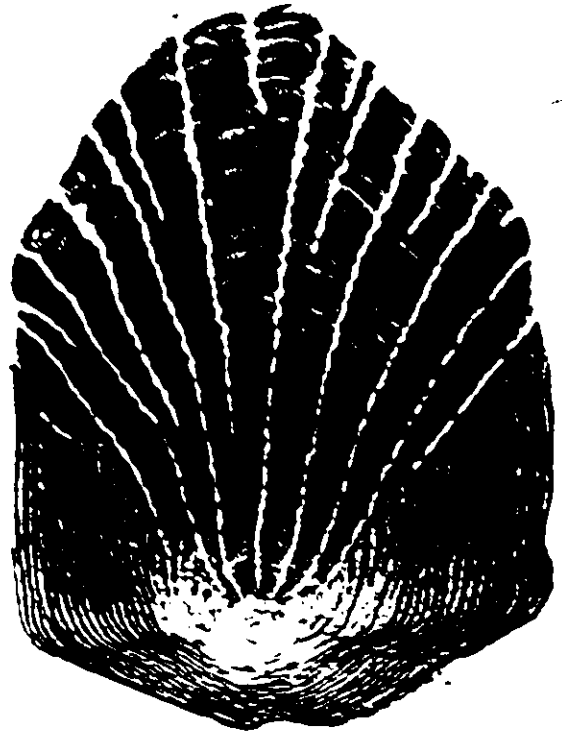
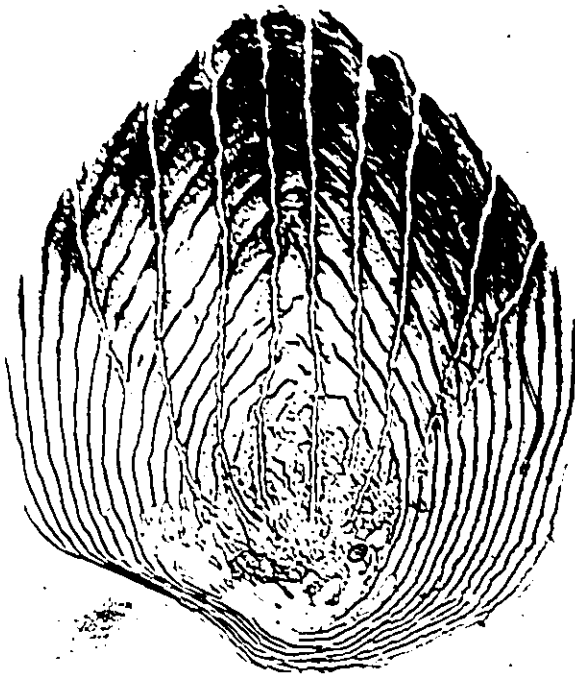


Figure 19. Caudal peduncle scales of Platygobio gracilis, 78 mm. S. L., scale length 2.6 mm; Platygobio gracilis, 165 mm. S. L., scale length 8.0 mm; Pogonichthys macrolepidotus*, 105 mm. S. L., scale length 2.4 mm; Ptychocheilus oregonensis, 305 mm. S. L., scale length 4.9 mm.

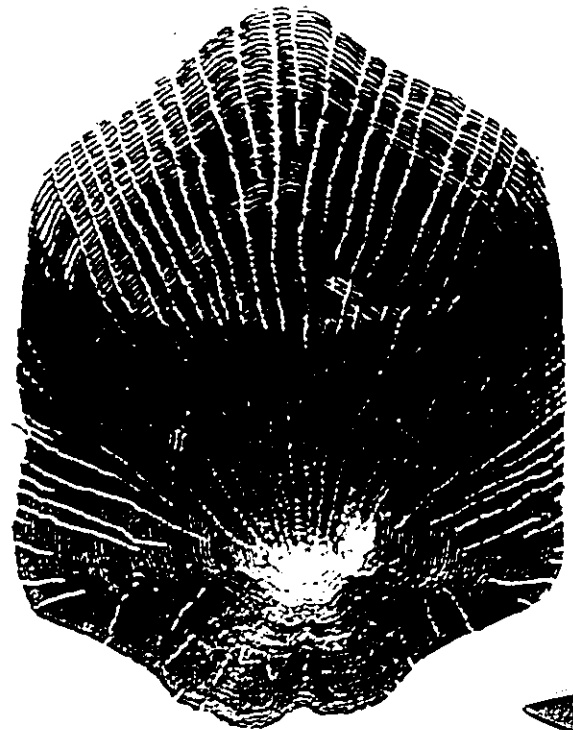
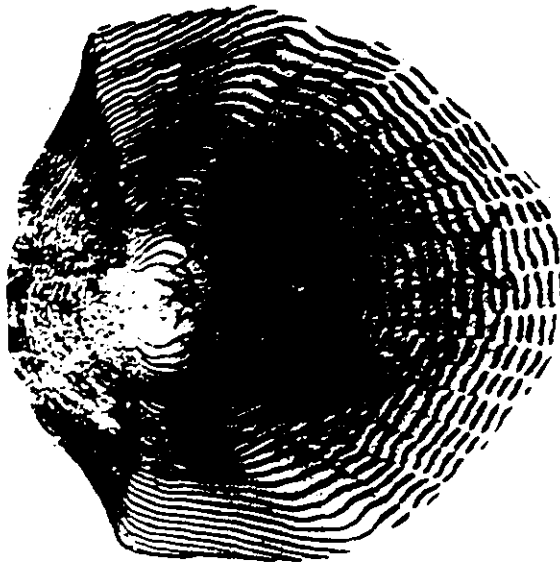


Figure 20. Caudal peduncle scales of Relictus solitarius, 41 mm. S. L., scale length 1.3 mm; Rhinichthys evermanni, 65 mm. S. L., scale length 1.4 mm; Rhinichthys falcatus, 64 mm. S. L., scale length 1.3 mm; Rhinichthys osculus, 52 mm. S. L., scale length 1.2 mm.

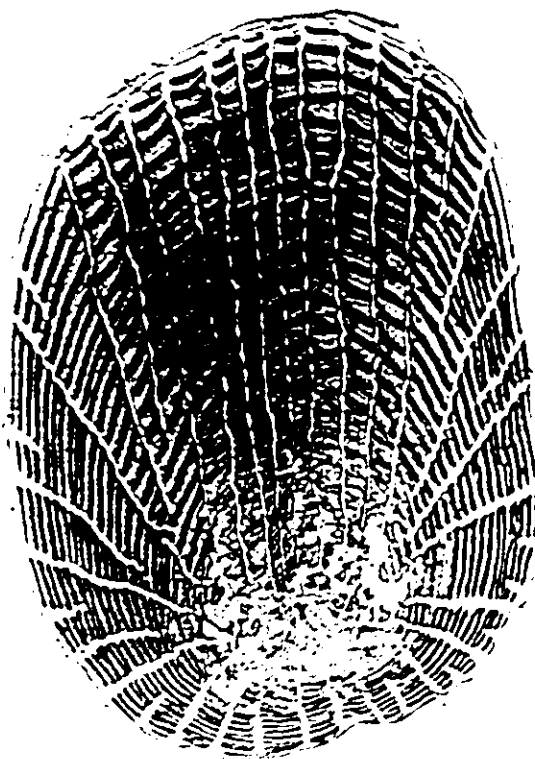
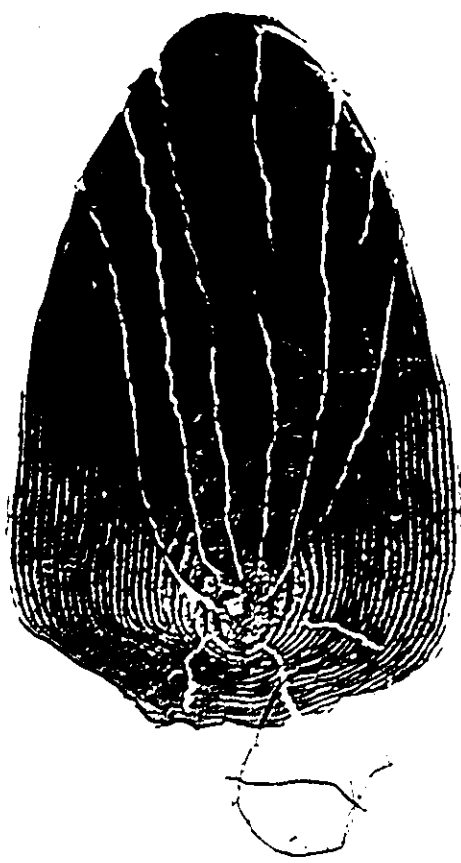
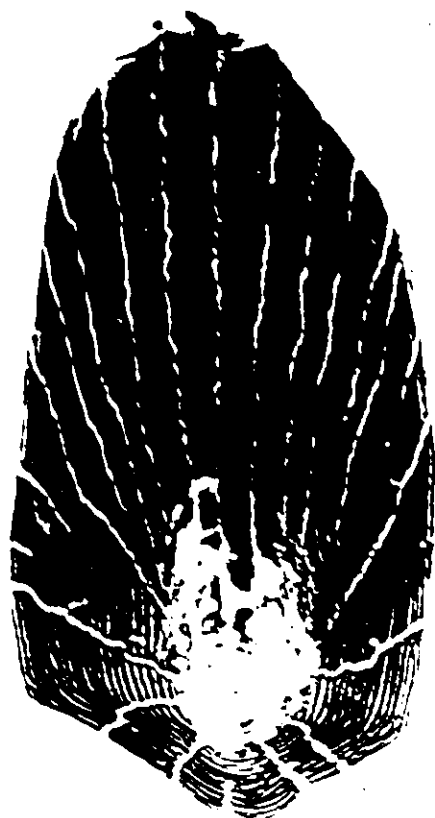
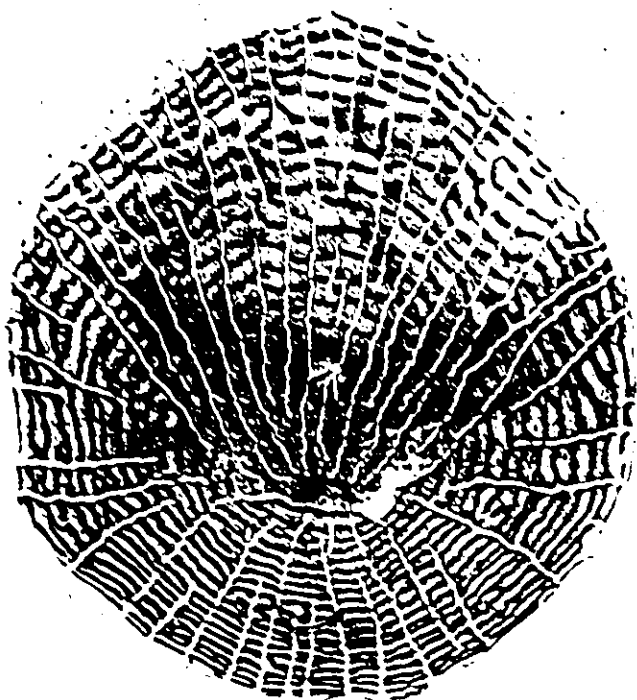


Figure 21. Caudal peduncle scales of Richardsonius balteatus*, 62 mm. S. L., scale length 1.2 mm; Semotilus atromaculatus, 121 mm. S. L., scale length 3.3 mm; Semotilus corporalis, 232 mm. S. L., scale length 8.8 mm; Tiaroga cobitis*, 67 mm. S. L., scale length 0.6 mm.

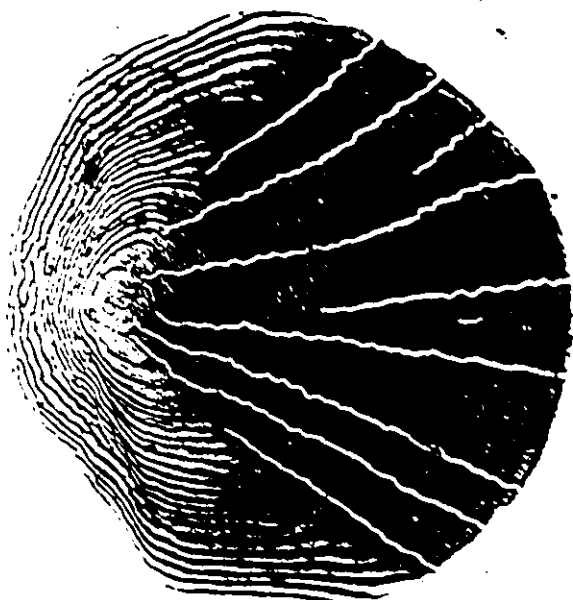
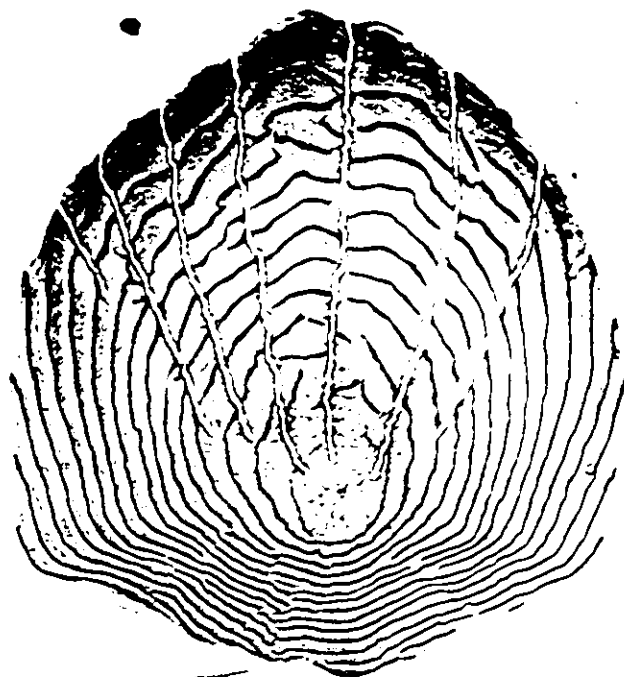


Figure 22. Caudal peduncle scales of Xystrosus popoche, 110 mm. S. L., scale length 2.6 mm; Xystrosus popoche, 110 mm. S. L., scale length 2.9 mm; Hybopsis (Yuriria) alta, 44 mm. S. L., scale length 1.3 mm.



Osteological Studies

INTRODUCTION

Comparative osteology has been used for many years in tracing systematic relationships in the higher categories of fishes. Uyeno (1961) and Buhan (1970) have used comparative osteology at the generic and species level in attempts to clarify relationships of certain North American genera of cyprinids, principally Gila, Ptychocheilus, Richardsonius, Clinostomus and Semotilus s.l.

The present study surveys certain osteological features of the majority of North American cyprinid genera and also some genera from Eurasia. It does not purport to be a complete osteology of the N. American cyprinids and some of the more inaccessible bone elements were not examined in detail.

The first part of this section of the thesis is a detailed study of the osteology of the golden shiner, Notemigonus crysoleucas (Mitchill), a monotypic genus, for which a variety of specimens was available. It forms a basis for the comparative studies on the other N. American genera which comprise the second part. Osteological comparisons between certain N. American and Eurasian genera are summarized in the section on Palaearctic-Nearctic relationships in Cyprinidae.

MATERIALS AND METHODS

Bone preparations

All stained osteological preparations were made on preserved specimens. The technique used was modified after Hollister (1934). Each specimen was immersed initially in distilled water to remove as much of its preservative as possible. The sex and standard length were determined and the contents of the body cavity removed through a slit in the abdominal wall. The specimen was then placed in a 2% solution of potassium hydroxide. A few drops of alizarin in ethanol were added when the flesh began to clear. Changes of potassium hydroxide and addition of more alizarin were carried out when deemed necessary. The specimen was cleared in a 50% ethanol - 50% glycerol mixture and stored in this mixture until dissected. Preparation time varied from a few days to several weeks depending on specimen size.

Certain data, such as those on vertebral numbers, were determined from X-ray plates. The time, voltage and amperage was varied with the size of the specimen according to a table in the Ichthyology Unit of the National Museum of Canada, Ottawa. Kodak Type M X-ray film was used in a Softex EMB X-ray machine.

Dissection technique

Each stained specimen was dissected in the following manner for reasons of convenience. The position, arrangement

and shape of the interneural and intermuscular bones were noted before the axial musculature was peeled off. The caudal skeleton, vertebral column and median fins were examined in situ. The pectoral and pelvic girdles were dissected out and examined separately. The relationship of the various sensory head canals to other head structures was noted before the left and right bones of the oromandibular region, the opercular series, the suborbital series, the symplectic and the hyomandibular were detached as a unit for study. The hyoid region, except the hyomandibular, symplectic and opercular series, was removed with the bones of the branchial region. All the bones listed above were disarticulated if necessary for more detailed examination. The prevomer, parasphenoid and ethmoid complex were observed in place on the cranium and after disarticulation. Otoliths were removed from the cranium by detaching the basioccipital and exoccipital. The Weberian apparatus was studied when the Weberian vertebrae were still attached to the skull and after removal and separation of these vertebrae from the skull and posterior vertebrae.

Bone terminology

The terminology and detailed descriptions closely follow those used by Harrington (1955) and Buhan (1970) but differ in several respects from that adopted by Uyeno (1961). The synonymy below provides the usage in the present work where it differs from Uyeno's.



Uyeno

Present study

Urostyle	Fused first and second urodermals
First hypural	Haemal spine
Several hypural etc.	Sixth hypural etc.
Actinosts of pectoral fin	Pectoral radials
Pterygiophores of pelvic fin	Pelvic radials

Harrington (1955) discusses the relationships of the complex herein termed the supratemporal-intertemporal.

Figures

The figures were drawn with the aid of a camera lucida attached to a Wild M5 microscope and are based on adult specimens judged to be typical of the species. The bones in the figures are labelled with abbreviations. The full names are given in the figure captions. Certain bones are drawn after disarticulation.

Material examined

A detailed list of the specimens examined is given in the Appendix. Wherever possible specimens of both sexes and all age groups were chosen from the range of the species. In this way an attempt was made to eliminate variation due to sex, age or location. Nevertheless statements on osteology are limited in certain cases by the availability of specimens as may be seen by examination of the specimen list. Forty-seven genera, 88 species and 448 specimens were studied. A brief listing of these alizarin specimens with number examined in parentheses follows: -

North American cyprinids

- Acrocheilus alutaceus (5)
- Agosia chrysogaster (10)
- Algansea monticola (4)
- Algansea tincella (4)
- Campostoma anomalum (4)
- Chrosomus eos (20)
- Chrosomus erythrogaster (8)
- Chrosomus neogaeus (14)
- Chrosomus oreas (4)
- Clinostomus funduloides (2)
- Couesius plumbeus (12)
- Dionda episcopa (8)
- Eremichthys acros (10)
- Ericymba buccata (8)
- Hybopsis (Erimystax) dissimilis (8)
- Hybopsis (Erimystax) x-punctata (2)
- Exoglossum maxillingua (4)
- Hybopsis (Extrarius) aestivalis (9)
- Gila alvordensis (2)
- Gila atraria (2)
- Gila bicolor (4)
- Gila orcutti (2)
- Gila robusta (2)
- Hemitremia flammea (2)
- Hesperoleucus symmetricus (14)
- Hybognathus hankinsoni (5)

Hybognathus hayi (1)
Hybognathus nuchalis (7)
Hybognathus placitus (4)
Hybopsis (Hybopsis) amblops (11)
Iotichthys phlegethontis (5)
Lavinia exilicauda (9)
Lepidomeda mollispinis (5)
Lepidomeda vittata (4)
Hybopsis (Macrhybopsis) gelida (3)
Hybopsis (Macrhybopsis) meeki (4)
Semotilus (Margariscus) margarita (5)
Meda fulgida (5)
Moapa coriacea (10)
Mylocheilus caurinus (4)
Mylopharodon conocephalus (5)
Nocomis asper (2)
Nocomis biguttatus (1)
Nocomis effusus (3)
Nocomis leptcephalus (3)
Nocomis micropogon (3)
Nocomis platyrhynchus (2)
Notemigonus crysoleucas (15)
Notropis atherinoides (6)
Notropis atrocaudalis (2)
Notropis bifrenatus (2)
Notropis blennius (2)
Notropis cornutus (2)

Notropis hudsonius (2)
Notropis labrosus (3)
Notropis lutrensis (2)
Notropis procne (2)
Notropis proserpinus (2)
Notropis texanus (2)
Notropis umbratilis (3)
Notropis venustus (2)
Notropis volucellus (4)
Opsopoeodus emiliae (2)
Hybopsis (Oregonichthys) crameri (4)
Orthodon microlepidotus (8)
Parexoglossum laurae (4)
Phenacobius mirabilis (4)
Phenacobius uranops (4)
Pimephales notatus (2)
Pimephales promelas (2)
Pimephales vigilax (4)
Plagopterus argentissimus (9)
Platygobio gracilis (4)
Pogonichthys macrolepidotus (1)
Ptychocheilus oregonensis (2)
Relictus solitarius (4)
Rhinichthys atratulus (10)
Rhinichthys cataractae (11)
Rhinichthys evermanni (4)

Rhinichthys falcatus (5)
Rhinichthys lariversi (= osculus ?) (9)
Rhinichthys osculus (6)
Richardsonius balteatus (2)
Semotilus atromaculatus (4)
Semotilus corporalis (5)
Tiaroga cobitis (13)
Xystrosus popoche (5)
Hybopsis (Yuriria) alta (4)

Eurasian cyprinids

Abramis ballerus (5)
Abramis brama (7)
Abramis sapa (5)
Alburnoides bipunctatus (10)
Alburnus alburnus (10)
Blicca bjoerkna (3)
Tribolodon hakonensis (4)
Vimba vimba (5)

RESULTS

Detailed osteology of Notemigonus crysoleucas (Mitchill).

The skeleton is divided into several areas for convenience. These are the cranial skeleton, vertebral column skeleton, median fin skeleton and the paired fin skeleton. The pectoral fin skeleton is intimately associated with the cranial skeleton.

CRANIAL SKELETON

The cranial skeleton is subdivided into seven regions after Harrington (1955) with minor modifications. The regions are the olfactory, orbital, otic, basicranial, oromandibular, hyoid and branchial.

The neurocranium provides a supporting and protective framework for the olfactory, optic, otic and part of the acoustico-lateralis organs and encases the brain. The splanchnocranium is suspended from the neurocranium and includes bones of the hyoid, branchial and oromandibular regions associated with feeding and respiration..

OLFACTORY REGION

Supraethmoid (Figures 24, 26 and 27).

The supraethmoid is a median, dermal bone fused to the ethmoid. Harrington (1955) considers that it may have been paired but pairing is not evident in this species. The dorsal surface is concave in the mid-line. In dorsal view the bone has diverging anterior wings on either side of a median ethmoid notch. Posteriorly, gently diverging wings are sutured to the frontals which overlie them. A median spike is directed posteriorly ventral to the frontals in some specimens. The width is about equal to the length.

Ethmoid (Figures 26 and 27).

The ethmoid is a median, endochondral bone lying in the sagittal plane. It is composed of two vertical plates which merge anteriorly and antero-ventrally to form a posteriorly

opening cup. In posterior view therefore the lateral walls do not meet. The two plates articulate posteriorly with the lateral ethmoids and dorsally their joint roof is fused with the supraethmoid. A large, ventral, horizontal plate, confluent with the cartilaginous planum ethmoidale, overlies the prevomer. It is expanded anteriorly into rounded processes which follow the notch of the prevomer and forms the upper parts of the receptacles for the preethmoids. The kinethmoid has ligamentous connections with the median notch formed by the anterior processes. Part of the posterior edge of the ethmoid forms the border of the olfactory foramen with the lateral ethmoid. The vertical and horizontal plates are perforated.

Lateral ethmoids (Figures 24, 25, 26 and 27).

The lateral ethmoids are paired endochondral bones laterally fused to the prefrontals. The mesial part of each lateral ethmoid consists of a plate which articulates with its opposing partner and forms the anterior floor of the brain cavity. Posteriorly this plate articulates with and underlies the mesial half of the upper plate of the orbitosphenoid. The plate of the lateral ethmoid curves anteriorly and then laterally into a vertical plate and thence to a thin sheet of bone lying approximately perpendicular to the major axis of the head. Part of this sheet is the prefrontal. This sheet effectively separates the orbital and nasal cavities. The mesial portions of the sheet articulate anteriorly with the ethmoid and dorsally

with the frontal and supraethmoid. The more lateral portions articulate postero-dorsally with the supraorbital and frontal. The border of the anterior fontanelle is formed by this sheet of the lateral ethmoid. Antero-ventrally the sheet expands into a large ventral base which articulates with the prevomer, the ethmoid and the endopterygoid. The parasphenoid is associated with the ventral surface of this structure and a postero-dorsal projection of the autopalatine fits into a notch on its anterior surface. The anterior myodome, a slight central depression for the origin of the oblique eye muscles, is located on the posterior surface of the lateral ethmoid. The olfactory foramen is bounded by the lateral ethmoid and the ethmoid. The lateral ethmoids are not extensively perforated. An orbito-nasal foramen passes dorsolaterally from the orbit to the nasal cavity opening lateral to the olfactory foramen.

Preethmoids (Figures 24, 26 and 27).

The preethmoids are paired, oval, endochondral bones fused with spoon shaped receptacles on the dorsal surface of the anterior process of the prevomer. The fused preethmoids and the prevomer are covered dorsally, laterally and anteriorly by cartilage which is continuous with that of the planum ethmoidale. A lateral preethmoid as distinct from a mesial preethmoid is rarely found (Buhan, 1970). It is not fused to the mesial preethmoid. The preethmoids are minutely perforated.

Kinethmoid

The kinethmoid is a median dermal bone lying anterior to the ethmoid and posterior to the upper jaw. It is comma-shaped in lateral view with the thickest part ventral and facing anteriorly. It connects the upper jaw to the skull via ligamentous attachments from its dorsal end to the ethmoid and from its ventral end to the premaxillaries. The dorsal end of the kinethmoid is forked and lateral ridges are apparent particularly at the ventral end. The bone is perforated. Nasals (Figures 23 and 24).

The nasals are paired dermal bones which are the most anterior portions of the supraorbital sensory canals. They are tubular and may have small ventral plates particularly at the anterior end. They lie in the skin lateral to the posterior wings of the supraethmoid, dorsal to the nares and partly covering the frontals. They usually have three pores.

Prefrontals

The prefrontals are paired dermal bones fused at right angles to the lateral ethmoids. They lie anterior to the supraorbitals and form the boundaries of the orbits lying immediately anterior to the sclerotic bones.

Prevomer (Figures 24, 25 and 26).

The prevomer is a thin median dermal bone lying ventral to the olfactory region. It is triangular in shape and longer than wide. The antero-lateral corners project and

form cup-shaped depressions. The preethmoids lie in these depressions and are fused to the prevomer. A notch between the depressions follows that of the ethmoid and its median lip curls posteriorly. Well developed lateral wings articulate with the lateral ethmoids. The pointed posterior end underlies the anterior end of the parasphenoid. Dorsally the prevomer articulates with the ethmoid and posteriorly bears a ridge which fits into a depression on the ventral surface of the ethmoid.

ORBITAL REGION

Lachrymals (Figures 23 and 30).

The lachrymals are paired dermal bones lying lateral to the maxillae. They are the first bones of the suborbital series. The shape of each lachrymal is variable but often approaches a hexagon. Posteriorly along the shortest side of the bone it is connected to the jugal or second suborbital by ligaments. The ventral side follows the line of the maxilla to which it has ligamentous connections. A short, free, postero-ventral side connects the ventral and jugal sides. The posterior edge is connected by a ligament to the lateral ethmoid with which it is closely associated. Dorsally the lachrymal borders the naris. Anteriorly it overlies the maxilla and is associated with a process of the autopalatine. A decurved sensory canal passes from the jugal across the lachrymal to terminate near the anterior edge of the latter. There are usually four or five pores

in this canal. The lachrymal itself is perforated.

Second to sixth suborbitals (Figures 23 and 30).

The suborbitals are paired dermal bones following the ventral and posterior margins of the orbit. They provide a support for the suborbital sensory canal. The canal is covered with bone and the suborbitals form thin sheets on either side of the canal bones. The ventral sheet is the larger of the two. The second suborbital may also be termed the jugal and the sixth suborbital the dermosphenotic. The second suborbital articulates anteriorly with the lachrymal and posteriorly with the third suborbital. The sensory canal usually has three or four pores. The third suborbital is the longest of the series and curves around the postero-ventral margin of the orbit. There are usually five pores in its sensory canal. The fourth and fifth suborbitals may be fused and the line of fusion is not apparent. Four or five pores are carried by its sensory canal. The dermosphenotic articulates ventrally with fused suborbitals four and five while dorsally it curves caudally. The sensory canal, with two pores, continues onto the supratemporal-intertemporal. The dermosphenotic is the smallest of the suborbital bones and narrows dorsally to the width of the sensory canal bone. It is not fused to the supratemporal-intertemporal and may not be ossified in young specimens.

Supraorbitals (Figures 23, 24, 25 and 26).

The supraorbitals are paired dermal bones lying above

the orbit, lateral to the frontal and partially overlying it. The lateral edge is straight and the mesial edge is curved to follow the edge of the frontal. Anteriorly each supra-orbital articulates with the lateral ethmoid. It may be singly perforated.

Scleral bones (Figure 23).

The scleral bones are two paired dermal ossifications lying within the anterior and posterior sclera of the eye. The lateral edge of each bone is truncated and the bones are concave on their orbital sides.

Orbitosphenoid (Figures 25 and 26).

The orbitosphenoid is a median endochondral bone forming part of the floor and side walls of the braincase. Laterally it forms a major part of the mesial border of the orbit. It is hexagonal in shape with two concave mesial faces descending to a thin, central, interorbital septum. The large septum articulates with a small raised ridge on the parasphenoid. Anteriorly the orbitosphenoid sutures broadly, and with some overlap, to the lateral ethmoids. Posteriorly it sutures with the pterosphenoid. Dorsally it joins both frontals. A notch in the centre of the postero-ventral edge forms part of the margin of the optic foramina. The optic foramina are posteriorly confluent with the hypophyseal foramen. The bone is not extensively perforated and the septum does not continue anteriorly between the lateral ethmoids and the parasphenoid. The lateral wall of the orbitosphenoid is not strongly ridged.

Pterosphenoids (Figures 25 and 26).

The pterosphenoids are paired endochondral bones with an irregular hexagonal shape. Anteriorly they are sutured with the orbitosphenoid and do not meet in the mid-line. Ventrally it borders the optic foramen while dorsally it is sutured to and overlain by the frontals. The pterosphenoids are connected by a cartilaginous epiphysial bar which runs over the brain and separates the anterior and posterior chondrocranial fontanelles. Posteriorly each pterosphenoid articulates with the prootic ventrally and the autosphenotic dorsally. The former articulation contains the foramen for the trigeminal nerve. There is a postero-ventrally directed spike over the trigeminal foramen. The internal structure of the pterosphenoid is characterised by arching tubules (Buhan, 1970) similar to those of the preopercula. They are best developed along the anterior and dorsal margins. The lateral walls are weakly ridged.

Frontals (Figures 23, 24, 25 and 26).

The frontals are paired, dermal bones roofing the major part of the skull. Their mutual suture forms a wavy line down the middle of the skull. Their greatest width is formed by lateral wings lying free over the orbits where length in width is 1 in 2. A zig-zag anterior margin overlaps the supraethmoids. The laterally expanded anterior edge overlaps a major part of the lateral ethmoids before turning posteriorly to form a notch in which the supraorbital lies.

Each frontal sutures posteriorly with the parietal and laterally with the autosphenotic and the supratemporal-intertemporal. The parietal suture involves mutual overlap, the degree of which is variable. Two parallel ridges on each ventrolateral side provide articulations for the dorsal edges of the orbitosphenoid and the pterosphenoid. The epiphysial bar lies between parallel ridges also. Each frontal bears the major extent of the supraorbital sensory canal lying over the line of articulation with the orbitosphenoid and pterosphenoid. There may be six or seven pores along the canal. The canal passes onto the parietal. Several small foramina penetrate the frontals particularly postero-dorsally. A small lateral expansion or shelf is found posterior to the lateral wings lying over the eye and bounding a lateral temporal fossa on the autosphenotic.

OTIC REGION

The otic region is composed of a complex of dermal and endochondral bones. It lies posterior to the optic region and encloses the inner ears and the posterior part of the brain. It also provides a base for suspension of the elements of the lower jaw, hyoid and branchial regions.

Supraoccipital (Figures 23 and 26).

The supraoccipital is composed of both dermal and endochondral bone. It is a median bone lying at the posterior end of the cranium. It consists of an endochondral plate

and a dermal, vertical supraoccipital crest fused to the mid-line. The anterior edge is complexly sutured to the parietals which partly overlap and are, themselves partly overlapped by the supraoccipital. Two processes diverge antero-laterally from the supraoccipital under the parietals. The lateral edges articulate with the epiotics and, below a ventral flexure, with the exoccipitals. The supraoccipital crest projects posteriorly over the hind end of the cranium. The posterior edge is serrated and the dorsal edge is laterally expanded to form wings. The overall shape is triangular.

Parietals (Figures 23 and 24).

The parietals are paired dermal bones of the posterior cranium roof. Each parietal is an irregular, quadrilateral plate of bone completely suturing with its neighbour in the mid-line. The right parietal markedly overlaps the left parietal anteriorly. The degree of overlap decreases caudal and in the posterior quarter of the suture this overlap is reversed. There is considerable individual variation in suture details and complexity. Anteriorly each parietal is sutured with a frontal. The degree and extent of overlap of either bone by the other is variable. Posteriorly the parietals overlies the supraoccipital and epiotic bones and laterally the autopterotic. The dorsal surface of the posterior end of each parietal is fused to the supratemporal sensory canal. The posterior ends of the

supraorbital sensory canal bones extend onto, and are fused with, the parietals. Each canal has two pores on the parietal. The parietals have many small foramina.

Medial extrascapulars (Figures 23, 24 and 26).

The medial extrascapulars are paired, dermal bones which form the supratemporal sensory canal. They may be continuous across the parietal-parietal suture or interrupted at this point. They are fused to the dorso-posterior end of the parietals and continue laterally in front of the dorsal portion of the posttemporal to join the infra-orbital canal. On the ventral portion of the posttemporal they form the lateral extrascapular canal. After leaving the parietal the bone lies free in the skin. There are usually three pores in each medial extrascapular.

Autosphenotics (Figures 24, 25 and 26).

The autosphenotics are paired endochondral bones lying latero-ventral to the posterior end of the frontals. Each autosphenotic is composed of a basal plate and a laterally directed process. Dorsally the plate is overlain anteriorly by the frontal and posteriorly by the supratemporal-inter-temporal. The anterior edge is sutured to the frontal and the posterior to the autopterotic. Ventrally the autosphenotic forms a suture with the prootic. The lateral process also forms a suture with the posterior edge of the lateral wing of the frontal. Mesially it borders the orbit. Mesial to the process, the autosphenotic is sutured to the ptero-

sphenoid. The dorso-mesial edge of the autosphenotic lying under the frontal contributes to the anterior border of the posterior fontanelle. Posteriorly the dorso-mesial edge continues into the cartilaginous tectum synoticum under the supratemporal-intertemporal and parietal. The head of the hyomandibular articulates with two facets. The anterior facet is formed from the ventral edge of the autosphenotic and parts of the prootic and pterosphenoid. The posterior facet is the larger and is composed partly of the lateral edge of the autosphenotic and the dorsal edge of the prootic but the autopterotic provides the major contribution. The anterior semicircular canal passes posterior to the lateral process of the autosphenotic and a short section of the horizontal semicircular canal is also present in the autosphenotic. The plate and process of the autosphenotic are not extensively perforated.

Autopterotics (Figures 23 and 25).

The autopterotics are paired endochondral bones lying posterior to the autosphenotics. Each autopterotic is a strut arching over and forming the dorso-lateral borders of the sub-temporal fossa. The strut encloses the horizontal semicircular canal and mesially it borders the tectum synoticum. Dorsally the strut is fused to the supratemporal-intertemporal but a small post-temporal fossa runs between them and communicates with the sub-temporal fossa via a tubular foramen in the autopterotic. Anteriorly the strut expands to articulate with the autosphenotic and the prootic.

A portion of the antero-lateral corner provides part of the facet for the posterior head of the hyomandibular. Posteriorly the strut expands to articulate with the exoccipital and mesially with the prootic. Postero-laterally a spatulate process articulates with the posttemporal. The origin of this process is dubious, it may be part of the supratemporal or the autopterotic. The process is basally perforated. The opisthotic lies postero-mesad to the process.

Prootics (Figures 25 and 26).

The prootics are paired endochondral bones, approximately square in shape, lying in the antero-ventral section of the otic region. The bulla acustica utricularis forms a swelling on the ventro-lateral surface of each prootic. It lies anterior to the sub-temporal fossa and encloses the lapillus. Anteriorly each prootic sutures with the pterosphonoid around the trigeminal foramen. The foramen for the facial nerve lies between that of the trigeminal nerve and the bulla acustica utricularis. Between these two foramina a small antero-ventral ridge articulates with the wing of the parasphenoid and forms the anterior edge of the foramen for the carotid artery. Further details of the nervous and arterial relations in this region are given by Mahy (1975a). Dorso-laterally the prootic articulates anteriorly with the autosphenotic and posteriorly with the autopterotic. The dorso-lateral edge contributes to both facets for the hyomandibular. Ventrally the prootics suture in the mid-line and this basal

portion forms the floor of the braincase. Anteriorly the ventral parts of the prootics form the posterior border of the optic foramen. Lateral to the mid-line suture, the prootic develops wings which curve mesially around the hypophyseal foramen. The wings do not meet in the ventral mid-line but are sealed over by the posterior part of the parasphenoid. The hypophyseal foramen is confluent with the optic foramen anteriorly. The posterior edge of the prootic articulates dorsally with the exoccipital and ventrally with the basioccipital. Several struts are apparent on the prootic at these articulations. Posterior to the bulge of the bulla acustica utricularis the prootic inflects and curves dorso-mesially to form the anterior, and part of the mesial, walls of the sub-temporal fossa. The dorso-posterior internal edge articulates with the tectum synoticum. The mesial surface of this part of the prootic forms the postero-lateral surface of the cranial cavity. In addition to the foramina mentioned there are small perforations of the prootic near its articulation with the parasphenoid.

Tecta synotica

Each tectum synoticum is a thin sheet of cartilage lying dorsal to the prootic and exoccipital bones between the autopterotic, autosphenotic, epiotic and supraoccipital bones. Posteriorly it roofs the sub-temporal fossa and anteriorly part of the cranial cavity. The anterior edge borders the posterior fontanelle and forms part of the anterior semicircular canal.

Epiotics (Figures 23, 24 and 26).

The epiotics are paired, endochondral bones situated at the postero-lateral corners of the cranium. They cover the sub-temporal fossa and anteriorly border the tecta synotica. Laterally each epiotic articulates with the autopterotic and postero-ventrally with the exoccipital. Mesially it articulates with the supraoccipital. Antero-mesially it is overlain by the parietal and antero-laterally it is complexly sutured with the supratemporal-intertemporal. The suture is overlain by the supratemporal canal bone but there is no fusion. A laterally directed epiotic process is connected to the posttemporal by ligaments. It is not well developed and its anterior edge follows the posterior edge of the parietal. The posterior semicircular canal crosses the postero-mesial corner of the epiotic.

Opisthotics (Figures 23, 24 and 25).

Opisthotics are paired endochondral bones lying between the exoccipitals and the spatulate processes of the autopterotics. Each opisthotic is a thin irregularly shaped bone. The antero-mesial section of the bone is thinnest and lies mesial to the autopterotic. A posterior spike is usually evident.

Exoccipitals (Figures 23, 24, 25 and 26).

The exoccipitals are paired endochondral bones of the posterior end of the cranium. Each exoccipital consists of

a plate of bone whose ventral and posterior edges are sutured to the basioccipital. The plate forms part of the wall of the bulla acustica lagenaris and also contributes to the sub-temporal fossa wall. Anteriorly this plate is sutured to the prootic and dorsally to the tectum synoticum. The posterior portion of the plate curves laterally as a thin sheet of bone with a centrally developed strut. The strut articulates anteriorly with the autopterotic and dorsally with the epiotic. It encloses part of the horizontal semicircular canal. Posterior to the strut a ring of bone encloses the lateral occipital foramen. The base of the ring lies above the bulla acustica lagenaris and its anterior portion lies in the lateral plate of the exoccipital. The ring curves dorso-mesially from the plate and then posteriorly paralleling the opposite ring before curving ventrally to the bulla. The dorsal part of the ring is a thin sheet of bone and is wider than other sections. The dorsal and posterior external edges of the ring are square cut. The ring sutures with the supraoccipital dorsally. Laterally the rings enclose the foramen magnum. Cartilage closes this foramen dorsally. Mesad to each bulla the exoccipitals send thin sheets of bone which suture in the mid-line forming the floor of the foramen magnum and the roof of the cavum sinus impar. The cranial cavity is thus separated from that containing the sacculus and lagena and the basioccipital is excluded from the foramen magnum. Anterior to the lateral plate in the ventral portion of the exoccipital there are two foramina. The most anterior one is for the glossopharyngeal

nerve and the posterior foramen is for the vagus. The vagal foramen is the larger of the two.

Supratemporal-intertemporal complexes (Figures 23, 24 and 26).

The supratemporal-intertemporal is a paired complex of fused dermal bones lying dorso-laterally in the otic region (Harrington, 1955). Mesially each complex is fused to the autopterotic. Anteriorly the complex overlies a portion of the autosphenotic and posteriorly it has an intricate interdigitating suture with the epiotic process. In some specimens, the autosphenotic intervenes between the frontal and the supratemporal-intertemporal on the dorso-lateral skull surface. The dorsal edge sutures with the parietal and the ventral edge fuses indistinguishably with the autopterotic. Ventro-laterally the infraorbital sensory canal runs along the lateral surface of the complex. There are usually 4 pores and the complex is minutely perforated. Bullae and semicircular canals (Figures 23, 25 and 26).

The bullae and semicircular canals of the inner ear are bounded by bones of the otic region.

The bulla acustica utricularis is a large ventro-lateral protrusion of each prootic. The lapillus is contained in the utriculus. The bulla acustica lagenaris is smaller than the bulla acustica utricularis and on each side of the cranium is a ventro-lateral protrusion of the basioccipital and exoccipital bones at their lateral suture. The sacculus and lagena lie within it containing the sagitta and asteriscus respectively.

There are three semicircular canals on each side of the head. Their courses can be traced in the otic region bones where they form rounded ridges. The anterior and posterior canals are orientated in the vertical plane and the horizontal canal in the horizontal plane. The anterior canal is visible in the prootic lateral to the bulla acustica utricularis and extends dorsolaterally through the autosphenotic, dorsally along the anterior edge of the tectum synoticum and supraoccipital and then curves ventromesad. The posterior canal lies in the exoccipital lateral to the lateral foramen and continues antero-mesially through the epiotic and supraoccipital. After approaching the anterior canal in the supraoccipital it curves meso-ventrally. The horizontal canal lies behind the anterior canal in the autosphenotic, passes through the lateral edge of the autoptero-tic bounding the subtemporal fossa and continues into the exoccipital.

Otoliths (Figure 28).

The otoliths are three paired structures of the inner ear. They appear as white structures seen through the red, alizarin-stained bones of the otic region. They are unstained because they are primarily calcium carbonate and lack the calcium phosphate for which alizarin is specific.

Asteriscus

Each asteriscus lies in the recessus sacculi with the sagitta. The asteriscus is orientated vertically and lies

lateral to the sacculus. It is disc-shaped with a crenelated edge. The lateral side is smooth and convex but the mesial side has a central depression bounded by a ridge. The depression opens anteriorly and the ridges end abruptly at the anterior edge.

Lapillus

Each lapillus lies in the recessus utriculi which is bounded by the bulla acustica utricularis. The lapillus is slightly smaller but thicker than the asteriscus and has a smoother margin. It lies approximately in the horizontal plane and is longer than broad. The anterior half of each lapillus is thickest and the anterior edge is rounded. Posteriorly it narrows to a thin plate and the posterior edge is sharply rounded. The antero-dorsal surface is grooved.

Sagitta

Each sagitta is a thin elongate structure lying mesial and mostly anterior to the asteriscus. Its anterior end projects over the postero-mesial surface of the prootic. The sagitta consists of a central strut with fragile expansions in the sagittal and horizontal planes. These wings are reduced posteriorly.

The post-temporals and supracleithra could be included in the otic region but are dealt with under the description of the pectoral girdle.

BASICRANIAL REGION

The basicranial region is composed of two bones, the parasphenoid which supports and connects the skull elements and the basioccipital which connects the skull to the vertebral column.

Basioccipital (Figures 23, 24, 25 and 26).

The basioccipital is a single median endochondral bone at the postero-ventral end of the cranium. It encloses the posterior myodome with the prootics. The anterior and dorsal edges are sutured with the prootic and exoccipital bones respectively. From these edges the basioccipital curves ventro-mesad. Two ventral ridges on either side of the mid-line interrupt the curving plates. Posteriorly the ridges merge with the masticatory process and anteriorly they decrease in size to merge with the anterior processes of the basioccipital underlying the parasphenoid. The two ridges form the anterior borders of the aortic canal which penetrates the masticatory process immediately below the proatlas. Posteriorly, above the masticatory process, the basioccipital terminates in a centrum shaped disc, the proatlas, with which the first vertebra articulates. Dorsal to the proatlas and extending anteriorly, the basioccipital forms the floor and side walls of the cavum sinus imparis and dorso-laterally is sutured to the exoccipital. The side walls and floor of

the recessus sacculi are also formed by the basioccipital. These are located on each side of the cavum sinus imparis with which they share a common wall. The lateral surfaces of the basioccipital form part of the walls of the bulla acustica lagenaris.

The masticatory process or basioccipital plate is a large, multi-perforated depression against which the pharyngeal teeth grind. It is posteriorly expanded into a median, perforated pharyngeal process for the origin of the pharyngeal arch retractors. The masticatory process surrounds the aortic canal. The posterior end of the process is rounded. Anteriorly a small process projects under the aortic canal in some specimens.

Parasphenoid (Figures 25 and 26).

The parasphenoid is a cross-shaped, median dermal bone located ventral to the cranium. The anterior arm is the longest and its ventrally concave anterior end lies above the prevomer between the lateral ethmoids. The concavity of the anterior arm is lost posteriorly approximately at the orbitosphenoid-pterosphenoid suture. A weakly developed ridge on the parasphenoid articulates with a mid-ventral ridge of the orbitosphenoid. The anterior arm slopes antero-dorsally to the olfactory region from the posterior end of the optic region. The lateral wings of the parasphenoid are located near the posterior end of the bone and are sutured laterally with the prootics forming part of the

border of the carotid foramen. The parasphenoid is angulate at this point and forms a slight keel. Between the wings on the dorsal surface a thin central process projects dorsad from a small central ridge. The ridge and process divide the posterior myodome into two channels which are laterally bounded by the upcurved edges of the parasphenoid's posterior arm and wings. The ridge is connected to the prootic. The posterior arm of the parasphenoid is a dorsally concave sheet underlying the basioccipital and prootics to form the floor of the posterior myodome. The posterior tip is forked. The pharyngobranchials are attached ventrally to the posterior arm of the parasphenoid. The parasphenoid is often difficult to separate from the prootics at the lateral wings indicating some degree of fusion.

OROMANDIBULAR REGION

Upper jaw

The upper jaw as in all Cyprinidae is toothless and is composed of two pairs of dermal bones, the premaxillaries and maxillaries.

Premaxillaries (Figure 29).

The premaxillaries alone border the gape and in this genus are protrusible. They are L-shaped bones paralleling the maxillaries along their major axis. The minor axis curves mesially to parallel the minor axis of the opposite,

side rising postero-dorsally. Mesially ligaments connect the minor axes of both sides and join them to the kinethmoid. The premaxillary articulates with the maxillary both anteriorly and posteriorly. The narrow posterior end of the major axis fits into a groove on the lower surface of the maxillary formed by a mesial maxillary plate. There is a ligamentous connection at this point. The anterior articulation is found at the junction of the two axes of the premaxillary. Lateral and mesial processes of the maxillary bone accommodate the premaxillary.

Maxillaries (Figure 29).

The maxillaries are large curved bones lying dorso-mesial to the premaxillaries. The anterior articulation with the premaxillaries on each side is by a groove formed by a lateral plate and a mesial process. The process is longer than the plate. The posterior articulation is in a groove formed by a mesial plate. The antero-dorsal end of each maxillary has a blunt head covered by the small submaxillary cartilage, which articulates with the preethmoid anteriorly and the autopalatine posteriorly. A large, rounded ascending process arises half-way down the main body of the maxilla and a strong occlusion pushes it against the lateral ethmoid. The posterior end of the maxilla is connected by ligaments to the premaxillary and to the ascending process of the dentary. A small lateral and ventral ridge is present to brace the lachrymal which is attached

by a ligament to a point one third of the length of the maxillary from the anterior end. The ridge is apparently an extension of the lateral plate and ends abruptly as a notch at the point of ligament attachment.

Lower jaw

The unossified Meckel's cartilages form the bases for the lower jaw around which dermal and endochondral bones are organised. Each cartilage is a cylindrical, mesial rod of cartilage. Ossifications of the anterior end form the articular, mentomeckelian and part of the retroarticular bones. The coronomeckelian is a postero-mesial ossification of Meckel's cartilage.

Mentomeckelians (Figure 29).

Each mentomeckelian is fused to the mesial surface of the dentary and is an anterior ossification of Meckel's cartilage. Its form is cylindrical, tapering anteriorly.

Coronomeckelians (Figure 29).

Each coronomeckelian is a complexly-shaped posterior ossification of Meckel's cartilage lying mesial to the angular. It consists of a vertical plate which ventrally forms a curled plate partially overlying Meckel's cartilage dorso-mesially. The vertical plate lies in a depression of the mesial angular surface antero-dorsad to the articular.

Dentaries (Figures 23 and 29).

The dentaries are paired dermal bones, the largest of

the lower jaw. They do not bear teeth. Anteriorly they join at a symphysis, curving mesiad from their laterally placed and parallel arms. The dorsal edge of the dentary slopes laterally, the ventral mesially. A notch is found on the ventro-mesial surface posterior to the symphysis. The dorsal edge is also notched anterior to the ascending process. A single foramen, for the truncus mandibularis of nerve VII, of variable position, perforates the thin dorsal half of the dentary between the symphysis and a posterior dorsal ascending process. The blunt ascending process is attached to the maxillary by a ligament. In this genus it curves posteriorly and its anterior edge slopes posteriorly. The central portion of the dentary is the thickest and its mesial surface is fused anteriorly to the mentomeckelian behind which there is a groove containing Meckel's cartilage. The ventral portion of the dentary is a plate tapering to a thin mesial edge from the central portion. It is connected by a ligament to the retroarticular and is loosely associated with the angular. Laterally the ossified preoperculomandibular canal is fused to the dentary and passes, usually with an ossification on the angular, to the preopercular bone. There may be four or five pores on the mandibular part of the canal.

Articulars

The articulars are paired posterior ossifications of Meckel's cartilage completely enclosed by the dermal

angular bone. Their form is tubular and they lie along the axis of Meckel's cartilage.

Retroarticulars (Figure 29).

Each retroarticular is placed ventrally at the posterior end of the angular caudad of the dentary. The central part of these bones is endochondral and part of Meckel's cartilage but this is covered by dermal bone. In lateral view the bone is oval in shape and it is closely associated with the angular.

Angulars (Figure 29).

The paired dermal angular bones encase the articulars and are the most posterior lower jaw bones. A posterior facet articulates with the knob of the quadrate. The ventral lip of the facet is produced posteriorly. A notch on the ventral surface accommodates the retroarticular. Anteriorly the angular is mesial to a posterior projection of the dentary and lateral to Meckel's cartilage. A thin rounded or pointed process rises dorsally behind the ascending process of the dentary. The process' height varies with specimen size and is highest and most pointed in large fish. The most anterior extension of the angular, a thin trough-like plate, almost reaches the mentomeckelian. The coronomeckelian fits into a depression on the mesial surface of the angular antero-dorsal to the articular. It is a tri-lobed structure with two posterior wings and a larger wing directed anteriorly. The two posterior wings

are of similar size and shape. The angular may bear part of the preoperculomandibular canal bone.

Autopalatines (Figure 29).

The autopalatines are paired, endochondral bones which aid in the articulation of the upper jaw and the olfactory region. They are the most anterior bones of the primary upper jaw. Each autopalatine is rod-like and the anterior end is expanded into three small, plate-like processes. Two of these processes are directed mesially forming a shallow cup around the lateral surface of the preethmoid. The third process articulates with a depression in the maxillary. Laterally this process is expanded into a triangular shaped head which abuts the lachrymal. The postero-dorsal surface of the autopalatine bears a blunt projection which fits into a depression of the ventro-lateral edge of the lateral ethmoid. The posterior end of the autopalatine articulates with the endopterygoid and, by means of cartilage, with the ectopterygoid and the quadrate. A small dorsal depression and process has a ligamentous connection with the endopterygoid. There is a cartilaginous cap over the hind end of the autopalatine with which this connecting cartilage is continuous. There are several perforations in the autopalatines.

Endopterygoids (Figure 29).

The endopterygoids are paired dermal bones forming a major portion of the floor of the orbit. They are laterally concave and their outline is sub-quadrilateral. Anteriorly

small lateral and mesial expansions form a cup-like articulation for the autopalatine. The dorsal corner is pointed and located dorsal to the posterior end of the autopalatine where it is attached by a ligament to the dorsal process. The posterior margin of the endopterygoid is laterally overlain by the anterior margin of the metapterygoid. This overlap extends onto the posterior one third of the ventral edge of the endopterygoid. Anteriorly the ventral edge is overlain laterally by the quadrate. The lower third of the anterior edge is covered laterally by the posterior edge of the ectopterygoid. There is a small gap, the quadrate-metapterygoid fenestra, where there is no overlap of the ventral edge of the endopterygoid. A small lateral ridge extends ventrally from the socket for the autopalatine. It curves posteriorly a short distance above the ventral edge terminating at the posterior margin of the endopterygoid. Ventral to this ridge the bone inclines mesially. The ridge provides an edge for articulation of the ectopterygoid, quadrate and metapterygoid. Mesially below the socket, there is a thin walled pocket which is variably perforated. The endopterygoid is perforated posterior to the socket for the autopalatine and irregularly over the major surface of the bone.

Ectopterygoids (Figure 29).

The ectopterygoids are paired dermal bones lying antero-lateral to the endopterygoid. Their outline is that of an

elongate oval with the most pointed end directed antero-dorsally. The ectopterygoid articulates posteriorly with the endopterygoid and the quadrate. It lies lateral to the endopterygoid but mesial to the quadrate. It may adhere closely to the quadrate or fit into a small depression. A single small perforation is found in the centre of the bone of some fish.

Quadrates (Figure 29).

The quadrates are paired endochondral bones consisting of a sub-quadrangular plate bearing a long posteriorly-directed process on its ventral surface. The posterior end of the process terminates bluntly where the dorsal ramus of the preopercular begins to ascend. The symplectic fits into a depression on the dorso-mesial surface of this process obscuring a posterior notch between the plate and the process. A mesial ridge along the middle of the process forms an articulation line for the preopercular which extends as far as the mid-line of the quadrate plate. The anterior end of the symplectic terminates slightly posterodorsally to the end of the preopercular. The dorsal edge and upper half of the anterior edge of the quadrate are lateral to the endopterygoid and ectopterygoid respectively. The process for articulation of the ectopterygoid has been referred to above and occurs approximately half way down the anterior edge of the quadrate. Below this point the quadrate is notched before it expands into a major saddle-

shaped process which articulates with the articular. The posterior edge of the plate is the anterior border of the quadrate-metapterygoid fenestra which is bounded ventrally by the symplectic. Several small foramina perforate the plate of the quadrate which is pitted irregularly. A foramen is found on the ventral surface of the anterior end of the process. The ectopterygoid may be fused closely with the quadrate and the articulation described may not be present. The quadrate is smaller than the endopterygoid and larger than the ectopterygoid.

Metapterygoids (Figure 29).

The metapterygoids are paired endochondral bones characterised by a concave anterior edge lying lateral to the posterior and part of the ventral edges of the endopterygoid. This anterior margin is irregular. The antero-ventral edge curves convexly to the symplectic and has the characteristic darkened appearance of an articulating edge. However part of the metapterygoid does not articulate with a similar opposing edge of the quadrate and a weak quadrate-metapterygoid fenestra is present. There may be some cartilage in this space. Ventrally the metapterygoid articulates with the symplectic and the manner of this articulation is dealt with later. Posteriorly the metapterygoid narrows to about one half its anterior depth. The dorsal corner bears a strut which extends diagonally towards the mid-point of the bone. The ventral corner bears a small articulation point. This

point may be supported by a small strut but if it is present it is very short and does not meet the dorsal strut. The dorsal strut articulates with the hyomandibular while the ventral articulation lies at the junction of the symplectic, hyomandibular and interhyal.

HYOID REGION

The hyoid region is composed of both dermal and endochondral bones. The dermal bones all belong to the opercular series, which support the gill covers. The endochondral bones contribute primarily to the methostylic jaw suspension. Opercula (Figures 23 and 30).

The opercula are sub-quadrilateral bones overlying the gills. The posterior edge of each operculum is free over the posttemporal and cleithrum, the ventral edge overlies and is attached by a membrane to the suboperculum. The dorsal edge is straight or scalloped. The antero-dorsal corner is elongated into an anterior process dorsal to the preoperculum and lateral to the head of the hyomandibular. The convex anterior edge is overlain by the preoperculum excepting the anterior process. Posterior to the process a portion of the preoperculomandibular canal runs dorsally. The operculum has its major articulation mesially with a posterior head of the hyomandibular. This articulation is supported by a very short diagonal mesial strut, which extends onto the anterior process, and by a longer thickening of the

anterior edge of the operculum. Below and slightly posterior to the socket of the hyomandibular articulation is a foramen which branches ventrally and dorsally. The ventral branch becomes a ventrally directed tube within the anterior thickened strut. There are several lateral openings of this tube which ends mid-way between the hyomandibular articulation and the ventral edge of the operculum. The dorsal branch passes under the articulation to open on the mesial face of the opercula and, via several tubular foramina, onto the lateral surface of the upper part of the operculum.

Preopercula (Figures 23 and 30).

The preopercula overlap the anterior edge of the opercula and, ventrally much of the interopercula to which they are connected by a Membrane. The preoperculomandibular canal of each side is fused to the lateral surface of each preoperculum. The bone is approximately right-angled with anterior and dorsal rami, the latter being the longer of the two. The dorsal ramus reaches to the level of the hyomandibular-opercular articulation. There is a membranous attachment to the hyomandibular along the posterior side of the lateral ridge. The anterior ramus lies ventral to the longitudinal shaft of the metapterygoid and lateral to the interoperculum. The sensory canal extends the whole length of the preoperculum and is fused to it throughout. There are about twelve pores but perforations are very irregular. Arching tubules are present within the bone anterior to the

sensory canal (Buhan, 1970). These are best developed in the angle of the bone.

Subopercula (Figures 23 and 30).

The subopercula are partially overlain by the ventral edge of the opercula and the posterior edge of the interopercula. There is no ridge marking the extent of overlap of the opercula. There are membranous connections with the opercula and interopercula of the same side. The dorsal edge of each suboperculum is concave, the ventral edge convex and from a square anterior face the bone tapers to a rounded posterior point. The antero-dorsal corner protrudes slightly as a rounded projection.

Interopercula (Figures 23 and 30).

The interopercula are lateral to the hypohyals, ceratohyals and epihyal. The anterior ramus of the preoperculum is lateral to much of the dorso-lateral surface of each interoperculum and the extent of this overlap is marked by a slight lateral ridge. The posterior end of the interoperculum is lateral to the suboperculum. Ligaments connect the anterior end of the interoperculum to the angular and the retroarticular. Anteriorly the interoperculum terminates in a point. The dorsal edge is convex and the ventral concave. The postero-ventral corner is rounded and curves up to a sharp, dorsal point. The dorsal arm is considerably shorter than the anterior arm. The interoperculum is longer than the suboperculum.

Branchiostegals (Figures 23 and 31).

The branchiostegals are three pairs of thin, arc-shaped bones covering the ventral branchial cavity. They are mesially concave and laterally convex. The anterior two branchiostegals articulate with the ceratohyal, the most posterior branchiostegal with the ceratohyal and the epihyal. The first branchiostegal is the most lateral. The third or anteriormost branchiostegal bears a slender, dorsally directed shaft which articulates with the ceratohyal. The first and second branchiostegals have a similar shape; the third is more slender. They become progressively longer posteriorly.

The following are all endochondral bones of the hyoid region: -

Hyomandibulars (Figures 23 and 31).

Each hyomandibular is a sub-triangular bone which narrows ventrally. There is a lateral, dorso-ventral strut. The articular head for the opercular is approximately one third of the way down the posterior edge of the hyomandibular. The hyomandibular branch of the facial nerve passes through a mesial foramen at the level of the opercular articulation. An elongated, oval exit for this nerve is found laterally. It is located near to the ventral end of the hyomandibular and the nerve passes through a canal running along the main strut. Two other lateral exits are found below and above the articular head. The ramus opercularis

superficialis leaves the hyomandibular via the foramen at the base of the opercular condyle and enters another foramen on the anterior edge of the operculum. Ventrally the hyomandibular articulates via a ligament with the symplectic and interhyal. Anteriorly it articulates with the two posterior heads of the metapterygoid. The dorsal end of the hyomandibular bears an anterior and posterior condyle separated by the downthrusting anterior semicircular canal. The anterior head is the smallest. These heads articulate with the otic region of the skull at the hyomandibular facet. The facet is composed of sections of the autosphenotic, prootic and autopterotic bones. The hyomandibular bears the origins of various muscles. The dilator operculi muscle has its origin on the upper third of the lateral face of the bone dorsal to a weak lateral ridge. The levator operculi originates in the posterior depression above the articulation with the operculum. Below this articulation is the mandibularis part of the adductor mandibulae origin. The levator arcus palatini occupies much of the lower anterior two thirds of the bone (Uyeno and Miller, 1965).

Symplectics (Figure 29).

The symplectics lie mesial to the posterior process of the quadrates. Their ventral edge is convex and each symplectic as a whole is gently arched. The anterior portion lies in a notch of the quadrate. The posterior end arti-

culates via a ligament with the hyomandibular and mesially with the interhyal. Its dorso-posterior edge may closely adhere to the metapterygoid. Immediately posterior to the quadrate-metapterygoid fenestra a small peg projects dorsally into a socket on the metapterygoid. The metapterygoid may have a peg posterior to that of the symplectic which fits into a socket on the dorsal edge of the symplectic but arrangement of pegs and sockets and even their presence is variable.

Interhyals (Figure 31).

The interhyals are small, ovoid bones found in close lateral proximity to the postero-dorsal notch of each epihyal. Ligaments connect each interhyal ventro-mesially to the hyomandibular and the symplectic.

Epihyals (Figure 31).

The epihyals are sub-triangular in outline with the base of the triangle anterior. The apex of each epihyal is postero-dorsal and bears a large notch near which lies the interhyal. Antero-mesially the epihyal articulates with the ceratohyal but only dorsally such that a postero-ventral notch is formed. The first branchiostegal lies lateral to the notch. A ligament connects the epihyal to the retro-articular.

Ceratohyals (Figure 31).

The ceratohyals are longer bones than the epihyals to

which they have a broad postero-lateral articulation. The middle section of each ceratohyal is narrow expanding antero-mesially into two heads which articulate with the upper and lower hypohyals and enclosing a large foramen. The branchiostegals articulate with the ceratohyal and epihyal as previously described.

Upper hypohyals (Figure 31).

The upper hypohyals are curved, tubular bones articulating laterally with the dorsal head of the ceratohyals and ventrally with the lower hypohyals. There is a ligament connecting each upper hypohyal to the posterior end of the basihyal and the anterior end of the first basibranchial. The upper hypohyals are noticeably perforated.

Lower hypohyals (Figure 31).

The lower hypohyals are also tubular bones but are larger than the upper hypohyals. The dorsal portion of each hypohyal articulates with the dorsal head of the upper hypohyal and the ventral portion with the ceratohyal. Ligamentous connections extend to the basihyal, urohyal and the lower hypohyal of the opposite side of the head. The lower hypohyals are perforated but not as extensively as the upper hypohyals.

Basihyal (Figure 32).

The basihyal is a thin, elongate unpaired bone supporting the tongue. Anteriorly it lies free in the oral cavity. Pos-

teriorly it narrows to where it lies dorsal to the hypohyals. Ligaments connect this bone to the dorso-mesial surfaces of the upper hypohyals and to the anterior end of the first basibranchial.

Urohyal (Figure 33).

The urohyal is an unpaired median bone lying at the base of the head below the basibranchials. It consists of a broad, flat plate with a dorsally directed median plate. The median plate extends dorso-posteriorly to the base plate and has small lateral wings at its tip. The urohyal may be perforated where the two plates converge. Anteriorly the bone narrows both laterally and dorsally before forming two heads separated by a deep vertical cleft. Ligaments from these heads connect the urohyals to the upper hypohyals. Posteriorly the sternohyoideus muscles are inserted but there is no marked expansion of the bone. There is a shallow cavity on the ventral surface of the urohyal.

BRANCHIAL REGION

The bones which constitute the branchial region support the gills, aortic arches and, as a modified fifth branchial arch, the pharyngeal teeth. The branchial arches also support the gill rakers, there being two rows on the first four arches and one on the fifth. Each raker is ossified only in its distal portions. In shape the gill raker is a slender process arising perpendicular to a small base.

Pharyngobranchials (Figure 32).

The pharyngobranchials are two pairs of thin, endochondral bones lying in the mid-line between the epibranchials at the roof of the branchial cavity. They suspended the gill arches from the cranium. The first pair lie ventral to the second and are smaller. Each pharyngobranchial is a half-moon shaped bone with the rounded edge placed laterally. The articulations of the pharyngobranchials with the epibranchials are described below.

The pharyngobranchials are loosely attached to the ventral surface of the parasphenoid posterior to the lateral wings. The second pharyngobranchial is posteriorly attached to a pharyngobranchial cartilage.

Epibranchials (Figure 32).

The epibranchials are four pairs of endochondral bones articulating mesially with the ceratobranchials. From this articulation they curve antero-mesially to overlies the ceratobranchials. The first epibranchial is articulated with the first pharyngobranchial, the second with pharyngobranchials one and two and the third with pharyngobranchial two. The fourth epibranchial has a cartilaginous connection with the second pharyngobranchial. The second and third epibranchials are curved plates of bone forming a dorso-lateral trough. The curvature of the first epibranchial is such that a ventro-mesial trough is formed. The fourth epibranchial is a thinner strut of bone without curved plates forming

a trough. The epibranchials are similar to the ceratobranchials near their articulation but are mesially modified. Near the mesial end of the first and second epibranchials the posterior edge abruptly inflects to continue mesially as a narrow process for articulation with the pharyngobranchial. The process of the second epibranchial is distally expanded into a plate. The third epibranchial is similar to the second but the posterior corner of the inflection is better developed as a small process. The fourth epibranchial is mesially similar to the third but has a well developed anterior inflection process. The lateral portions of the bone do not form a rectangular plate but a thin strut bearing a perforated posterior plate. The plate merges with the expanded end articulating with the ceratobranchial. Cartilaginous fifth epibranchials are present in Notemigonus crysoleucas, posterior to the fourth epibranchial.

Ceratobranchials (Figure 32).

The ceratobranchials are four pairs of endochondral bones, the largest bones of the branchial region. Their shape is that of an elongate rectangle, with a concave ventral surface. Laterally they articulate with the epibranchials and mesially the first three pairs articulate with the hypobranchials while the last articulates with a median basi-branchial cartilage. The ceratobranchials are perforated. The fifth ceratobranchials are modified and bear the pharyngeal teeth.

Pharyngeal arch and teeth (Figure 33).

The fifth pharyngeal arch is derived from a modified pair of ceratobranchials (Chu, 1935). They are larger than the preceding ceratobranchials and mesially they bear teeth. The teeth have a distinct origin from ectoderm and mesoderm in contrast to the purely mesodermal arch (Chu, 1935). Each arch consists of two rami, one directed anteriorly, the other curving mesially to the dorsally placed basioccipital process. The anterior arms come to lie close together at their tips and are connected by ligaments to the basibranchial cartilage. Each arm is mesially notched near the tip and the posterior end of the basibranchial cartilage terminates in the articulation thus formed. The junction of the two arms is developed as a ventro-lateral keel. The keel is perforated by large foramina which pass through onto the mesial surface of the base of the teeth. The number of foramina varies and may differ on the right and left arches. There is a single row of five teeth on each arch in Notemigonus crysoleucas. The tips of the teeth are hooked caudo-dorsally and the caudo-dorsal edge is serrated.

Hypobranchials (Figure 32).

The hypobranchials are paired endochondral bones lying lateral to the posterior ends of the basibranchials. They articulate with the first three ceratobranchials. The first two pairs of hypobranchials are small irregular masses of bone but the third has a distinct comma shape. The base of

the comma is situated lateral to the third basibranchial and the thin tail curls cranioventrally. The distal portion of the tail inflects caudad. From the inflection a ligament connects the third hypobranchial with the second hypobranchial and the second basibranchial. The second hypobranchial may bear a small ventral process to which the ligament attaches. Each member of the third hypobranchial pair is connected distally with its neighbour by a ligament. Basibranchials (Figure 32).

The basibranchials are median, endochondral bones having the form of short cylinders. They lie on the floor of the pharynx. There are three basibranchials, the most anterior one articulating with the posterior end of the basihyal. Basibranchials two and three articulate in line posterior to basibranchial one. The articulation between the first and second basibranchials is formed by expanded heads. The first basibranchial is the smallest and it bears a ventral process. Its posterior face is roughly triangular in outline and the postero-lateral edges are more massive than the antero-lateral edges. Each basibranchial may be laterally perforated. Cartilage extends posteriorly from the last basibranchial to the ventromesial end of the fifth ceratobranchial.

Other cranial structures

Various cranial structures have been mentioned in passing above. These are discussed in more detail here but

reference should also be made to previous mentions.

Fontanelles

The anterior fontanelle is the anterior cranial cavity bounded by the lateral ethmoids, orbitosphenoids and part of the pterosphenoids. Dorsally these bones are unossified and are continuous with the epiphyseal bar which forms the anterior limit of the posterior fontanelle. The bar is slender and arched posteriorly. The posterior fontanelle is bounded by the pterosphenoids, autosphenotics, tecta synotica and the supraoccipital.

Fossae

A small lateral temporal fossa is located behind the orbit under the posteriormost orbital series bones. The subtemporal fossa is a large depression on the ventrolateral surface of the otic region. It is bounded by the autopterotic, epiotic, exoccipital, prootic and tectum synoticum. This fossa serves for the origin of the branchial muscles. The post-temporal fossa is small and located posterodorsally at the rear of the skull. Dorsally the fossa is covered by the posttemporal, epiotic process, and the supratemporal-intertemporal. The epiotic and autopterotic bones form the floor.

Myodomes

The anterior myodome on each side is found mesoposteriorly on the lateral ethmoids and serves for the origin

of eye muscles. The posterior myodome is a larger structure under the parasphenoid and extending back into the basioccipital. The prootics and basioccipital roof this median myodome and ventrally it is bordered by the parasphenoid and basioccipital. It also serves for the origin of eye muscles.

VERTEBRAL COLUMN

The vertebral column may be divided into several regions. These are the Weberian, abdominal, transitional and caudal regions as defined below. All the centra are amphicoelus. Weberian region (Figure 34).

The first four abdominal vertebrae are modified for transmission of sound from the gas bladder to the inner ear. This modification involves shortening of the vertebrae and the derivation of Weberian ossicles from the vertebrae. The four paired ossicles described below are the claustrum, scaphium, intercalarium and tripus. The Weberian apparatus is the major characteristic of the order Cypriniformes.

First vertebra or atlas

The atlas is basically a shortened cylinder of bone, the centrum, which is biconcave. Anteriorly it articulates with the proatlas region of the basioccipital and posteriorly with the second vertebral centrum. The posterior edge curves gently ventro-cranial making the ventral half of the centrum narrower than the dorsal half. A slight ventral lip projects

posteriorly. Laterally the centrum bears a short process directed ventro-laterally. Above the process a depression opening caudo-dorsally receives the head of the scaphium. Ventrally the centrum bears a depression larger than the lateral one. Dorsally the centrum is rounded.

Second vertebra

The second vertebra is longitudinally shorter than the first. Its anterior edge articulates with the atlas and is appropriately curved to fit. The posterior articulation with the third vertebra is vertical or sloping anteriorly and a little ventrally. The antero-lateral surface bears a long process which arises from a broad dorso-ventral base and curves dorso-caudad. Near its base the lateral process curves over part of the posterior end of atlas. The posterior dorso-lateral corner of the centrum bears a depression into which the ventral head of the intercalarium articulates. At the base of each lateral process there is a large depression and between the processes on the ventral surface a smaller depression. Two small cavities may also be found postero-laterally to the ventral depression. The base of the process is perforated.

The neural spine overlies the atrium sinus impar. It is a thin sheet of bone in the horizontal plane with laterally curving edges. The anterior edge has a median notch into which the posterior end of the exoccipital articulates and is connected by ligaments. The anterior edge is

level with the anterior edge of the atlas. The posterior edge articulates with the neural complex or spines of the third vertebra. The claustra articulate with the antero-ventral edges of the second neural spine. The dorsal process of each scaphium lies between the articulation of the second neural spine and the third neural arch.

Third vertebra

The third centrum is larger than the preceding two. It articulates anteriorly with the second vertebra and posteriorly with the fourth. The anterior and posterior articulations are approximately vertical. Laterally a deep groove runs diagonally to the postero-ventral corner. This groove forms a receptacle for the tripus. The ventral surface is composed of a ridge with several perforations on each side of the mid-line. The number and shape of these perforations varies but there is usually a major posterior oval foramen. There is no lateral process. The lateral surface anterior to the diagonal depression may be perforated. The base of the neural arch is fused to the dorsal and upper lateral edges of the centrum and is saddle-shaped. A suture line is clearly visible. The lateral edges of the arch arise some distance behind the anterior edge of the saddle and continue to the posterior edge. They consist of thin sheets of bone which project to a blunt point in the middle of their anterior edge. A process, sometimes with a forked tip, projects caudo-ventrally below the lateral edge of the arch bone.

The process may be absent. The tip has ligamentous connections to an anterior process of the pleural rib of the fourth vertebra. The posterior border of the arch is notched. Above the notch the arch articulates with the arch of the fourth vertebra. Dorsally the arch is fused to or closely associated with the neural complex or spine. Cranio-ventrally the dorsal process of the intercalarium rests on the lateral edge of the neural arch. Cranio-dorsally the dorsal process of the scaphium lies between the arch and the neural spine of the second vertebra. The second neural spine articulates with the third neural arch caudo-ventrally. The sides of the arch are perforated. The neural complex or spine of the third vertebra is ventrally sutured to the neural arch. The anterior edge lies free except for a ventral section articulating with the neural spine of the second vertebra. The postero-ventral edge articulates with the spine of the fourth vertebra. The spine has a complex shape. From the wide, saddle-shaped base the spine anteriorly and dorsally divides into lateral sheets which meet broadly at the anterior edge of the spine. Dorsally these sheets are not closed over and a hollow results. The margins and general shape of this hollow are variable in form. The anterior rounded edge of the spine slopes anteriorly and overhangs the first and second vertebrae, terminating in a point. Below this point and the rounded edge of the joined lateral sheets, two

other thin sheets may enclose a depression similar to that on the dorsal edge. They are bounded ventrally by the articulation with the neural spine of the second vertebra. This structure is not strongly developed in some specimens. The neural complex is variably perforated.

Fourth vertebra

The centrum of the fourth vertebra articulates anteriorly with the centrum of the third vertebra and posteriorly with the centrum of the first abdominal or fifth vertebra. It is shorter than the third vertebra and the ventral portion is slightly wider than the dorsal. Latero-ventrally and latero-dorsally the body of the centrum is obscured by the articulation depressions for the parapophyses and the neural arch respectively. Ventrally the parapophyses almost completely obscure the centrum. Arising from a solid base the parapophysis of each side forks into a stout, lateral, pleural rib curving gently craniad and a mesial os suspensorium. The junction of these two bones has a horizontal mesially projecting plate of bone which is ligamentously connected to that of the other side. This plate is much perforated with minute holes. A ridge is developed on the anterior edge of the parapophysis. Laterally it merges with the rib, mesially it continues as a process overlying the third vertebra and connected by ligaments to the neural arch of that vertebra. The os suspensorium lies against the gas-bladder. Ventrally each os suspensorium is closely associated with its neighbour but dorsally they enclose a

foramen. A large foramen lies between the bases of the parapophyses and is bounded ventrally by the os suspensorium. The parapophysis is perforated in the base before the fork.

The neural arch and spine is less complex than that of the preceeding vertebrae. It articulates anteriorly with the ventral portions of the neural spine of the third vertebra along the posterior edge of the latter. It also articulates narrowly with the neural arch of the third vertebra. Ventral to the anterior projection which effects this articulation is a large foramen, bounded by the neural arches and centra of vertebrae three and four. The neural spine of the fourth vertebra extends dorsally from the anterior edge of the arch. It may rise to a level higher than that of the preceding spine. It consists of a strut of bone with a small, median, posterior plate. Posterior to the base of the spine the neural arch is open dorsally. Its dorso-posterior edge bears one or two small projections (neural postzygapophyses). The posterior edge of the arch falls vertically to the base. This edge is interrupted by a small gap which anteriorly expands into a foramen in the lateral wall of the arch. The gap may be closed. The base of the arch also has a large foramen.

Weberian ossicles (Figures 34 and 35).

The Weberian ossicles are a series of paired bones connecting the inner ear to the gas-bladder. They are derived from elements of the Weberian vertebrae and are termed the claustrum, scaphium, intercalarium and tripus from anterior

to posterior. The claustrum is derived from the neural spine of the first vertebra and the scaphium is derived from the neural arch. The intercalarium has its origin from the second neural arch and the tripus is derived from the third parapophysis.

Claustra

Each claustrum lies dorsal to the first centrum and contributes to the wall of the atrium sinus impar. The claustrum consists of two parts, a dorso-posterior median plate and an antero-ventral cup. The dorso-posterior edge of the plate articulates with the second neural spine while the cup articulates mesially with the dorsal and posterior edges of the cup of the scaphium. Antero-dorsally the plate terminates in a point and postero-ventrally in a blunt process. The dorsal and posterior walls of the cup form a ridge.

Scaphia

Each scaphium lies lateral and partially ventral to the claustrum and dorso-lateral to the first centrum. It is composed of an anterior cup and a dorso-posteriorly directed spine. A slight mesial depression in the lateral surface of the cup divides the cup into dorso-posterior and antero-ventral halves. The cups of the scaphia form part of the walls of the atrium sinus impar. The spine lies between the first neural spine and the second neural arch. A blunt projection is directed postero-ventrally from the base of the two cups. An interossicular ligament connects the projection with the intercalarium.

Intercalaria

The intercalarium lies between the scaphium and the tripus to which it is connected by interossicular ligaments. The scaphium and tripus are connected to the lateral ramus of the intercalarium, the largest of three rami which comprise this bone. The lateral ramus may be forked at the tip. The point of attachment for the ligament from the tripus is expanded. A short ventral arm of the intercalarium terminates in an articulating head which fits into a socket on the lateral edge of the second centrum. The dorsal arm is smaller and ends in a point articulating with the ventral edge of the neural arch of the third vertebra. The overall shape of the intercalarium varies from a "Y" to almost a triangle.

Tripes

The tripes are the largest Weberian ossicles. Anteriorly each tripus is attached by a ligament to the intercalarium. Posteriorly it is connected to the gas-bladder by the transformator process. Each tripus lies lateral to the Weberian vertebrae. The bone is composed of a triangular plate, which is mesially concave. The anterior corner terminates broadly and the posterior corner terminates in a thin elongate transformator process. The process lies between the fourth pleural rib and the os suspensorium, curving mesially to the swim-bladder. Dorsally the body of the tripus is twisted so that the dorsal edge lies in the transverse plane. The

edge slopes laterally downwards and dorsally articulates with a small plate of the parapophysis of the fourth vertebra. Anterior to this articulation the tripus follows the curvature of the third centrum so that dorsally it is laterally concave. The junction of the complexly folded dorsal portion and the simple ventral plate is composed of several struts.

Abdominal region (Figures 36 and 37).

The abdominal vertebrae are generalised vertebrae lying between the Weberian and transitional vertebrae. They bear pleural ribs and lack haemal spines.

Centra

The centra are longer and more regular than those of the Weberian region. Each centrum bears a neural arch with paired neural prezygapophyses and a neural spine on its antero-dorsal surface. Posterior to this complex there are a pair of neural postzygapophyses. The antero-lateral surfaces bear paired parapophyses with which the pleural ribs articulate.

Neural arches and spines

The neural arch of each vertebra is located on the antero-dorsal surface of the centrum and slopes dorso-posteriorly. Anteriorly the arch walls are expanded into small cranio-dorsally directed prezygapophyses. Posteriorly the walls form the caudo-dorsally directed neural spine.

The spine is thus formed from fusion of the lateral walls of the arch. The anterior and posterior edges of the spine are grooved near the arch but distally they disappear and the rounded spine terminates in a blunt or pointed tip. The epineural bones are laterally connected by ligaments to the neural spines. The interneural bones lie between the tips of those neural spines anterior to the dorsal fin.

Neural prezygapophyses and postzygapophyses

The prezygapophyses and postzygapophyses are small paired processes arising from the cranio-dorsal and caudo-dorsal corners of the base of the neural arch and the centrum respectively. Each prezygapophysis closely articulates with the postzygapophysis of the preceding vertebra.

Spinal foramina

The paired spinal foramina are located posterior to the neural arch in a thin plate of bone arising from the centrum. The foramina of anterior centra are unroofed dorsally and only the most posterior vertebrae have true enclosed foramina. The foramen provides an exit for the ventral root of the spinal nerve and the intersegmental artery.

Parapophyses and pleural ribs

Each lateral surface of a centrum bears a firmly fused parapophysis. Parapophyses are found in all abdominal vertebrae but become smaller towards the transitional vertebrae. A pleural rib articulates with each parapophysis and curves

postero-ventrally. They are widest near their base in the transverse plane and narrow to sharp or blunt points distally. The distal end of the anterior ribs curves mesially almost meeting its opposing neighbour. Posteriorly the ribs become shorter and less massive at the base. The last ribs are only partially ossified and are associated with the haemal arches of the transitional vertebrae.

Haemal postzygapophyses

Haemal postzygapophyses are small caudo-ventral spines of the centra. They only become apparent on the last abdominal vertebrae and the transitional vertebrae.

Number of abdominal vertebrae

A distinction is drawn between abdominal and caudal vertebrae after Jenkins and Lachner (1971). If a haemal spine is distinctly longer (by about 25% or more) than an adjacent anterior haemal element, the vertebra on which such a spine occurs is counted as the first caudal vertebra. Haemal spines bearing weak ribs are arbitrarily counted as abdominal vertebrae. The number of abdominal vertebrae varies from 20-21, this count including the four Weberian vertebrae.

Transitional region (Figure 37).

Transitional vertebrae are located between the abdominal and caudal vertebrae. They vary in number but there are usually two or three in N. crysoleucas. They lack fully developed pleural ribs and haemal spines thus distinguishing

themselves from abdominal and caudal vertebrae respectively.

The transitional centra are basically similar to those of the abdominal vertebrae but the lack of parapophyses reveals a horizontal lateral bar. Traces of this bar may be seen in the last few abdominal centra which have reduced parapophyses. A neural arch, prezygapophyses, postzygapophyses and a neural spine are present as in abdominal vertebrae. The spinal foramina are open or closed. The cranio-ventral corners bear the caudo-ventrally directed sides of the haemal arch. The arch is open and there is a connecting bar in the posteriormost vertebra. There is no haemal spine. Haemal postzygapophyses are present on the caudo-ventral corners of the centra.

Caudal region (Figures 37 and 38).

The caudal vertebrae are found posterior to the transitional region and are uniquely characterised by closed haemal arches bearing spines. The modified posterior caudal vertebrae supporting the caudal fin are described in the section dealing with caudal fin bones.

The centra are similar to those of the transitional vertebrae except those supporting the tail fin which are shortened. The horizontal lateral bar referred to above is well developed. Dorsally a neural arch, spine, prezygapophyses and postzygapophyses are present similar to those of the abdominal vertebrae. The spines often terminate more sharply than those in abdominal vertebrae. The spines become shorter posteriorly and their angle of inclination

to the vertebral column decreases. The spinal foramina are usually enclosed but an occasional foramen may be dorsally open.

Haemal arches and spines

Haemal arches are located cranio-ventrally on the centra. Their anterior corners bear paired prezygapophyses. The arch walls of each side merge to form a median spine directed caudo-ventrally. The spine may terminate in a point or bluntly and it is grooved on its anterior and posterior faces. The spines lie at an angle to the vertebral column in the same manner as the neural spines.

Haemal prezygapophyses and postzygapophyses

The prezygapophyses and postzygapophyses are small, paired, ventral processes of the haemal arches and the centra respectively. The prezygapophyses are absent from the anterior 3-5 caudal vertebrae. The postzygapophyses are best developed in the mid-caudal vertebrae and are absent from 0-3 of the last vertebrae.

Haemal foramina

Haemal foramina are located between the haemal arches and the postzygapophyses, similar to spinal foramina. They carry blood vessels from the caudal artery and vein. Only the most posterior ones are closed.

Numbers of caudal vertebrae

The number of caudal vertebrae (including the fused ural

and first preural centra as one vertebra) varies from 17-19.

Caudal vertebrae modifications

The second, third and fourth preural caudal vertebrae may bear modified neural and haemal spines and arches. The fourth preural neural and haemal spines are longer than those of more anterior vertebrae.

Neural arches and spines

Median plates are frequent on the neural spines where the neural arches fuse into the spine. On the fourth preural vertebra the plate is usually small and posterior. It may be absent. On the second and third preural vertebrae these plates tend to be best developed anteriorly and to be larger than the plate of the fourth preural vertebra. Their shape is variable. The third preural centrum of one specimen bore two neural arches and spines. The distal end of the neural spine may be split into anterior and posterior halves. The "plain" or non-splitting condition of Buhan (1970) predominates however.

Haemal arches and spines

The second and third preural haemal spines are more flattened than anterior spines and caudal fin rays articulate with their distal ends. Median processes are variably developed on the anterior and posterior faces of the spines. The processes tend to be longer and less pro-

nounced than those of the neural spines. Haemal prezygapophyses and postzygapophyses are variable in this region. Both may be absent or individually well developed.

Total numbers of vertebrae

A range in total vertebral number, including the four Weberian vertebrae and the fused ural and first preural centra as one vertebra, of 36-39 is recorded for this study, confirming literature reports.

Interneural bones

The interneurals are a series of median bones lying between the neural spines anterior to the dorsal fin. There are usually nine or ten irregular shaped interneurals extending from the Weberian vertebrae to the dorsal fin and following the curvature of the body. The first interneural lying above the Weberian vertebrae is the largest of the series and may be derived by fusion of several interneurals. Its shape is variable and irregular but it is longer than deep and may approach a rectangle in shape. In some specimens it is perforated. Its anterior end may occupy the dorsal hollow of the neural complex of the third vertebra. The remaining interneurals are deeper than they are broad and are regularly placed between the neural spines of the anterior vertebrae. They are inclined dorso-posteriorly. Their shape varies from an irregular rectangle to a thin sliver of bone. The series becomes smaller posteriorly. Their number is not correlated with the size of the fish,

although the interneurals of smaller fish are less developed than those of larger fish.

Intermuscular bones

The intermuscular bones are a series of small, splint-like bones found in the myocommata and best developed in adult fish. They project laterally from the neural (epineurals) and haemal (epipleurals) arches and spines to which they have ligamentous connections.

Epipleurals

The epipleurals lie in the ventral or hypaxial muscle of the urosome and extend from the level of the anterior edge of the anal fin onto the caudal peduncle. Anteriorly they are orientated postero-ventrally but on the caudal peduncle they come to lie parallel with the vertebral column. Ventrally each epipleural has a mesial fork and above the anal fin certain bones may be forked or expanded at their dorsal tip. The epipleurals of the caudal peduncle bear several branches at their posterior tips.

Epineurals

The epineurals lie in the dorsal or epaxial muscle and extend from the region of the Weberian vertebrae to the caudal peduncle. They are orientated dorso-posteriorly but come to lie parallel with the epipleurals at the caudal peduncle. There is a ventral mesial fork and the dorsal tips may be forked or expanded under the dorsal fin. The

epineurals of the caudal peduncle bear several branches at their posterior tips.

MEDIAN FINS

There are three median fins lying in the sagittal plane, the dorsal, the anal and the caudal. The caudal fin is situated at the posterior end of the body, the dorsal fin in the mid-line of the back and the anal fin in the mid-line of the tail region. Only the bones of these fins and the fin ray articulations are described. Details of the structure of the fin rays are not included. Both the dorsal and anal fins have a similar structure based on the pterygiophores, a serially repeated complex of small bones along the base of the fin. The complex is composed of distal, intermediate and proximal pterygiophores. The latter are elongate and lie between the neural (dorsal fin) or haemal (anal fin) spines.

Dorsal fin bones (Figure 39).

Proximal pterygiophores

The proximal pterygiophores are directed antero-ventrally. The most anterior ones are the largest and their size decreases posteriorly. Each pterygiophore has a cylindrical head inclined postero-dorsally which articulates distally with an intermediate pterygiophore. The first three or four proximal and intermediate pterygiophores are fused however. Ventrally each proximal pterygiophore consists of a thin, median plate of bone widest immediately below the head and

tapering to a narrow square end between the neural spines. The general tendency is for the anterior edge to taper gradually and the posterior edge to inflect sharply about halfway down the length of the pterygiophore. The edges may be smooth or slightly crenellated. At right angles to the median plates transverse plates run from the head of each proximal pterygiophores to the end. The transverse plate are not as expanded below the head as the median plates and they tend to narrow uniformly towards the end. There is a slight posterior curve evident in some transverse plates. The first proximal pterygiophore differs in shape from others in the series. The anterior edge of the median plate is expanded anteriorly as an antero-ventrally directed process. The dorsal edge of this process is thickened and laterally expanded. The last proximal pterygiophores (terminal complex of Buhan, 1970) lacks the lateral plate and is extended caudally to take on a triangular shape. Its dorsal half is thickened and hollow with ventrally directed openings. Proximal pterygiophores may be perforated.

Intermediate pterygiophores

The intermediate pterygiophores are small, dorso-ventrally flattened cylindrical bones articulating proximally with the proximal pterygiophore and distally with the distal pterygiophore. The anteriormost three or four intermediate pterygiophores are fused to their proximal pterygiophores. Posteriorly the series decreases in size. Each inter-

mediate pterygiophore bears small lateral and ventral plates and is centrally perforated.

Distal pterygiophores

Each distal pterygiophore articulates distally with a fin ray and proximally with an intermediate pterygiophore or fused intermediate and proximal pterygiophores. Each distal pterygiophore is medially divided into rounded rectangular shaped halves articulating mesially with each other. Each half tapers to a blunt posterior point. The ventral surface bears a shallow groove for the articulation of a projection from the fin ray half. The antero-ventral surface bulges ventrally in front of this articulation to form a head for articulation with the intermediate pterygiophore. The thinner posterior section of each distal pterygiophore overlies the head of the next proximal pterygiophore. The dorsal surface bears a laterally directed process which is attached via a ligament to the mesial surface of the fin ray half. The most anterior distal pterygiophores are compressed antero-posteriorly. The smallest distal pterygiophore is found at the base of the last two fin rays.

Ray articulations

Each complex of pterygiophores supports one fin ray with two exceptions. The first complex supports two small rays and the first unbranched ray and the ultimate complex supports two rays. The fin ray articulates with the distal pterygiophore by means of mesial processes, one from each fin ray

half. These processes are directed into ventral grooves of the distal pterygiophores. An antero-dorsal process on the fin ray creates a groove between it and the mesial process and the lateral edge of the distal pterygiophore articulates with this groove. The mesial surface of each fin ray half bears ligaments connecting it to the distal pterygiophore below it and with the distal pterygiophore of the next posterior fin ray. Each major fin ray bears a posteriorly directed process which obscures the distal pterygiophore in lateral view. The anterior edge of each fin ray half is notched and the lateral process of the distal pterygiophore articulates with it. The notch becomes more evident on the posterior fin ray halves. The modal number of dorsal fin rays and of pterygiophores is eight.

Anal fin bones (Figures 40 and 42).

Proximal pterygiophores

The proximal pterygiophores of the anal fin are structurally very similar to those of the dorsal fin and decrease in size posteriorly. The first four proximal pterygiophores are fused to their intermediate pterygiophores and the other proximal pterygiophores in the series articulate distally with their intermediate pterygiophores. Each proximal pterygiophore is orientated antero-dorsally and their lateral plates may curve anteriorly or posteriorly. The first proximal pterygiophore has an expanded median plate, ventrally thickened, but this is not as pronounced as

in the first proximal pterygiophore of the dorsal fin. The penultimate proximal pterygiophore has an expanded posterior median plate. The last proximal pterygiophore is similar to that of the dorsal fin being triangular in shape and lacking a lateral plate. It is also perforated and has several dorsally directed openings into a hollow ventral half. The heads of the proximal pterygiophores may be perforated.

Intermediate pterygiophores

The intermediate pterygiophores are structurally very similar to those of the dorsal fin. They are small cylindrical bones with lateral and dorsal plates. They may be minutely perforated. The series decreases in size posteriorly. The first four are fused distally to their proximal pterygiophores and the remainder articulate proximally with their proximal pterygiophores and distally with their distal pterygiophores.

Distal pterygiophores

Structurally and in their articulations the distal pterygiophores of the anal fin are the same as those of the dorsal fin.

Ray articulations

The first complex bears two small rays. The penultimate pterygiophore complex articulates with the last two rays, which, as in the dorsal fin, are closely approximated at their bases. The modal number of fin rays is variable and the range is 8-19 rays (Scott and Crossman, 1973).

Caudal fin bones (Figure 41).

Preural centra

The first preural centrum is fused with the ural centra and is dealt with in a separate section below. Preural centra two, three and four are found anterior to the caudal fin skeleton and are similar to other caudal vertebrae but bear expanded haemal and neural spines. The antero-posterior axis of these preural centra tends to be shorter also.

First preural and ural centra

The origin of the last centrum is compound arising from the fusion of the first preural centrum and the ural centra (Buhan, 1970). The compound centrum is shorter than those anterior to it and is the shape of a posteriorly directed cone. Anteriorly the compound centrum articulates with the vertebral column. Postero-ventrally the last haemal arch and spine arise from a clearly defined fusion line which partially encloses the area of fusion of the first hypural to the centrum. Posterior to these points of fusion the haemal spine and the first hypural closely parallel each other after a small initial space, the parhypural foramen (foramen parhypural, Monod, 1968). The hypural foramen lies dorsal to this foramen at the base of the first and second hypurals. There may be some degree of fusion between the two bones posterior to the space but usually they can be separated. Both bones narrow anteriorly before expanding to fuse with the centrum. The last haemal spine bears a short

lateral process, the hypurapophysis (Nursall, 1963). The haemal spine and the hypurals are in the form of wide flat vertical plates which terminate abruptly. The second hypural lies dorsal to the first hypural and is fused with the centrum, while the third hypural articulates with the centrum. The fused urodermals one and two are fused to the dorso-posterior edge of the centrum. Dorsally the centrum bears a reduced neural arch and spine which is irregular in shape. The arch is laterally perforated.

Hypurals

Normally there are six hypurals in cyprinids but N. crysoleucas may lack the sixth hypural. Hypurals appear to be modified haemal spines. They are numbered ventro-dorsally. Their posterior margin is truncated and contributes to the posterior convex curve of the tail skeleton. The first hypural and its articulation with the compound centrum and its partial fusion with the last haemal spine have been described above. Dorsally the first hypural abuts the second hypural. The third hypural is separated from the lower hypurals by a space or hypural diastema which divides the tail into two lobes. The third hypural articulates with the centrum in a depression such that it is partially overlapped by the bases of the second hypural and the fused first and second urodermals. The fourth, fifth and sixth hypurals are shorter than the ventral hypurals and are loosely articulated with the fused first and second urodermals. The fourth to sixth hypurals are broadest posteriorly

and are rounded and lying free anteriorly. These hypurals may be perforated. The sixth hypural may be present, absent or reduced to a speck. Further discussion about this bone is given on p. 238.

Urodermals

Two dermal urodermal bones are present but the most anterior and largest one is derived from fusion of the first and second urodermals (Buhan, 1973). The fused first and second urodermals form a slim elongate bone directed dorso-posteriorly. It articulates with the dorso-posterior corner of the centrum. Above this articulation a narrow neck splits into right and left plates which terminate in points level with the posterior ends of the other tail elements. The third urodermal is absent in N. crysoleucas. In other cypriids it lies in the region between the dorsalmost hypural and the fused first and second urodermal, partially overlapping both these bones. It has the form of a drawn out S'.

Epural

The epural is a single slender bone lying between the last fully developed neural spine of the caudal vertebrae and the fused first and second urodermal. Its antero-ventral end is gently rounded and may be closely associated with the neural spines of the compound centrum. Postero-dorsally it is truncated and lies close to the tips of the fused first and second urodermals.

Ray articulations

The upper lobe of the tail skeleton has ten major caudal fin rays (9 branched) articulating with it, the lower lobe nine (8 branched). More detailed distinction of articulations is complicated because certain rays overlap several bones. The following articulations are those commonly encountered but each ray may articulate slightly dorsal or ventral of the position indicated. The first and most dorsal major fin ray overlies the fused first and second urodermals and the sixth (when present) and fifth hypurals. The second ray articulates with the fifth hypural and its base may just reach the fused first and second urodermals. The third and fourth rays overlie both the fifth and fourth hypurals. Rays five and six overlie the fourth hypural only. The seventh ray is located at the junction of the fourth and third hypurals while rays eight and nine overlie the third hypural only. The tenth ray may be associated with the space between the third and second hypurals but usually lies nearer to the third hypural. Rays eleven and twelve overlie the second hypural; ray thirteen is associated with both the second and first hypurals. Ray fourteen articulates solely with the first hypural. Rays fifteen and sixteen overlie the first hypural and the last haemal spine. Rays seventeen and eighteen articulate with the haemal spine and the last major ray overlies both the last haemal spine and the penultimate haemal spine.

Several minor rays lie dorsal and ventral to the major rays described above. Dorsally a single ray is associated with the fused first and second urodermals. Two smaller rays dorsal to this ray articulate with the fused first and second urodermal and the epural. Four other rays are variably associated with the epural and the last two developed neural spines. Ventrally two rays articulate with the penultimate haemal spine and four more anterior spines, becoming progressively smaller ventrally, articulate around the tip of the neural spine preceding the penultimate one.

PAIRED FINS

The pectoral and pelvic or ventral fins are supported by pectoral and pelvic girdles. The pectoral and pelvic girdles are separate complexes of paired dermal and endochondral bones, as in other lower teleosts. The bones of these girdles and their articulation with the fin rays are described below. The fin rays are not described.

PECTORAL GIRDLE

The pectoral girdle forms the basis for support of the pectoral fins. Each half of the pectoral girdle proper is dorsally connected to the cranium by dermal suspensory bones, which also act to buffer the effect of head movements on the lateral line system where it passes from the head to the body. The girdle forms part of the border of the bran-

chial chamber and abuts the pharyngeal arch.

Suspensory Bones (Figure 42).

Posttemporals

Each posttemporal has a narrow antero-dorsal end overlying the epiotic and an expanded postero-ventral end overlying the supratemporal-intertemporal, pterotic and the dorsal quarter of the supracleithrum. The lateral extrascapular sensory canal bone is fused to the lateral surface of the posttemporal. It is continuous antero-dorsally with the supratemporal and infraorbital canals and postero-ventrally with the canal on the supracleithrum.

Supracleithra

Each supracleithrum connects the posttemporal with the cleithrum of the pectoral girdle proper. The wide dorsal end is connected by a ligament mesially to the posttemporal and the narrower, ventral end is similarly connected lateral to the cleithrum. The postero-dorsal corner of the opercular overlaps the supracleithrum. A small sensory canal bone is fused to the lateral surface just below the point of overlap by the posttemporal and its canal. Ventrally and posteriorly the canal is connected with the lateral line.

Pectoral Girdle Bones (Figure 43).

The pectoral girdle proper is composed of five major bones on each side. The largest of these is the cleithrum which is composed of two rami at right angles giving the girdle

its characteristic shape. The other major girdle bones articulate with the cleithrum.

Cleithra

The cleithra are paired, dermal bones, the anterior surface of which form the posterior walls of the gill cavities separating them from the abdominal cavity. The dorsal ramus of the cleithrum narrows to a point mesial and posteriad to the supracleithrum. The supracleithrum overlaps the cleithrum at an angle over the upper half of the dorsal ramus. The anterior ramus is directed antero-ventrally at an angle of slightly more than 90° to the dorsal ramus. The caudo-ventral angle of the cleithrum is produced posteriorly. Both cleithra are connected with each other and with the urohyal by ligaments. The dorsal ramus is a flat plate of bone bearing a lateral ridge on its anterior surface. The ridge merges with the dorsal ramus near its tip and runs down along the lateral edge of the anterior ramus. It has a posterior curl. The supracleithrum is connected to the dorsal ramus ridge by ligaments. A mesial ridge runs the length of the dorsal ramus and expands anteriorly as a small rounded projection beyond the anterior edge of the lateral ridge. A third ridge branches off the mesial ridge midway from the tip of the dorsal ramus and runs along the mesial surface of the anterior ramus in a sagittal plane as the dorsal edge. The coracoid articulates with ventro-mesial plates from the mesial ridge of the anterior ramus, anteriorly and posteriorly around a large oval space.

The mesocoracoid articulates with the cleithrum at the base of the mesial ridge.

Postcleithra

The postcleithra are paired, dermal bones of variable size and shape which ventrally provide the origin for the sternohyoideus muscle (Buhan, 1970). In N. crysoleucas they are quite small, often gently curved, slivers of bone articulating mesially with the caudo-ventral corner of the cleithrum.

Coracoids

The coracoids are paired, endochondral bones lying mesial to, and articulating with, the anterior rami of the cleithra. Each coracoid forms the anterior and ventro-mesial borders of a large foramen between it and the cleithrum. The anterior articulation with the cleithrum is narrower than the posterior one and both mesially overlap the cleithrum. The articulations are irregular. Posteriorly the coracoid articulates with the scapula and partly with the second and third radials. A mesial ridge bears the major part of the articulating surface for the mesocoracoid. The coracoid is perforated cranio-ventrally to this articulation.

Mesocoracoids

The mesocoracoids are paired, endochondral bones which articulate mesially in the lateral plane with the mesial ridge of the dorsal ramus of the cleithrum and with the dorsal edge of the scapula. A thin central portion expands

ventrally to articulate broadly with the coracoid and posteriorly to articulate narrowly with a ridge on the scapula. The central portion may be straight or show an 'S'-curve.

Scapulae

The scapulae are paired, endochondral bones situated mesial to the cleithra and lateral to the mesocoracoids. Each scapula has the outline of a triangle with curved sides. There is a large central foramen. The dorsal edge articulates with the lower surface of the mesial ridge of the anterior ramus at the junction of the two rami of the cleithrum. Antero-dorsally a small portion articulates with the laterally expanded head of the mesocoracoid. A ventrally directed side articulates with the coracoid and bears a mesial and dorsally directed projection which articulates with the mesocoracoid. The posterior edge bears the glenoid fossa into which the first pectoral ray articulates. The first two radials articulate with the scapula ventral to the glenoid fossa. The second radial also articulates partly with the coracoid.

Pectoral Radials

The radials are four, paired, endochondral bones at the posterior margin of the pectoral girdle connecting the fin rays to the girdle. The first radial is located ventro-mesial to the glenoid fossa. It is the shortest and thickest bone of the series. It articulates anteriorly with the sca-

pula and a lateral projection overlaps this bone. Posteriorly it may have one or two heads articulating with the fin rays. The first radial bears a notch on its dorsal edge which accommodates a projection from the first fin ray. The radial articulates ventro-mesially with the second radial.

The second radial partially overlaps the first. Its anterior end is notched and projections pass lateral and mesial to the joint between the coracoid and scapula. The second radial lies mesial to the third radial.

The third radial articulates with the coracoid anteriorly, the second radial laterally and the fourth radial mesially. Both the second and third radials consist of a plate which narrows posteriorly to a head which articulates with the fin rays.

The fourth radial is connected to the coracoid by a ligament and lies mesial to the third radial. Anteriorly it is pointed and posteriorly it bears an articulating head.

The radials may be perforated, particularly the second radial. Small accessory ossifications (Buhan, 1970) may be associated with the first radial. They are bounded laterally by the fin rays which are proximally split to articulate on the mesial and lateral surfaces of the radial.

Ray articulations

Articulations are difficult to determine because of the angle at which rays cross the radials. Consequently articulations were arbitrarily designated as the first radial

by a ray as seen from the mesial surface. The first pectoral ray articulates anteriorly with the glenoid fossa on the scapula and ventro-mesially with a depression on the first radial. The first radial articulates with three rays including the first ray and the second radial articulates with two rays. The third and fourth radials articulate with the remaining rays which curl ventrally around the posterior end of the fourth radial.

PELVIC GIRDLE (Figure 41).

The pelvic girdle lies in the ventral body wall divorced from other parts of the skeleton. It supports the paired pelvic or ventral fins.

Basipterygia

The basipterygia are paired endochondral bones forming the major structural elements of the girdle. They articulate mesially with each other by means of ligaments and are connected posteriorly to the radials. Each basipterygium is composed of a thin central plate bearing projections. Anteriorly two projections diverge gradually from the lateral and mesial corners of the basipterygium. The mesial projections converge but do not meet. They are loosely connected by ligaments. The projections are thin curved plates of bone lying in the sagittal plane. The lateral projection is concave on its lateral surface and the mesial projection is convex on its lateral surface. The lateral projection

merges posteriorly with the basipterygium while the mesial projection is more pronounced and merges posteriorly with a mesial process on its dorsal edge. The ventral edge ends posteriorly in a central raised process against which the lateral-most fin ray abuts. The mesial process is connected to its opposite neighbour by a ligament. Ventral to this process a projection, the posterior medial process, curves caudad. The thickened posterior ends of the basipterygium are perforated.

Radials

The radials are paired endochondral bones articulating anteriorly with the posterior end of the basipterygium and posteriorly with the pelvic fin rays. The first two radials are irregular in shape but bear a depression on their anterior surface where they articulate with the basipterygium. They are divisible into dorsal and ventral sections. The third radial is the largest and is L-shaped. The bone follows the curvature of the projection of the mesial process and terminates in a point just posterior to the end of the projection. The base of the third radial is thickened and bears a notch on its anterior surface which articulates with the postero-mesial end of the basipterygium.

Ray articulations

The first ray of each side articulates directly with the basipterygium. The ray is split into dorsal and ventral pro-

ximal halves which fit on either side of the basipterygium lateral to the first radial. The ventral half bends gently mesad and is slightly expanded. It abuts the raised process at the posterior end of the mesial projection. The dorsal half bends sharply at 90° or more and bears a ventral knob at its angle which articulates with the basipterygium. External to the first ray is the pelvic splint which runs from the basipterygium posteriorly for one third of the length of the first ray. The anterior end of the splint curves mesially into the abdomen.

The articulations of the remaining rays are difficult to determine because of the different degrees of bending of the dorsal and ventral halves. Also the bending causes each ray to cross several bones and to overlap each other such that the first ray is the only one to be seen in its entirety at the base. Only the ventral ray articulations are described where they first cross a radial. The mesal-most 5 rays are associated with the third radial while the most lateral rays, 4 in number, are variably associated with the first and second radials. Usually there are 2-3 rays with each radial, the outermost ray being more closely associated with the postero-lateral corner of the basipterygium. There is a modal number of 9 rays in each pelvic fin.

Figure 23. Lateral view of head and posterior view of cranium (posttemporals removed from latter). Scales: 1 cm. and 0.5 cm. respectively.

AC: aortic canal, BAL: bulla acustica lagenaris, BO: basioccipital, BPP: basioccipital pharyngeal process, BR₁₋₃: branchiostegals₁₋₃, CL: cleithrum, CS: cavum sinus imparis, D: dentary, EO: epiotic, EXO: exoccipital, F: frontal, FM: foramen magnum, H: hyomandibular, IO: infraorbital canal, IOP: interoperculum, L: lachrymal, LF: lateral occipital foramen, N: nasal, O: opisthotic, OP: operculum, P: parietal, PCL: postcleithrum, PM: preoperculo-mandibular canal, POP: preoperculum, PRO: proatlas, PSC: posterior semicircular canal, PT: posttemporal, PTF: posttemporal fossa, PTO: autopterotic, Q: quadrate, SB: scleral bone, SCL: supra-cleithrum, SI: supratemporal-intertemporal, SO: supra-orbital canal, SOC: supraoccipital, SOP: suboperculum, SP: supraorbital, ST: supratemporal canal.

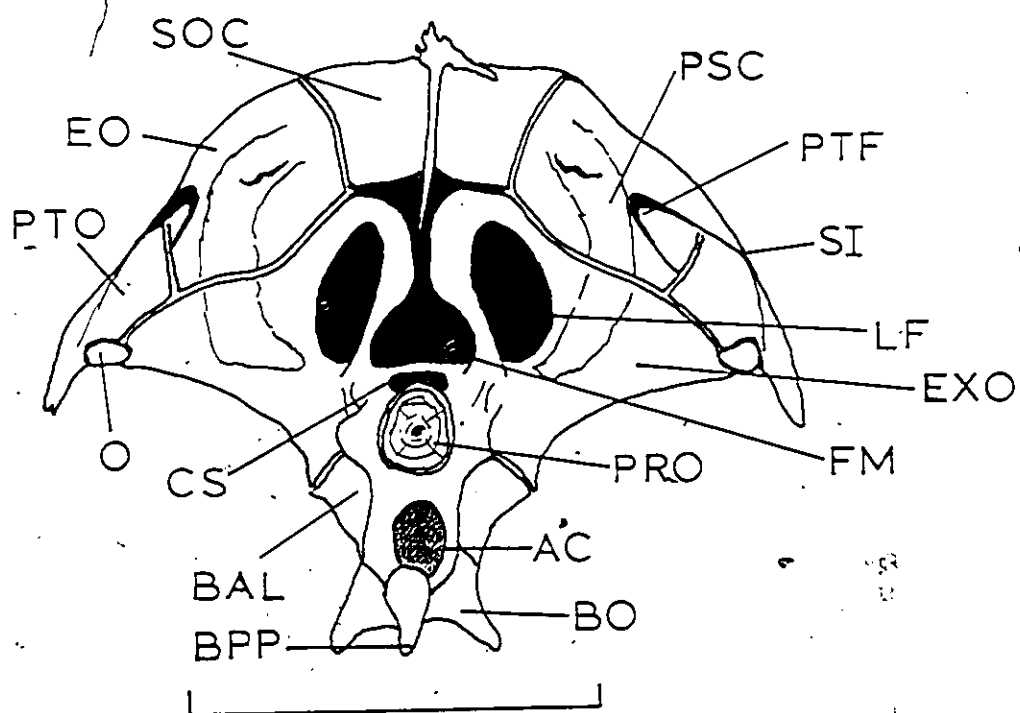
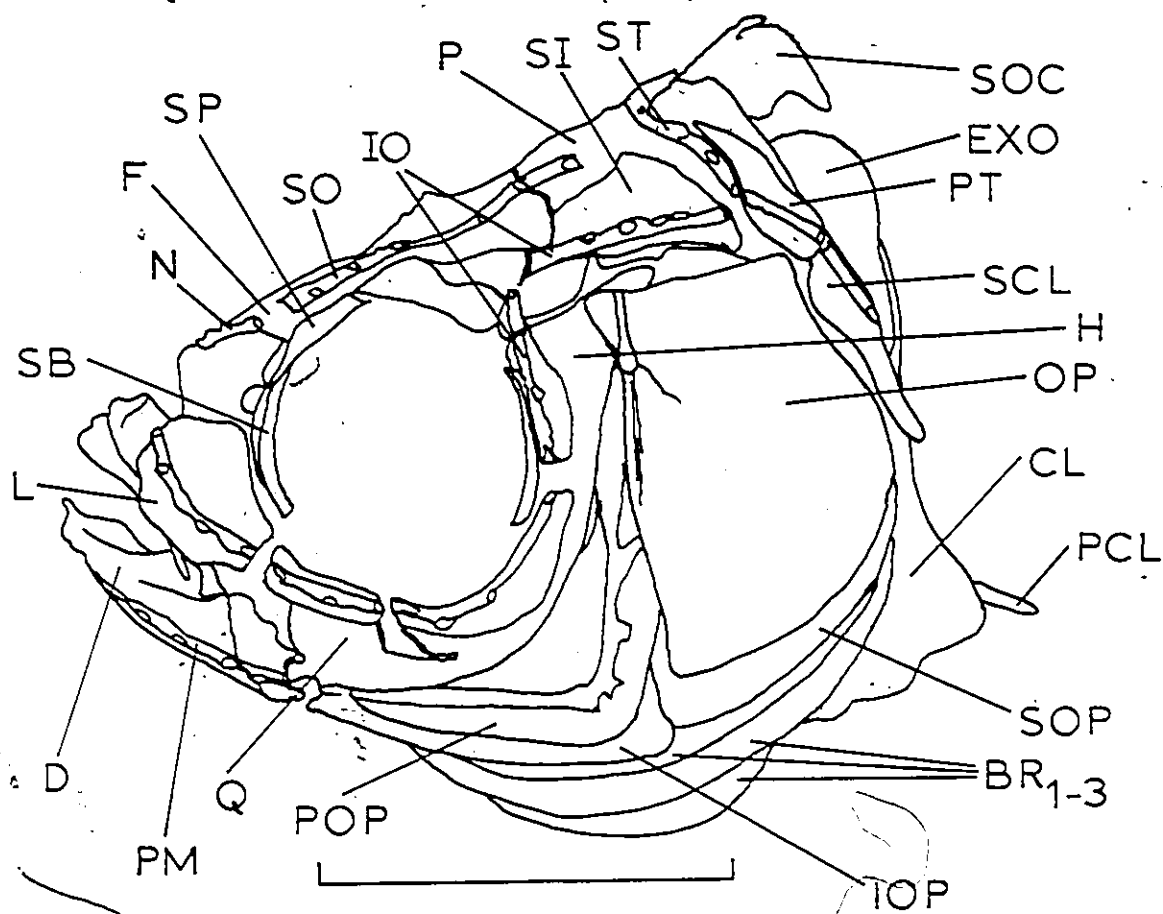


Figure 24. Dorsal view of the cranium (posttemporals removed).

Scale: 0.5 cm.

AS: autosphenotic, BO: basioccipital, BPP: basioccipital pharyngeal process, EO: epiotic, EPB: epiphysial bar, EXO: exoccipital, F: frontal, FM: foramen magnum, LE: lateral ethmoid, LF: lateral occipital foramen, N: nasal, O: opisthotic, P: parietal, PEC: preethmoid cornua, PV: prevomer, SE: supraethmoid, SI: supratemporal-intertemporal, SO: supraorbital canal, SOC: supraoccipital, SP: supraorbital, ST: supratemporal canal, STF: subtemporal fossa.

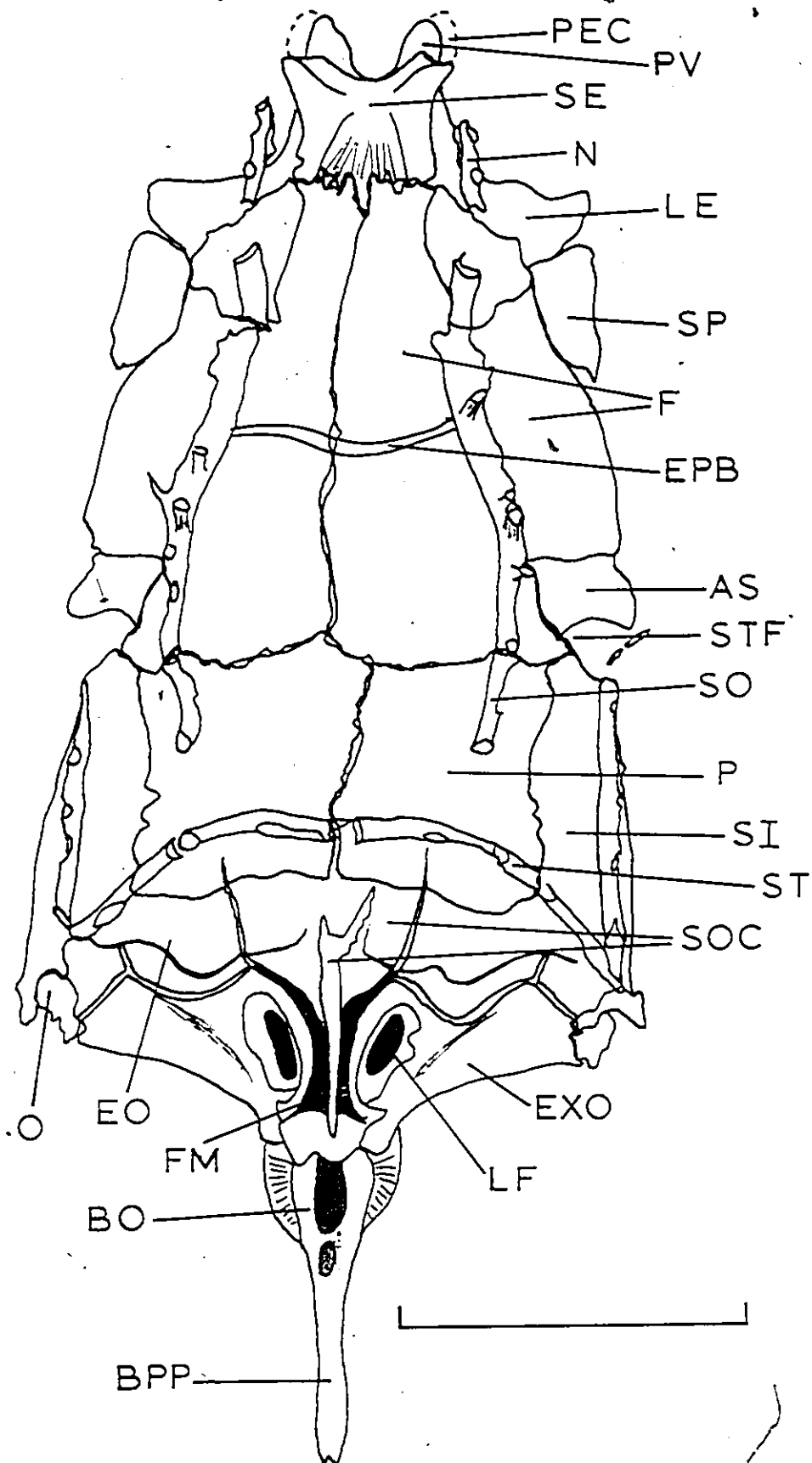


Figure 25. Ventral view of cranium (posttemporals removed).

Scale: 0.5 cm.

AS: autosphenotic, BAL: bulla acustica lagenaris,
BAU: bulla acustica utricularis, BO: basioccipital,
BP: basioccipital or masticatory plate, BPP: basi-
occipital pharyngeal process, CA: carotid artery
foramen, EXO: exoccipital, F: frontal, HSC:
horizontal semicircular canal, HYF: facet for
hyomandibular head, LE: lateral ethmoid, O:
opisthotic, OF: optic foramen, OS: orbitosphenoid,
PO: prootic, PS: parasphenoid, PTS: pterosphenoid,
PTO: autopterotic, PV: prevomer, SP: supraorbital,
STF: subtemporal fossa, lll: oculomotor nerve foramen,
lv: trochlear nerve foramen, V: trigeminal nerve
foramen, Vl: abducens nerve foramen, Vll: facial nerve
foramen, VLll: acoustic nerve foramen, lX: glosso-
pharyngeal nerve foramen, X: vagus nerve foramen.

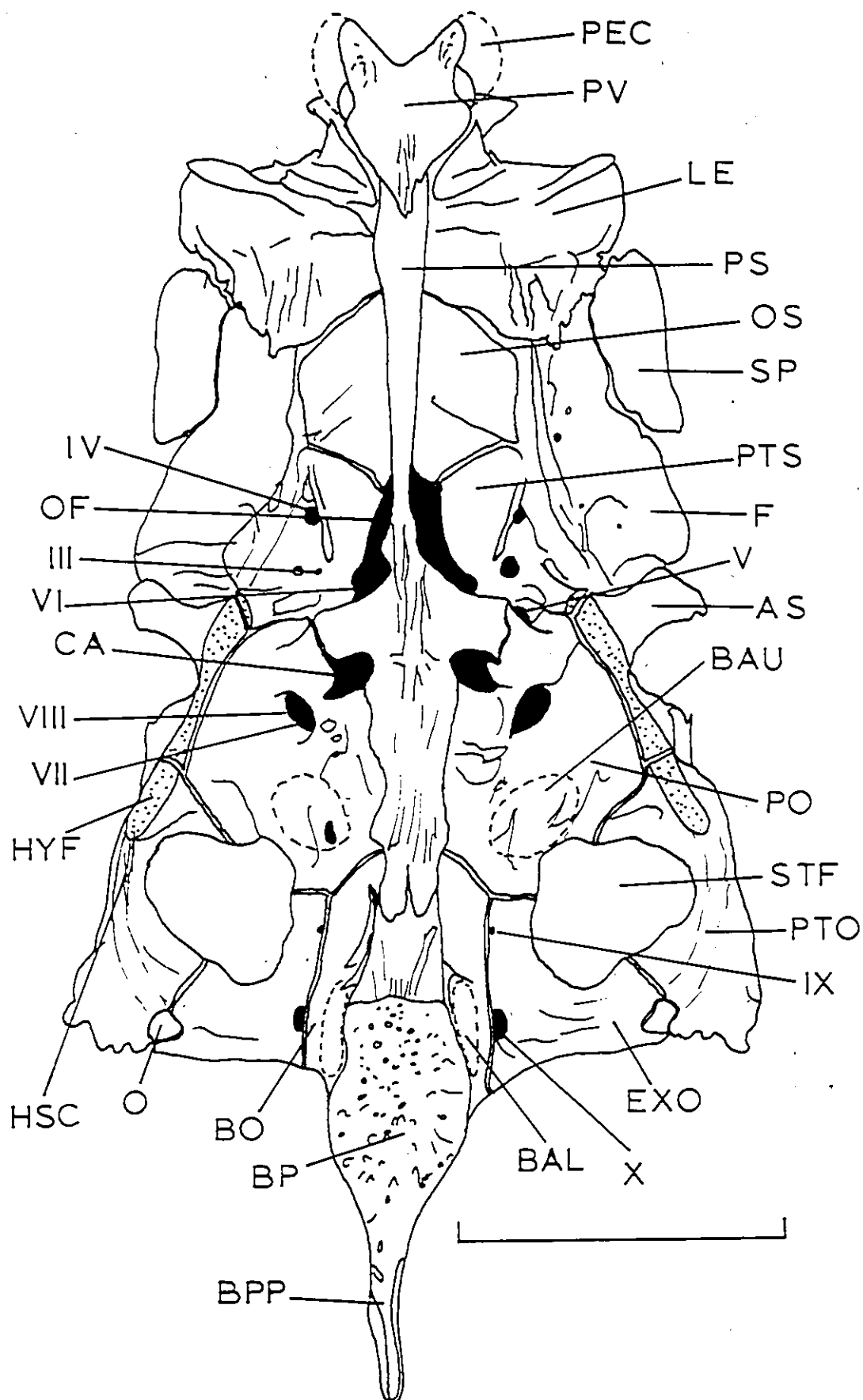


Figure 26. Lateral view of cranium (posttemporals removed).

Scale: 0.5 cm.

AS: autosphenotic, ASC: anterior semicircular canal, BAL: bulla acustica lagenaris, BAU: bulla acustica utricularis, BO: basioccipital, BPP: basioccipital pharyngeal process, CA: carotid artery foramen, E: ethmoid, EO: epiotic, EXO: exoccipital, F: frontal, HYF: facet for hyomandibular head, LE: lateral ethmoid, LF: lateral occipital foramen, OF: optic foramen, OS: orbitosphenoid, P: parietal, PE: pre-ethmoid, PEC: preethmoid cornua, PM: preoperculo-mandibular canal, PO: prootic, PS: parasphenoid, PTS: pterosphenoid, PV: prevomer, SE: supraethmoid, SI: supratemporal-intertemporal, SO: supraorbital canal, SOC: supraoccipital, SP: supraorbital, ST: supratemporal canal, I: olfactory nerve foramen, VI: abducens nerve foramen, VII: facial nerve foramen.

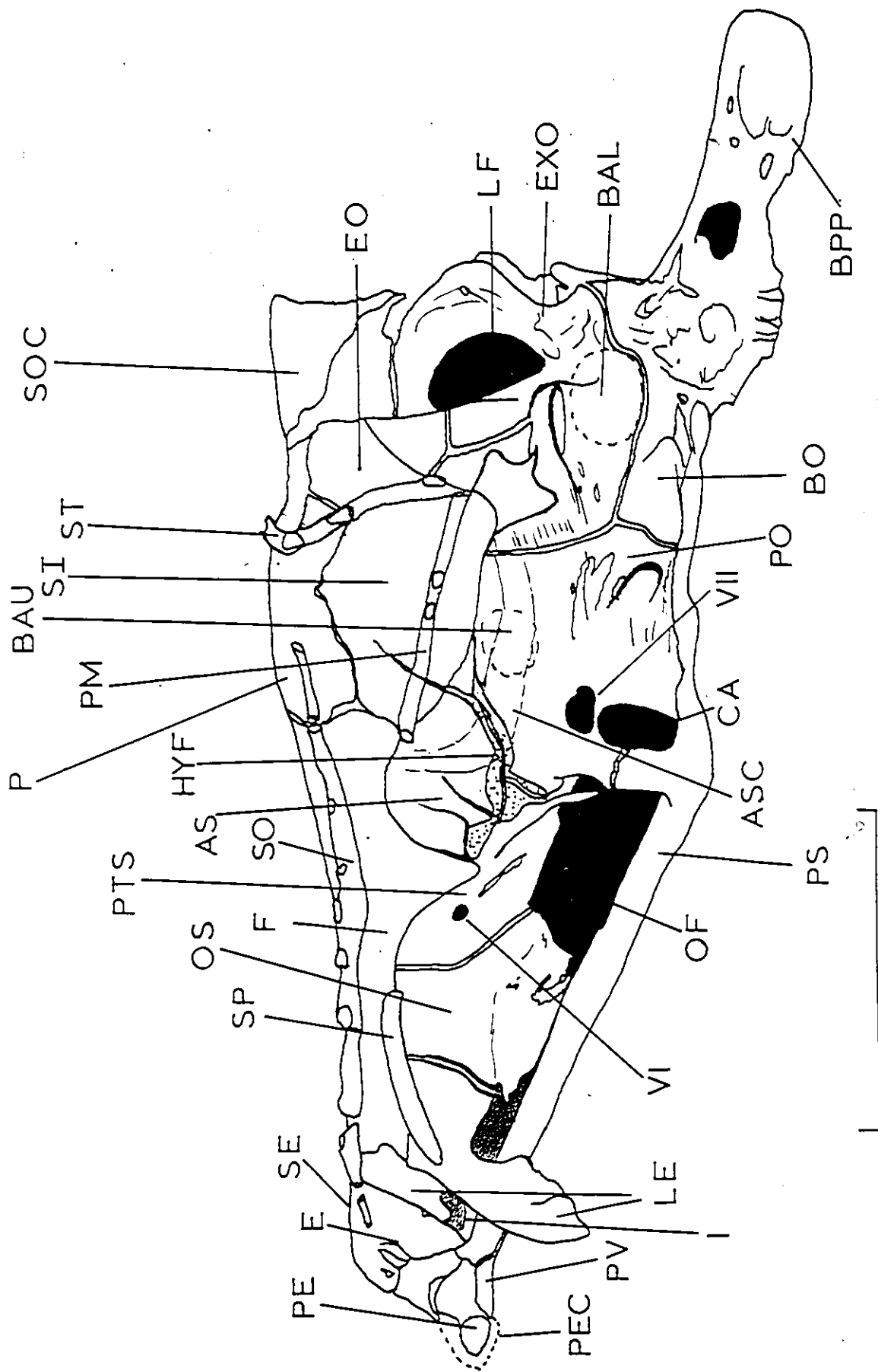


Figure 27. Lateral (A), ventral (B) and posterior (C) views of the ethmoid complex. Lateral ethmoids removed except in B. Scale: 1 mm.

E: ethmoid, LE: lateral ethmoid, PE: preethmoid (mesial only in this specimen), PEC: preethmoid cornua, PV: prevomer, SE: supraethmoid.

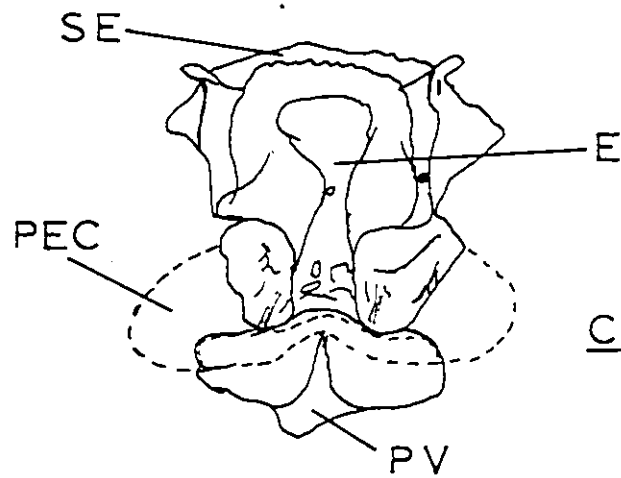
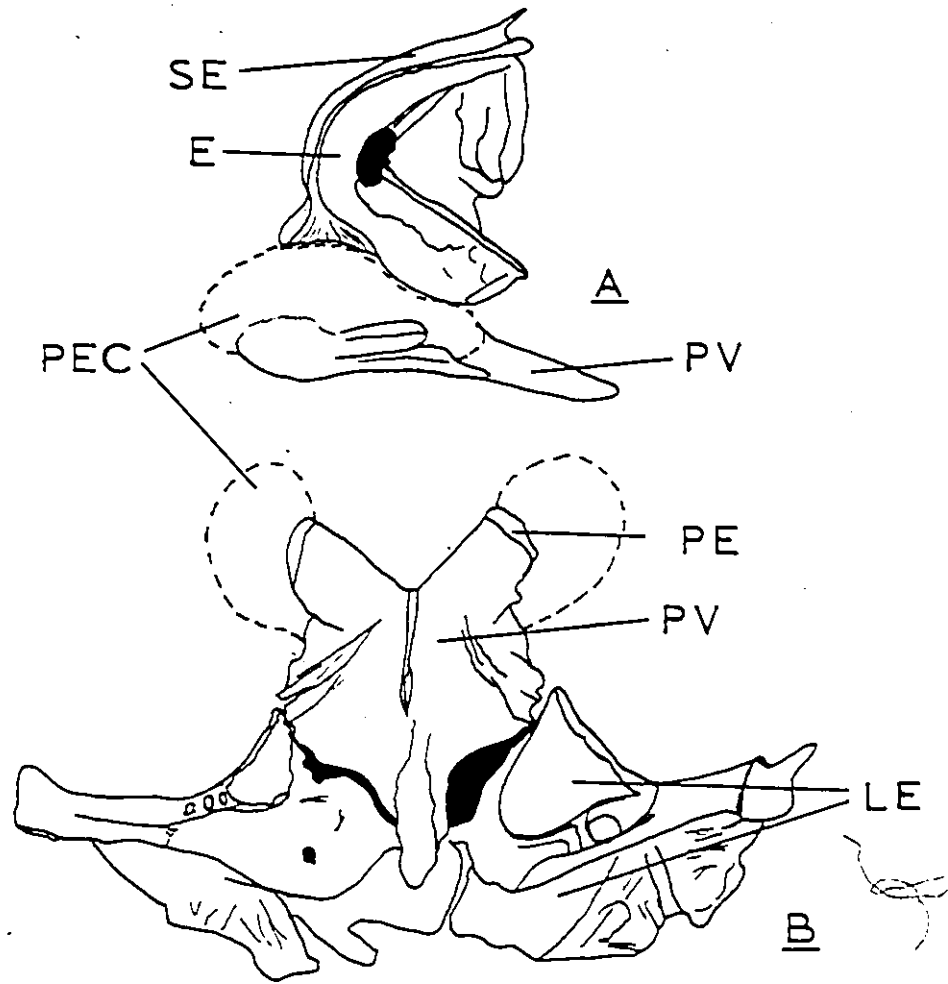
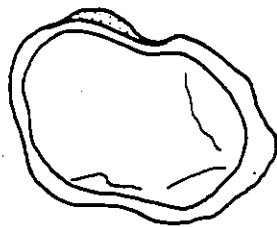




Figure 28. A- Ventro-lateral view of left lapillus, B- lateral view of right sagitta, partially fragmented, and C- mesial view of left asteriscus. Scale: 1 mm.

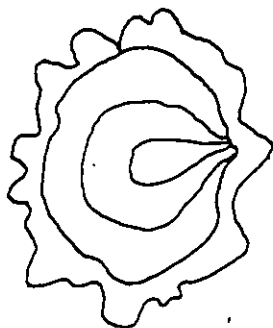
8



A



B



C



Figure 29. Lateral views of left maxillary and premaxillary bones; mesial view of left lower jaw; lateral view of remainder of oromandibular region plus symplectic. Scale: 0.5 cm.

A: angular, AP: autopalatine, CM: coronomeckelian, D: dentary, ECPT: ectopterygoid, ENPT: endopterygoid, M: mentomeckelian, MP: metapterygoid, MX: maxillary, PMX: premaxillary, Q: quadrate, RA: retroarticular, SY: symplectic.

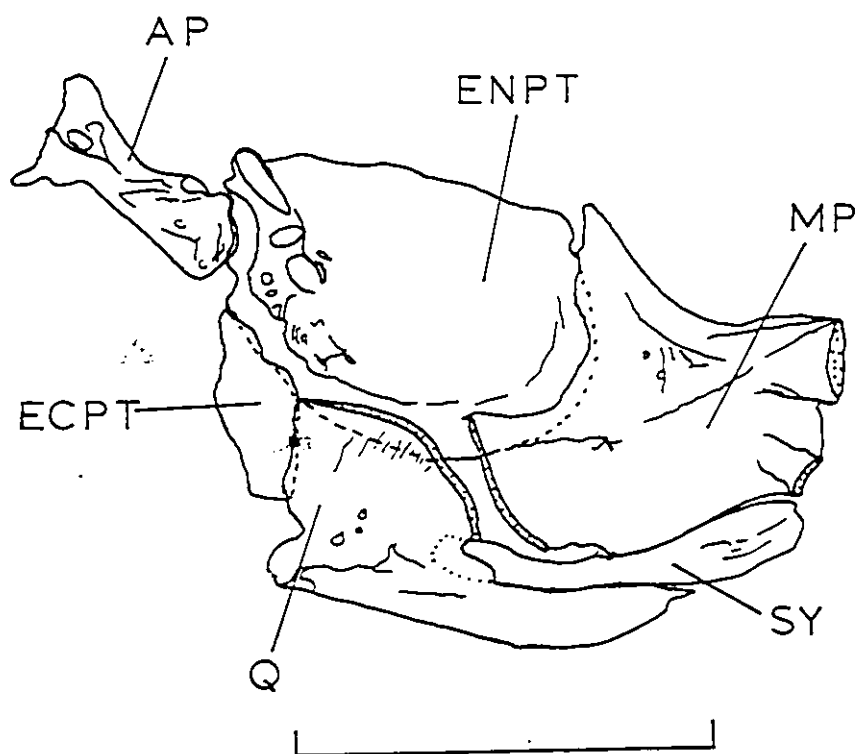
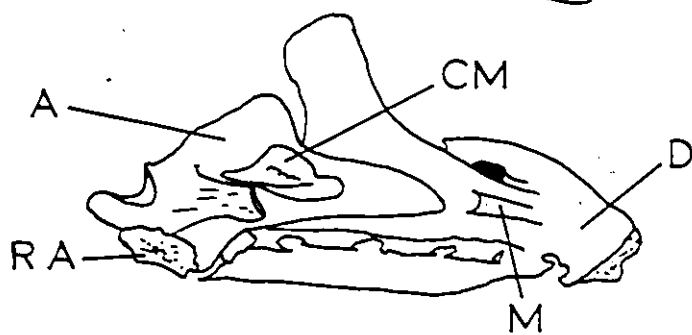
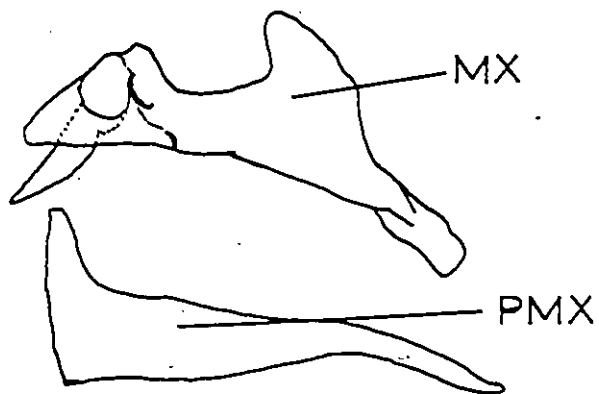


Figure 30. Lateral view of opercular and suborbital series of bones. Scale: 0.5 cm.

DS: dermosphenotic, IOP: interoperculum, L: lachrymal,
OP: operculum, POP: preoperculum, SO₂₋₅: suborbitals₂₋₅,
SOP: suboperculum.

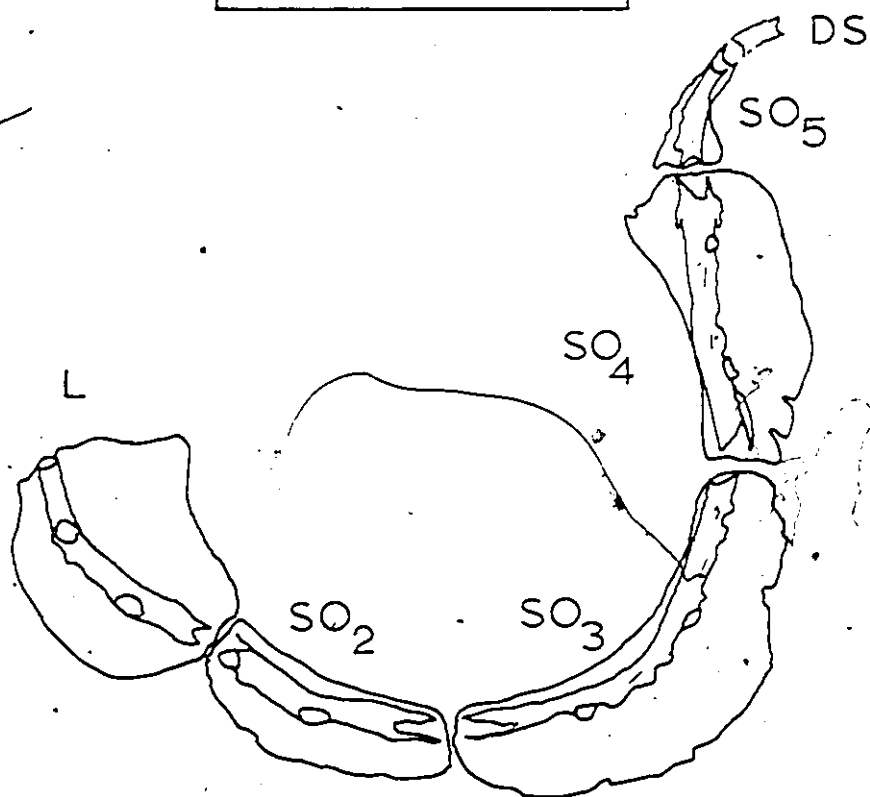
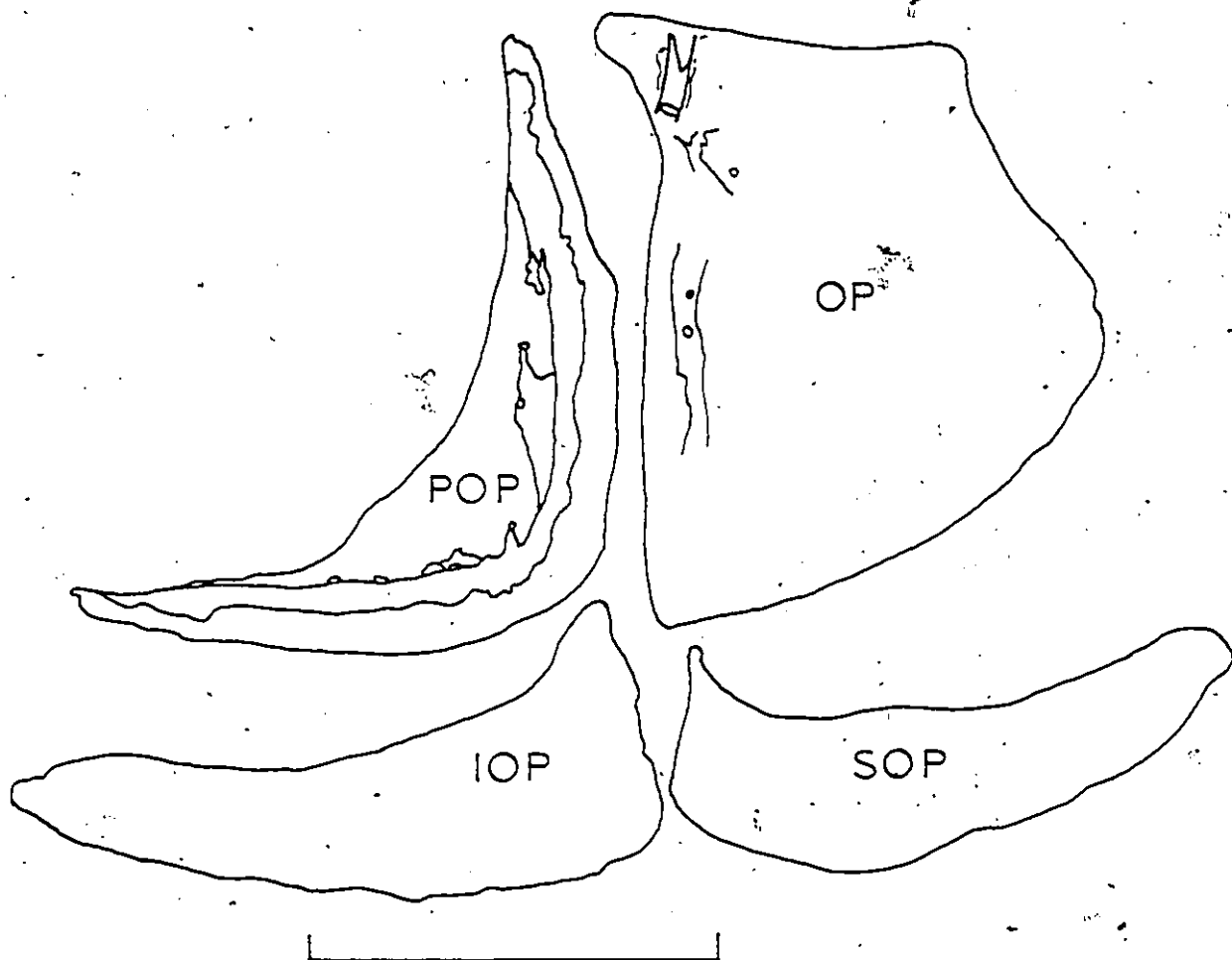


Figure 31. A- Dorsal and B- ventro-mesial views of upper and lower hypohyals and anterior end of the ceratohyal; C- Lateral view of hyomandibular; D- Lateral view of branchiostegals and associated bones of the hyoid region. Scale: 0.5 cm.

BR₁₋₃: branchiostegals₁₋₃, CH: ceratohyal, EH: epihyal, H: hyomandibular, IH: interhyal, LHY: lower hypohyal, UHY: upper hypohyal.

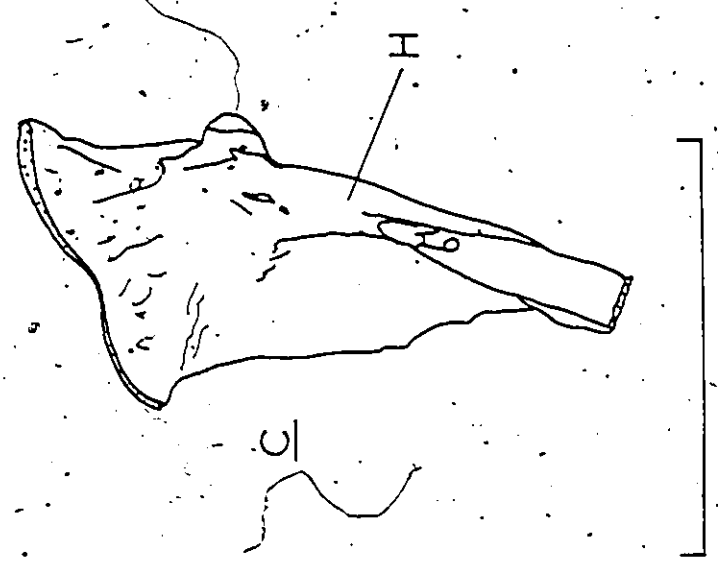
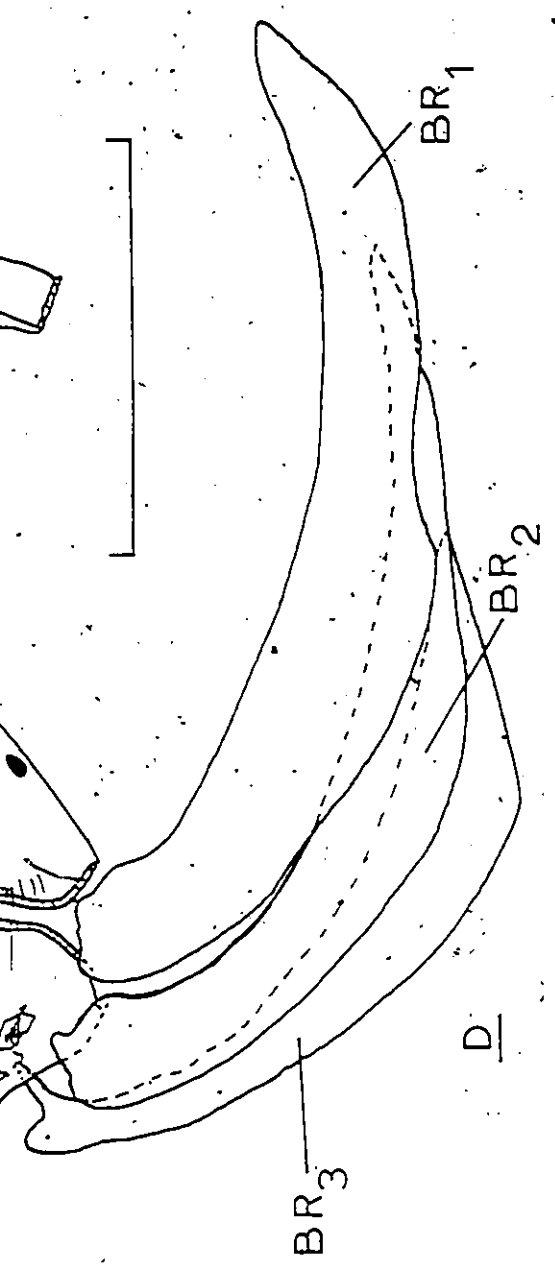
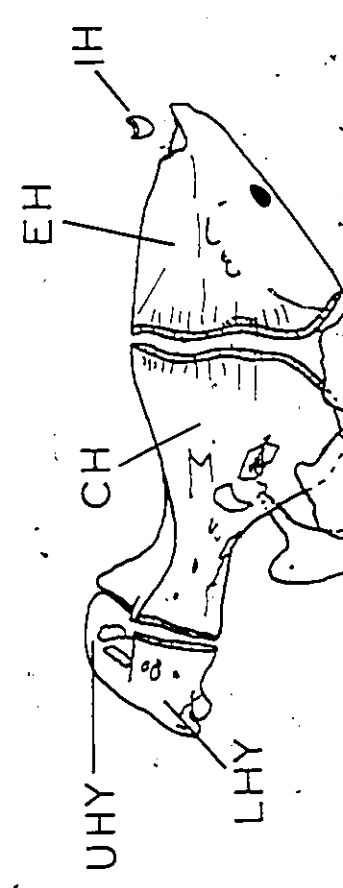
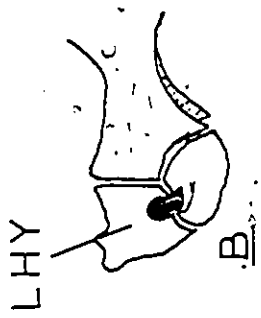
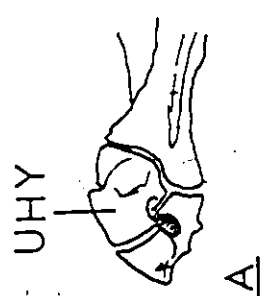


Figure 32. Dorsal view of the branchial region including basihyal but excluding pharyngeal arches and cartilaginous fifth epibranchial. Right epibranchials and pharyngobranchials laid to the right. Scale: 0.5 cm.

BB₁₋₃: basibranchials₁₋₃, BH: basihyal, CB₁₋₄: ceratobranchials₁₋₄, EB₁₋₄: epibranchials₁₋₄, HB₁₋₃: hypobranchials₁₋₃, PB₁₋₂: pharyngobranchials₁₋₂.

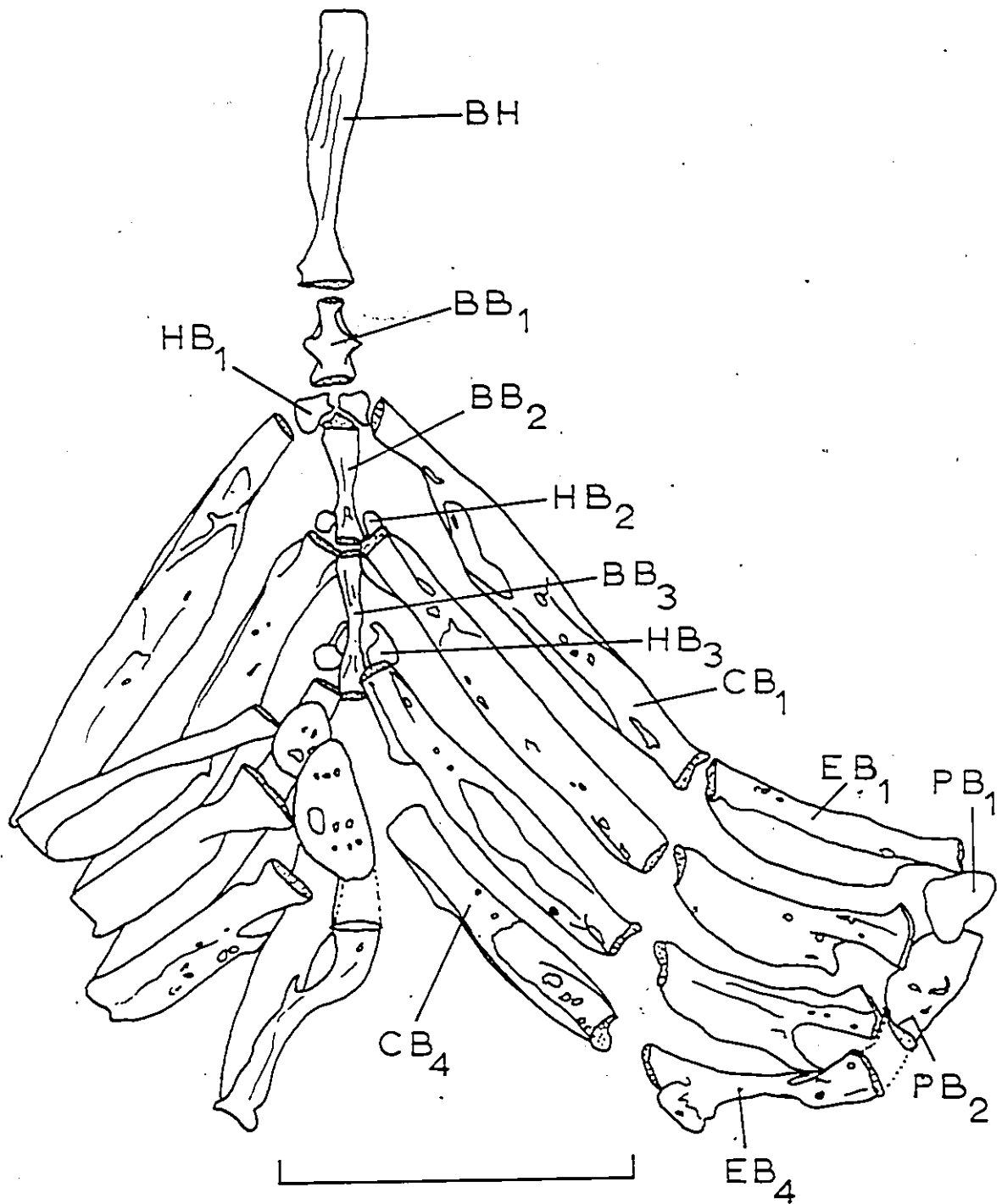
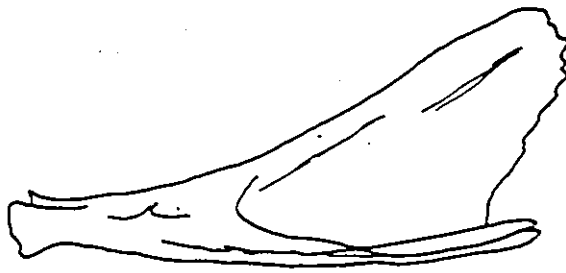
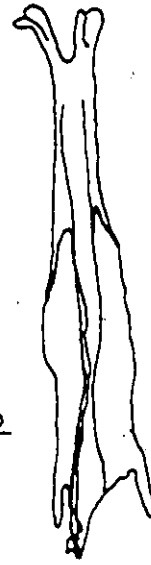


Figure 33. Lateral (A) and dorsal (B) views of the urohyal;
Ventral (A) and dorsal (B) views of right pharyngeal
arch. Scale: 0.5 cm.
PH: pharyngeal arch, UH: urohyal.

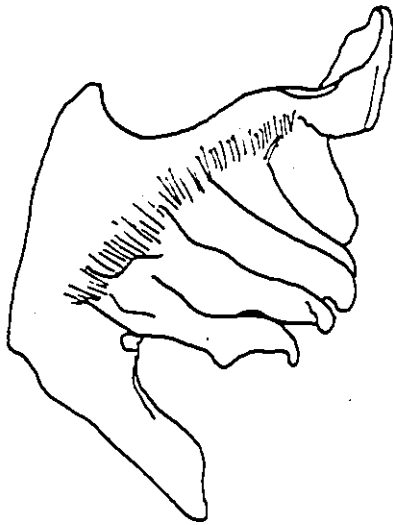


A

UH

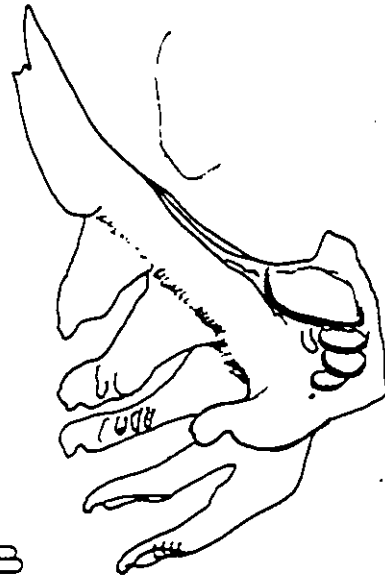


B



A

PH



B



Figure 34. Lateral view of Weberian vertebrae and ossicles.

Scale: 0.5 cm.

BO: basioccipital, C_1 and C_7 : first and seventh centra, CT: claustrum, I: intercalarium, IN: interneural, NA: neural arch, NC: neural complex, NEZ: neural prezygapophysis, NPZ: neural postzygapophysis, NS: neural spine, OSS: os suspensorium, PA: parapophysis, PRB: pleural rib, S: scaphium, T: tripus.

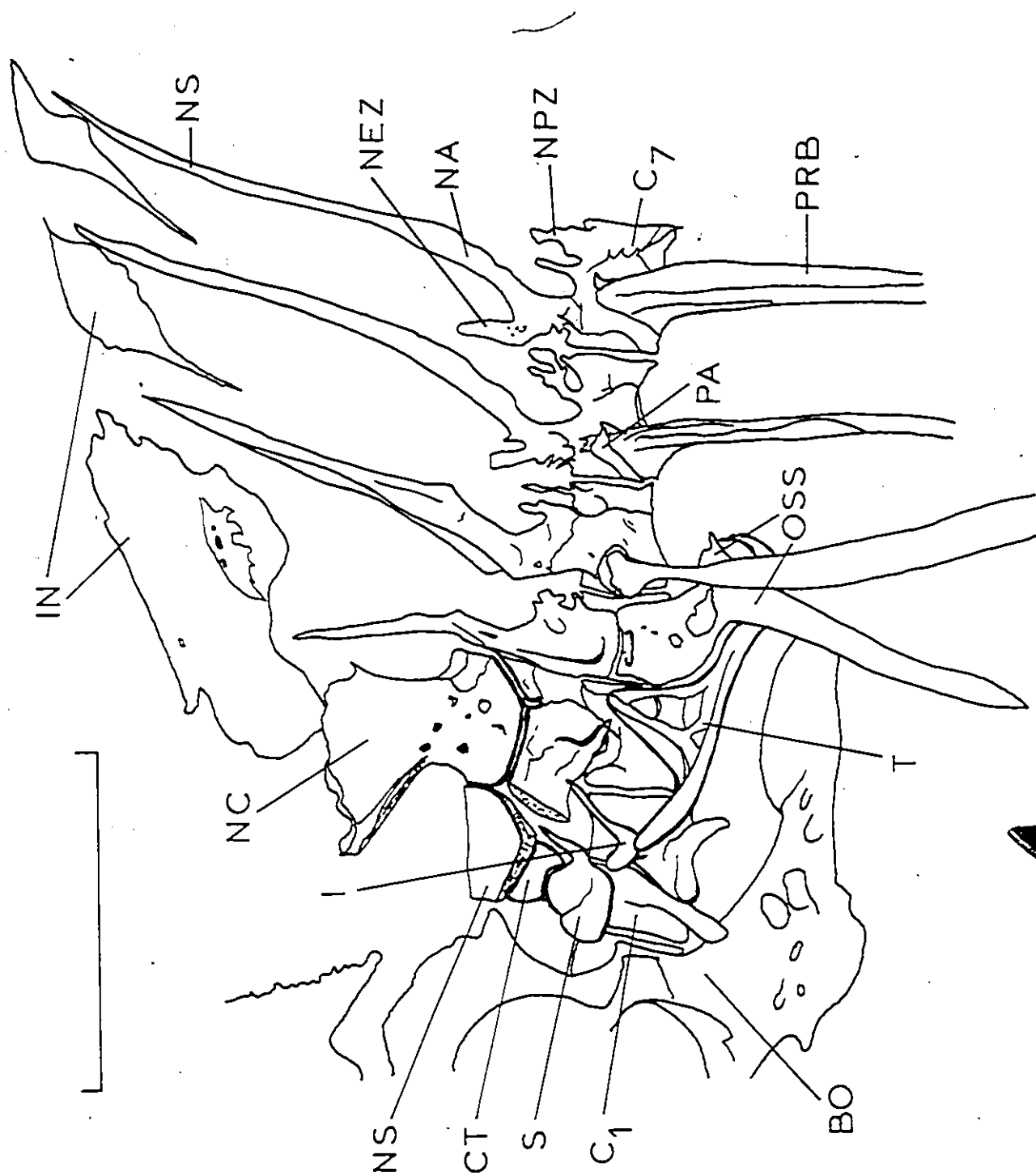
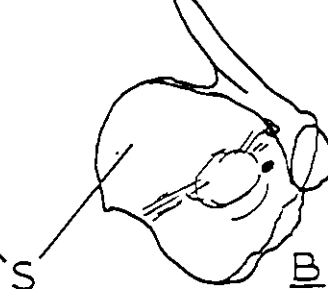
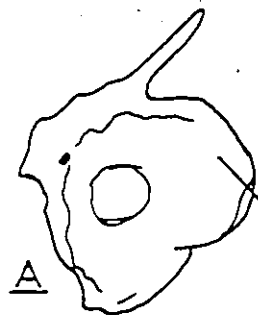
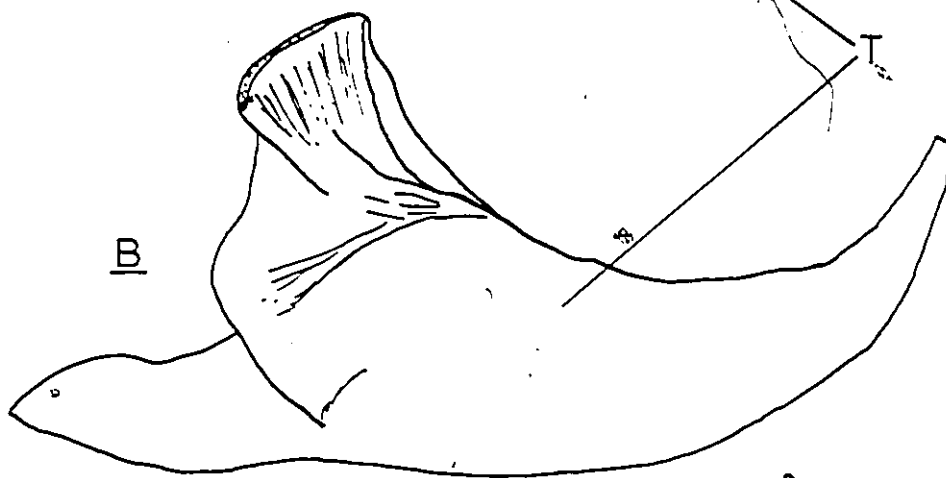


Figure 35. Lateral (A) and mesial (B) views of the Weberian ossicles (intercalarium in lateral view only).

Scale: 0.5 cm.

CT: claustrum, I: intercalarium, S: scaphium, T: tripus.





CT



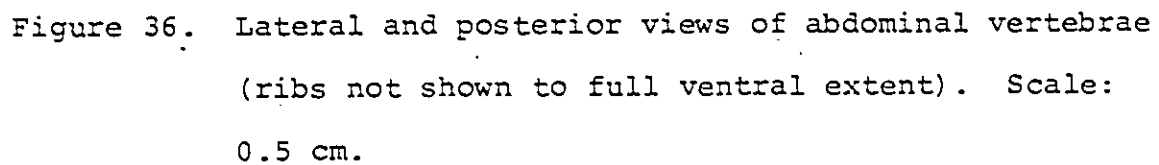


Figure 36. Lateral and posterior views of abdominal vertebrae
(ribs not shown to full ventral extent). Scale:
0.5 cm.

C₁₄₋₁₅: fourteenth and fifteenth centra, NA: neural
arch, NEZ: neural prezygapophysis, NPZ: neural
postzygapophysis, NS: neural spine, PRB: pleural rib.

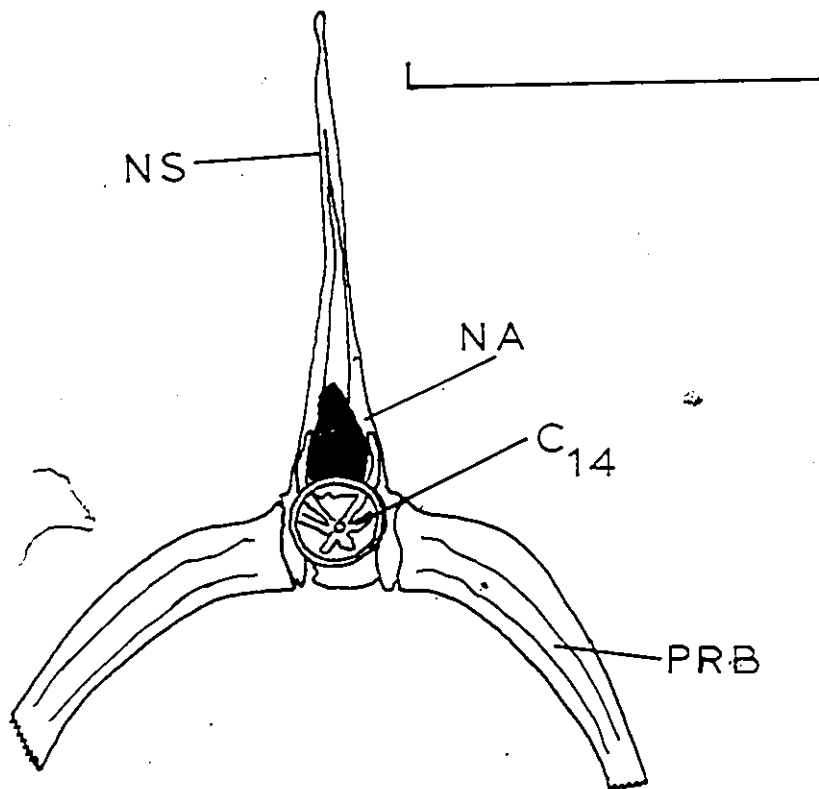
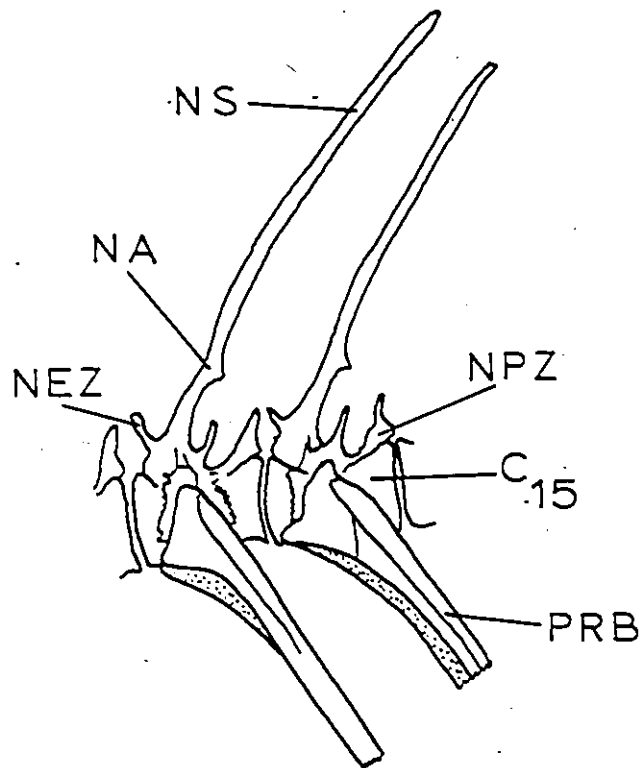


Figure 37. Lateral view of transitional and adjacent vertebrae (ribs not shown to full ventral extent). Scale: 0.5 cm.

C₂₃: twenty-third centrum, HA: haemal arch, HS: haemal spine, NA: neural arch, NS: neural spine, PRB: pleural rib, TV: transitional vertebrae.

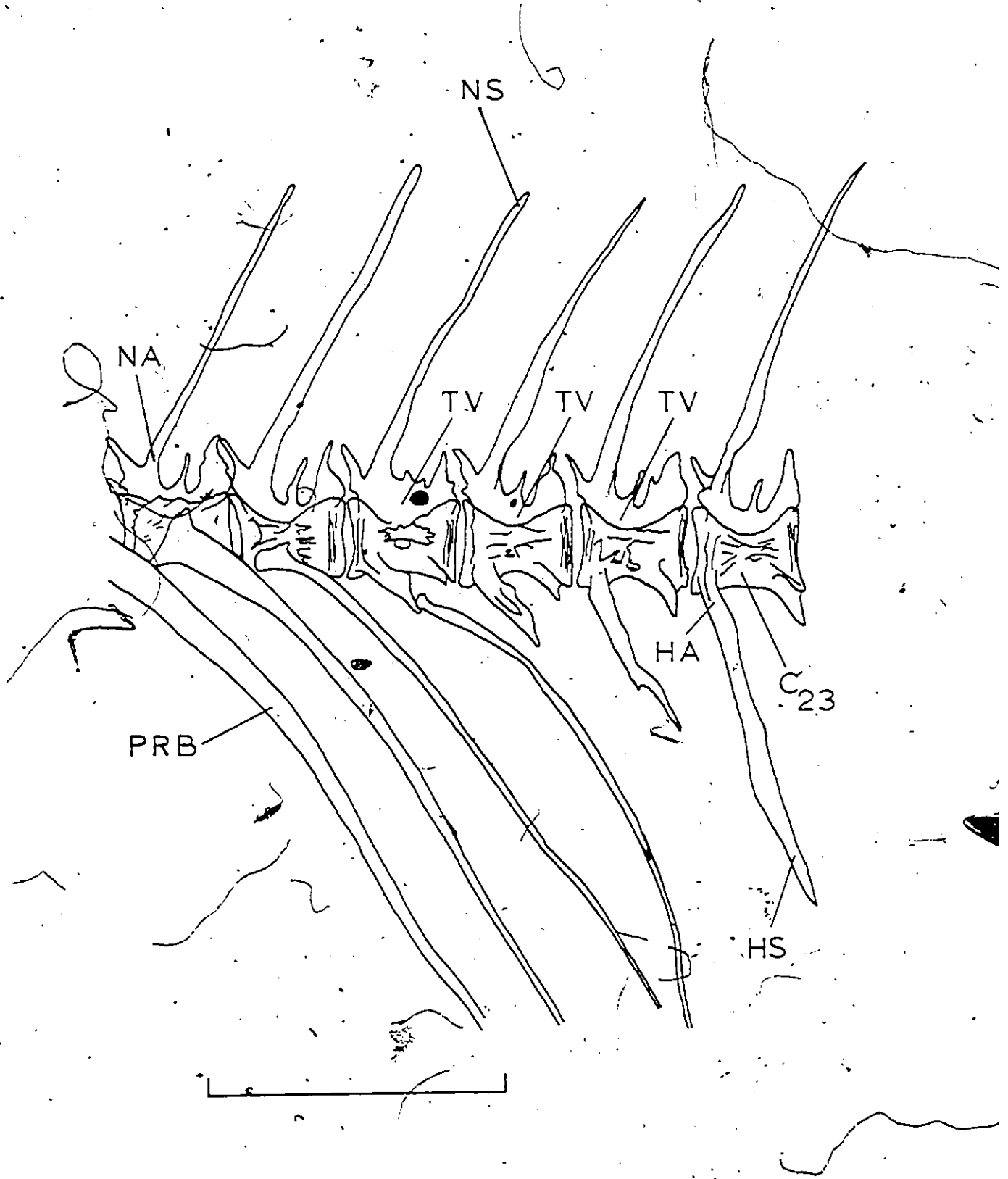


Figure 38. Lateral and posterior views of caudal vertebrae.

Scale 0.5 cm.

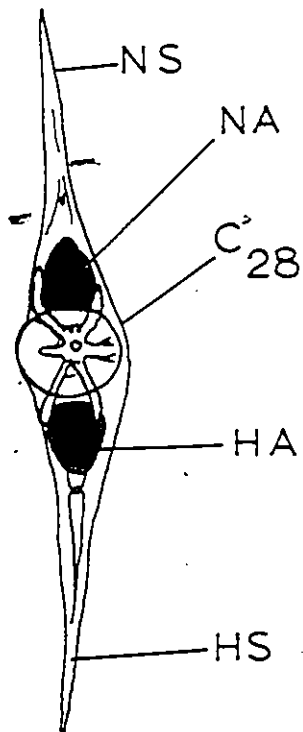
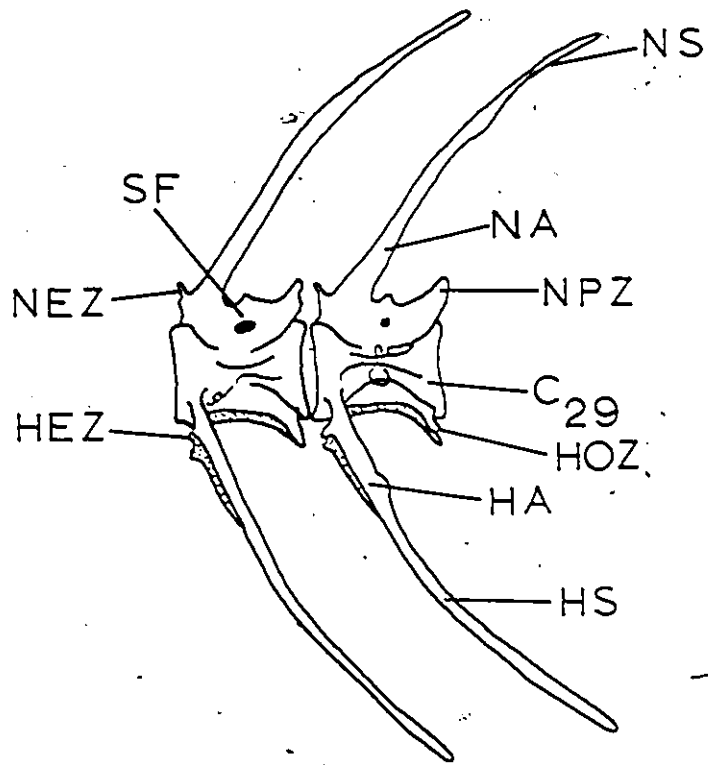
C₂₈ and C₂₉: twenty-eighth and twenty-ninth centra,

HA: haemal arch, HEZ: haemal prezygapophysis, HOZ:

haemal postzygapophysis, HS: haemal spine, NA: neural

arch, NEZ: neural prezygapophysis, NPZ: neural

postzygapophysis, NS: neural spine, SF: spinal foramen.



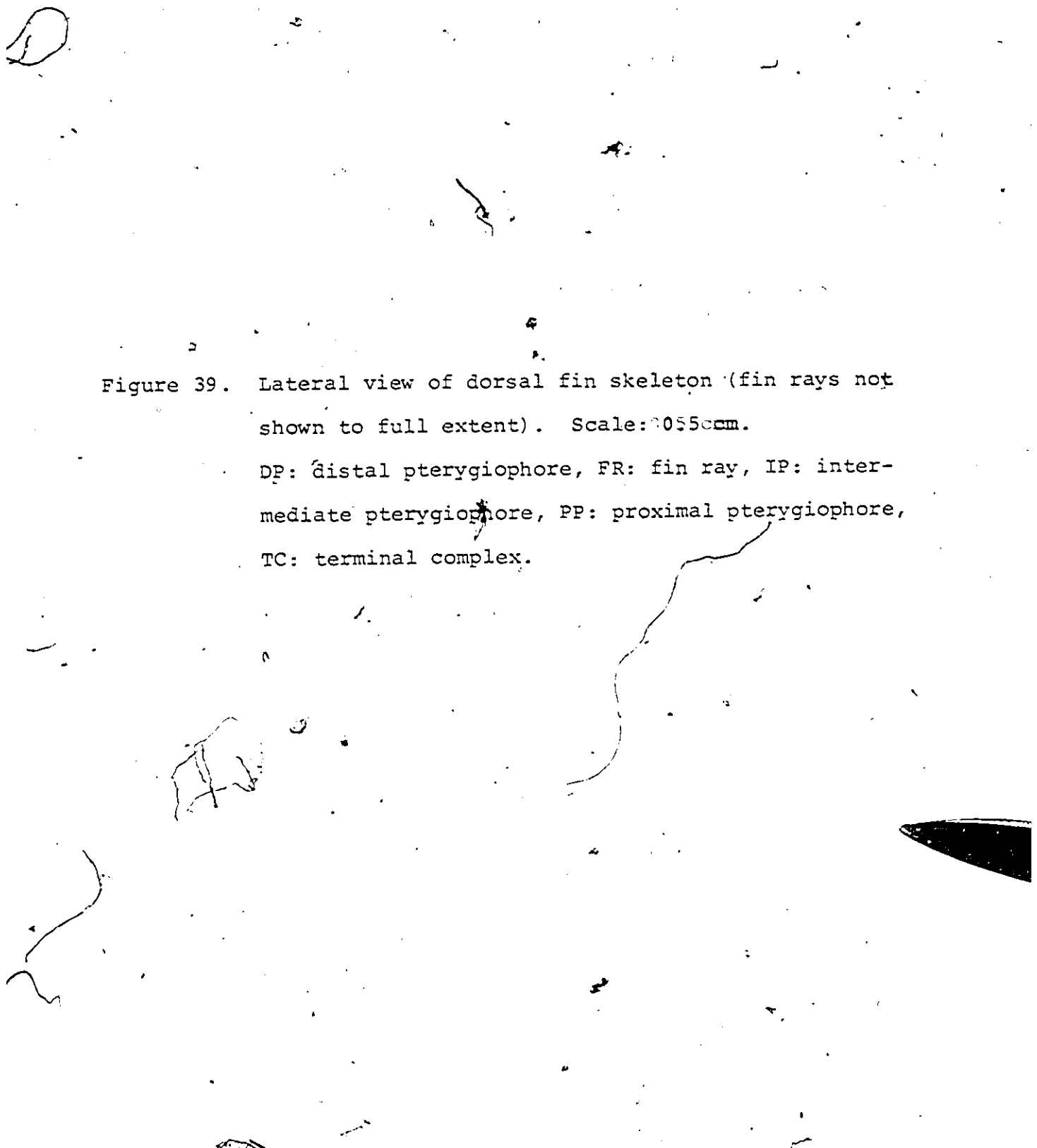


Figure 39. Lateral view of dorsal fin skeleton (fin rays not shown to full extent). Scale: 0.55cm.

DP: distal pterygiophore, FR: fin ray, IP: intermediate pterygiophore, PP: proximal pterygiophore, TC: terminal complex.

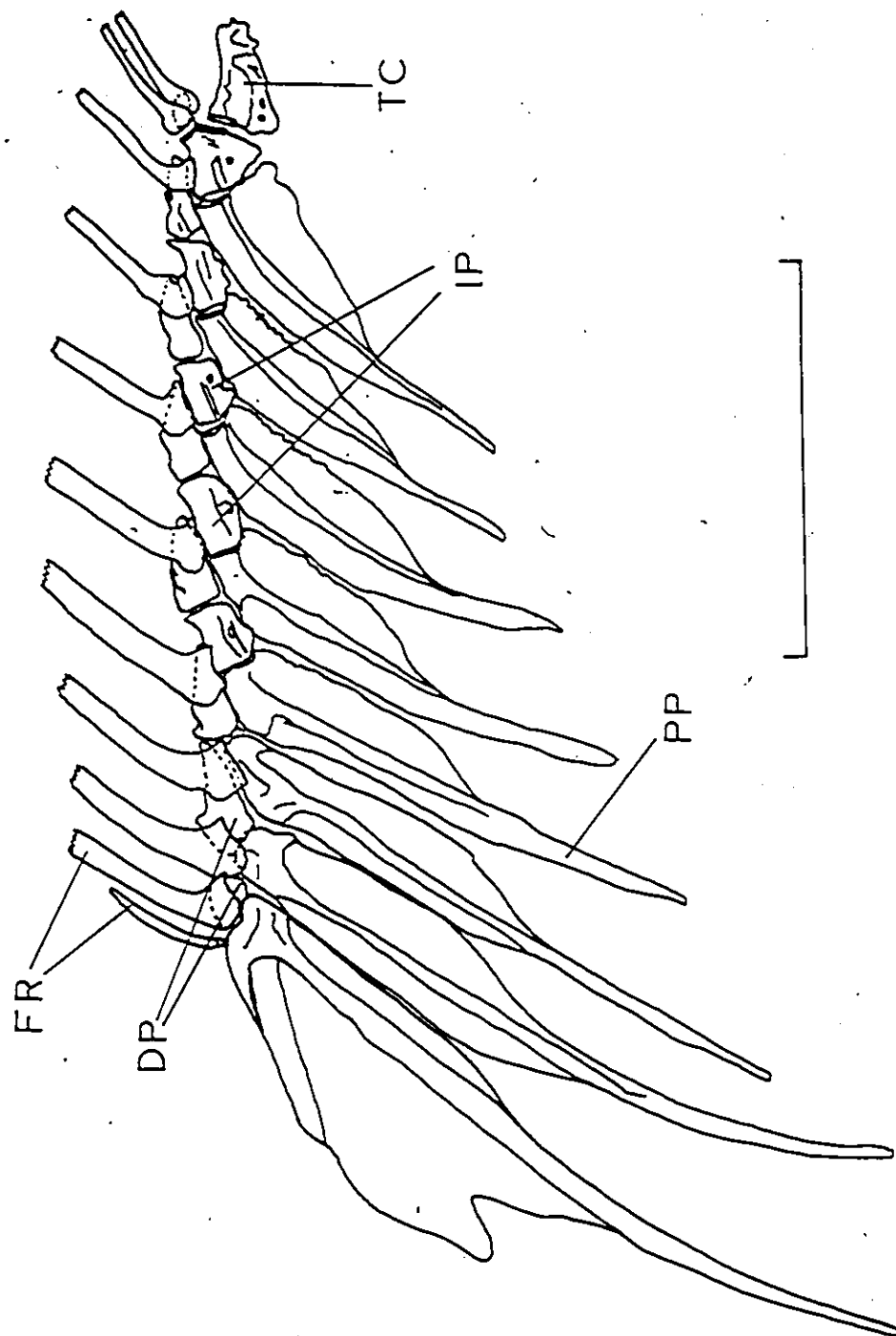


Figure 40. Lateral view of anal fin skeleton (fin rays not shown to full ventral extent). Scale: 0.5 cm.
DP: distal pterygiophore, FR: fin ray, IP: intermediate pterygiophore, PP: proximal pterygiophore, TC: terminal complex.

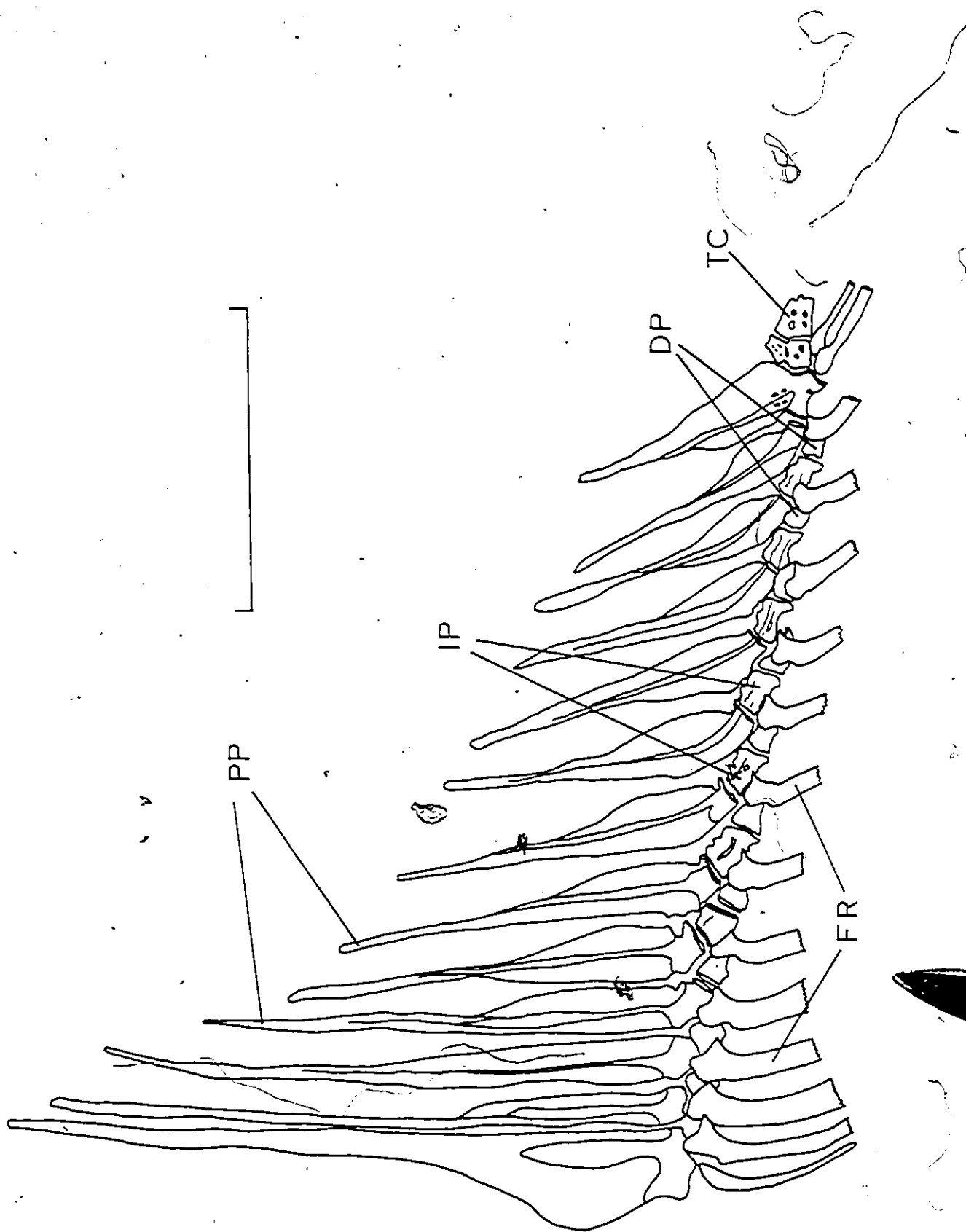




Figure 41. Lateral view of caudal fin skeleton (fin rays removed); dorsal view of left half of pelvic girdle (fin rays removed). Scale: 0.5 cm.

BPT: basipterygium, EP: epural, HS: haemal spine, HY₁ and HY₆: first and sixth hypurals, NS: neural spine, PC₄: fourth preural centrum, PUC: fused first preural centrum and first and second ural centra, UD: fused first and second urodermals, VR₁₋₃: pelvic radials₁₋₃.

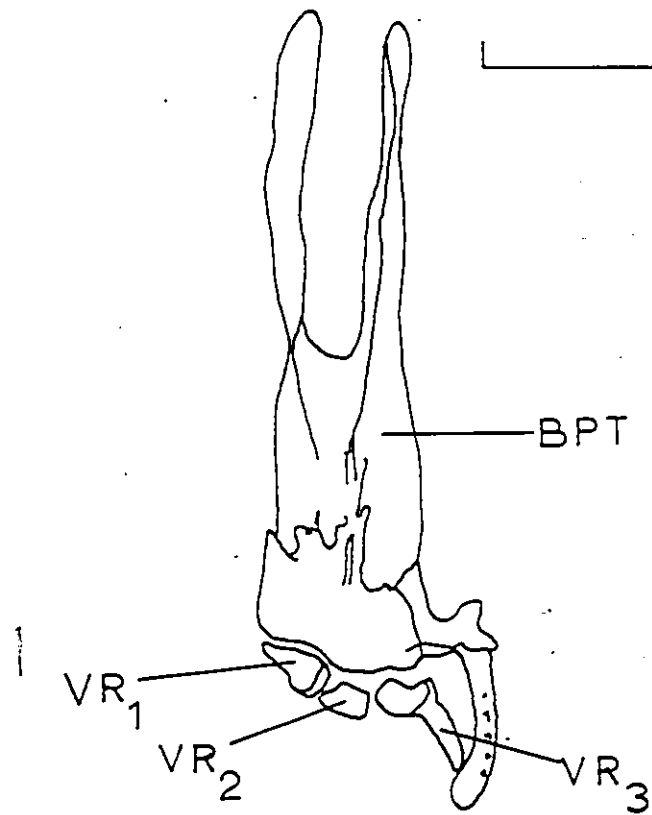
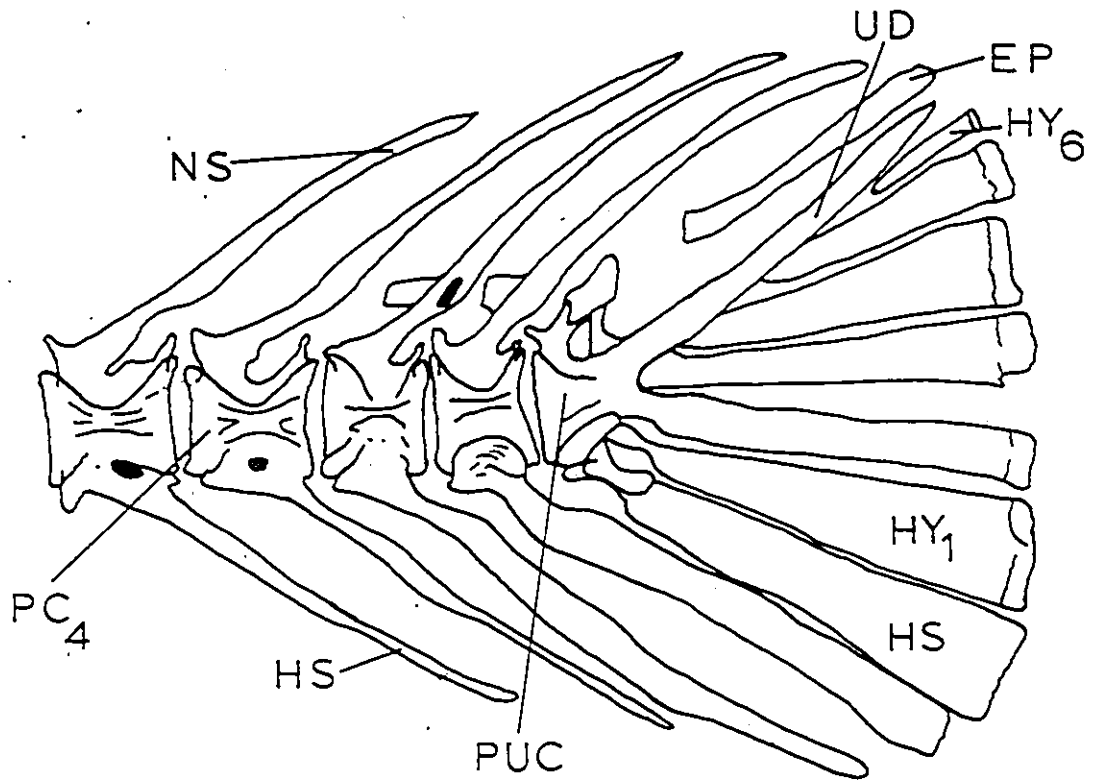


Figure 42. A- Anterior view of the first proximal anal pterygiophore; B, C and D- lateral views of three right supracleithra (note variation in lateral tube development). C has the posttemporal attached (PT)
Scale: 0.5 cm.

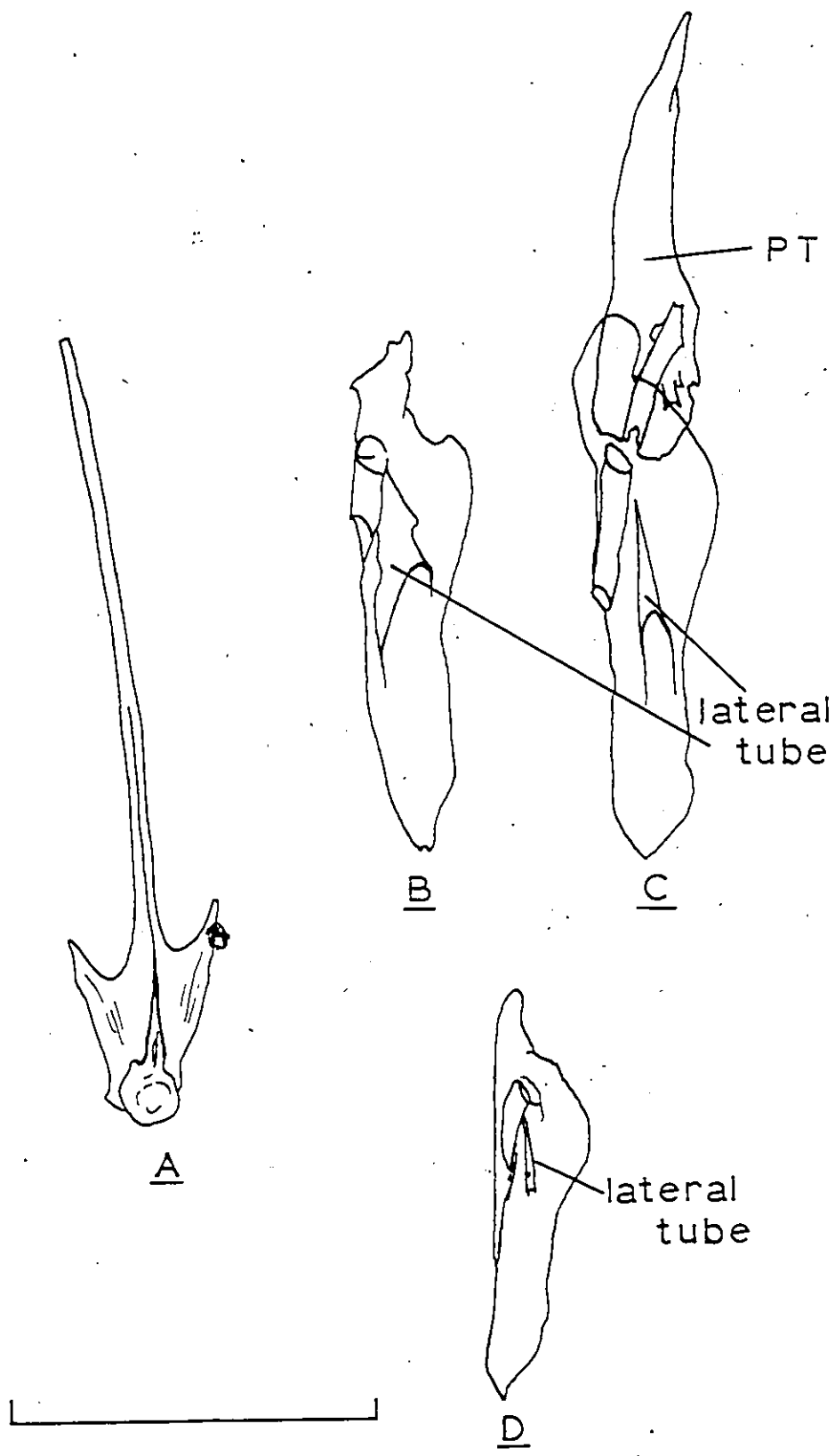
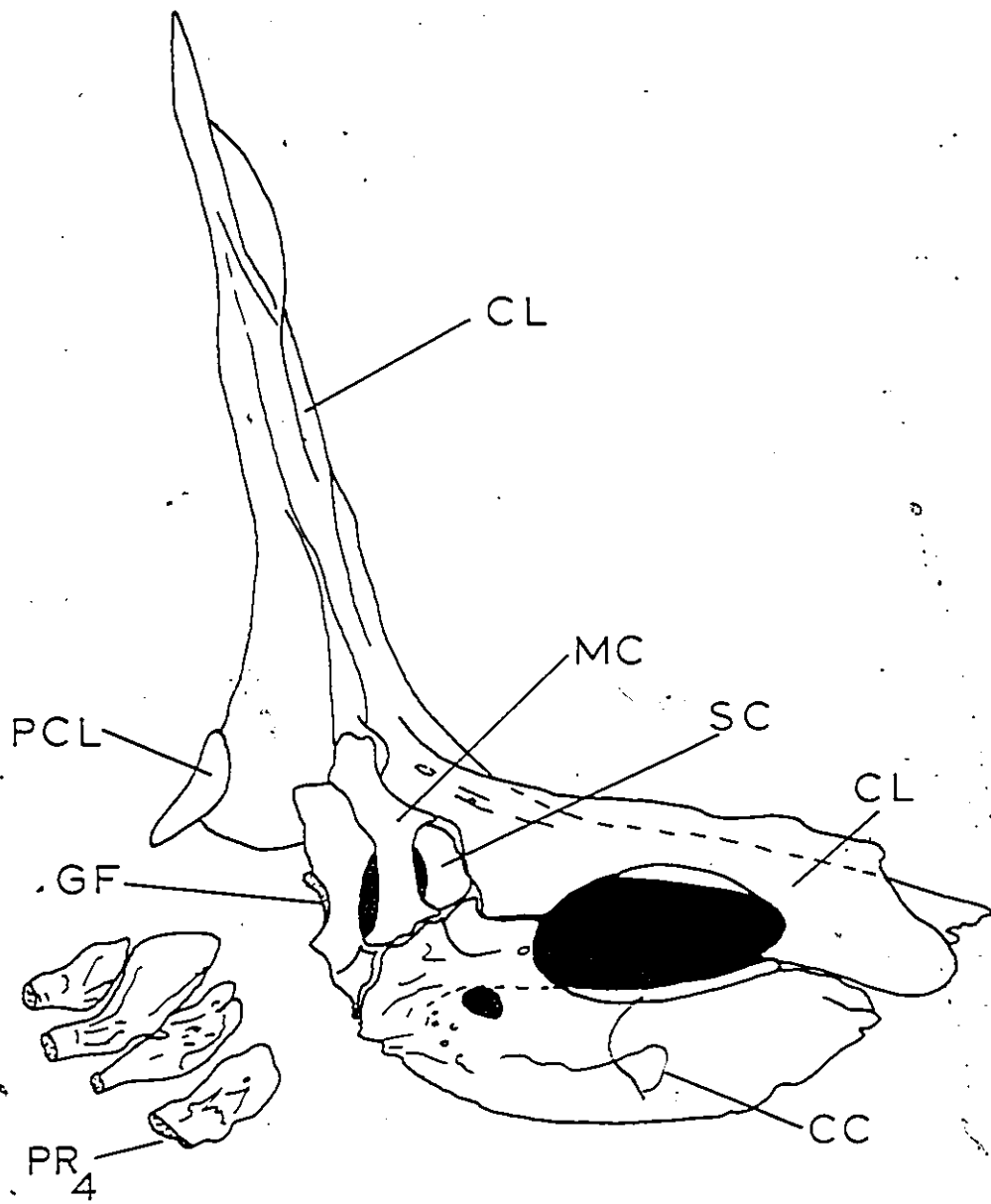


Figure 43. Mesial view of left pectoral girdle (fin rays removed), pectoral radials displaced postero-ventrally). Scale: 0.5 cm.

CC: coracoid, CL: cleithrum, GF: glenoid fossa,
MC: mesocoracoid, PCL: postcleithrum, PR₄:
fourth pectoral radial, SC: scapula.



Comparative osteology of North American cyprinid genera

Analysis of the osteological descriptions of the genera showed that articulations, relative positions and general shape of the bones were similar to those described for Notemigonus crysoleucas and so are not reiterated here. Many potential characters were found to be intra- or inter-specifically variable and their utility at the generic level was therefore limited, particularly where only a few specimens or species of a genus were available for study. They may be useful when analysing smaller groups of genera where it is more feasible to examine large and varied series of specimens. The analysis was further complicated by the size range of specimens studied. It was difficult to compare young fish of one genus to older fish of another genus because of size-related variations.

Therefore characters, whose variation was intra- or inter-specific or possibly size dependent, are referred to here by an exemplar genus or genera. Other, potentially more useful characters, are listed by state in all available genera.

For brevity characters are listed by genus alone without specific names unless intrageneric variation is being discussed. Data accuracy is limited by specimen availability (see abbreviated listing of alizarin preparations) e.g. "Dionda" refers strictly to D. episcopa but "Rhinichthys" includes all recognised species.

For the genera Gila, Ptychocheilus, Clinostomus, Richardsonius, Semotilus and Margariscus the reader is referred to Uyeno (1961) and Buhan (1970). Specimens of these genera were only re-examined to confirm data of use in the character analysis. The genera Evarra and Stypodon were not available for osteological examination.

CRANIAL SKELETON

OLFACTORY REGION

Supraethmoid (Figure 44).

The supraethmoid may be longer than wide, length and width may be approximately equal, or width may exceed length. Intraspecific variation in this character is noted in Notropis and elsewhere there is some evidence that these proportions are size dependent. The dorsal surface is concave in the anterior mid-line except in Orthodon and less strongly in Xystrosus where it is convex. Posteriorly the supraethmoid articulates jaggedly with the frontal and usually two postero-lateral wings are developed. These wings are poorly developed or absent in e.g. Hemitremia, Macrhybopsis, Moapa, Opsopoeodus, and Phenacobius probably because these are small specimens.

Ethmoid (Figure 44)

The ethmoid usually has a large horizontal plate though it appears to be small in e.g. Campostoma, some Eremichthys, Eriocymba, Exoglossum, Extrarius, Hybognathus, Macrhybopsis, Meda, Pimephales and Yuriria. Without a series of measure-

ments such relative characters are difficult to assess and this particular character was not studied further. The space beneath the supraethmoid in the ethmoid is generally small but is large in e.g. Mylocheilus, some Notropis, Orthodon, Parexoglossum, and Xystrosus. One distinctive character of the ethmoid is that the lateral walls meet or partially meet in the mid-line when viewed posteriorly in Chrosomus (variably), Dionda, Ericymba, Erimystax, Extrarius, Hybognathus (partially), Hybopsis, Iotichthys, Macrhybopsis, Nocomis (partially), some Notropis, Opsopoeodus, Oregonichthys, Phenacobius, Pimephales (variably), Relictus, Rhinichthys, and Tiaroga. In other genera the walls may be widely separated or approach each other in varying degrees.

Lateral ethmoids (Figure 45).

The lateral ethmoid articulates with the prevomer and its lateral plate (or prefrontal) with the supraorbital. The latter articulation is variably present or absent in Agosia and Rhinichthys, and is absent in Ericymba, Exoglossum, Moapa, Parexoglossum and Tiaroga. The orbitosphenoid sends a mesial process under the lateral ethmoid, e.g. in Acrocheilus, Algansea, Couesius, Hesperoleucus, Hybopsis, Meda, Mylocheilus, Mylopharodon, some Nocomis, weakly in Notemigonus, some Notropis, Oregonichthys, Orthodon, Phenacobius, Pogonichthys, Relictus, Rhinichthys evermanni and Yuriria. The process may act as a strengthening device at the junction of the orbitosphenoid and lateral ethmoid. Its development varies from strong to weak and is often little more than a flexure in the two bones mesially such that the orbitosphenoid projects anteriorly.

Preethmoid (Figure 45).

Buhan (1974) has described and discussed the systematic significance of the development of the lateral preethmoid in some N. American cyprinids. It is usually present but not fused to the mesial preethmoid. In size it varies from a minute ossification to a large structure occupying most of the preethmoid cornua, e.g. in Agosia. The lateral and mesial preethmoids appear to be fused in Dionda and variably in Erimystax and Rhinichthys. No lateral preethmoid is seen in Hemitremia, Margariscus, Meda, Mylopharodon, Orthodon, Paraxoglossum, Plagopterus, Semotilus, Xystrosus, and Yuriria and its presence is interspecifically variable in Clinostomus, Nocomis, Notropis and Richardsonius (see Buhan, 1974) and intraspecifically in Notemigonus.

The prepalatine of Weisel (1955b) is the lateral preethmoid.

Kinethmoid

The kinethmoid is invariably present as a comma-shaped bone, dorsally cleft. It is not compared in detail between the genera.

Nasals

The nasal bones enclosing the anterior part of the supraorbital sensory canal are usually developed as a tubular structure over the nostril. They are not always fully ossified.

Prefrontals

The prefrontals are mesially fused to the lateral ethmoid and are dealt with under that heading.

Prevomer (Figure 45).

The prevomer is a triangular-shaped bone with a pointed, rounded or weakly-jagged posterior end, weak or strong lateral processes and with the two preethmoid cornua anteriorly separated by a curved notch. The notch is deeply concave, more rarely shallow, e.g. in Plagopterus. The prevomer is longer than broad usually, but only slightly in e.g. Acrocheilus, Eremichthys, Lepidomeda, Platygobio, Orthodon, while in Relictus length and breadth are approximately equal and in Iotichthys breadth exceeds length.

ORBITAL REGION

Lachrymals (Figures 47 and 48).

The lachrymal is generally similar to that of Notemigonus with minor variations in shape and sharpness of angles.

However in Brimystax, Extrarius, Macrhybopsis, Nocomis, Phenacobius, Platygobio, Rhinichthys, and weakly in Hybopsis, Plagopterus and Tiaroga it is an elongate bone with the canal bone terminating ventrally rather than on the posterior edge. The suborbital bones also commence ventral to the posterior edge of the lachrymal in these genera and are split into

several small bones. An elongate lachrymal appears to be associated with an elongate snout.

Second to sixth suborbitals (Figures 47 and 48).

The suborbital bones are generally similar to those in Notemigonus. Evident variation in shape and development could be related to specimen size as could the presence and degree of ossification of the dermosphenotic. Canal bones are usually fused to the underlying plate but the plates may be absent or canal bones not fused in some small species, e.g. Chrosomus, Iotichthys. Occasionally the suborbital bones posterior to the lachrymal were divided into a series of small bones rather than just five e.g. in some Moapa there might be up to 11 post lachrymal bones. The suborbitals of Algansea and Xystrosus are unusual and characteristic (see also Gila crassicauda in Miller, 1963b). The lachrymal in them is followed by 3 to 6 small bones, a large bone ($SO_3?$), $SO_4?$, $SO_5?$, the dermosphenotic ? or SO_6 , plus an additional 1 or 2 bones. In Xystrosus the bone tentatively designated as SO_5 touches the supraorbital and in both genera much of the lateral temporal fossa is roofed over by the posterior members of the suborbital series. The unique canal system and associated bones of Ericymba have been described by Hoyt (1972).

Supraorbitals (Figure 47).

The supraorbital bones show marked variation in shape,

size and position between individuals of a species. In general they are rounded, oval and antero-posteriorly elongated. Each supraorbital lies lateral to the frontal process of the orbit, either free or in a frontal notch. Anteriorly large supraorbitals project in front of the frontal and articulate with the lateral ethmoid.

Scleral bones

The scleral bones are usually similar in shape to those described for Notemigonus except in some Macrhybopsis and rarely in Algansea the posterior one is smaller than the anterior one and the lateral edge of either one could be rounded instead of truncate, e.g. in some Exoglossum.

Orbitosphenoid

The orbitosphenoid bears a moderate ventral interorbital septum in most genera but it is small in Macrhybopsis, Nocomis, Plagopterus, Platygobio, Relictus, Rhinichthys, Tiaroga and Xystrosus and is weak to moderate in such genera as Algansea, Exoglossum, Orthodon and Phenacobius. The heads of these genera show varying degrees of dorso-ventral depression, at least anteriorly, a condition probably acquired independently in some of them. In Mylopharodon there is an evident posterior spike developed on the orbitosphenoid, lateral to the pterospheno-

Pterosphenooids

Both the pterosphenooid and orbitosphenoid bear ridges on

their lateral surfaces, sometimes developed as distinct wings in large specimens or weak to absent in small specimens. Wings are seen in Mylocheilus, Nocomis, Orthodon and Platygobio. Mesially the pterospheneoids do not meet except in some Erimystax rarely in large Notropis, Orthodon, and Xystrosus.

Frontals (Figures 47 and 50).

The sutures between each frontal are simple or complex but both extremes grade in to each other in certain individuals and species rendering assessment of character states difficult if not impossible. The major curve in the suture appears to be over the epiphyseal bar and most complex sutures are found in larger specimens. Length in interorbital width is variable but size related variation may account for some of the differences observed. Most genera fall in the category where width is less than length i.e. $\frac{1}{2}$ - $\frac{3}{4}$ in 1, but some show approximately equal length and width, e.g. Campostoma, some Chrosomus, Exoglossum, Mylopharodon, Orthodon, Platygobio, or length is 1 - $1\frac{1}{2}$ times in width, e.g. Macrhybopsis, Oregonichthys, Parexoglossum and Yuriria, or is 2 or more in width, e.g. some Chrosomus, Ericymba, Erimystax, Moapa, Pogonichthys, and Tiaroga.

Usually the supratemporal-intertemporal anteriorly meets the frontal but in some genera the autosphenotic intervenes, e.g. in Algaea monticola, Chrosomus, some Couesius, Dionda, some Erimystax, Extrarius, some Hemitremia, Hybognathus (not

seen in H. hankinsoni) Hybopsis, Iotichthys, some Lavinia, Macrhybopsis, some Nocomis, some Notropis, Opsopoeodus, Oregonichthys, large Orthodon, some Pimephales, some Placopterus, Platygobio, Pogonichthys, some Rhinichthys, some Tiaroga and some Yuriria. The condition is intra- and inter-specifically variable and thus a poor character at the generic level.

The epiphysial bar is visible dorsally under the frontal. It is most commonly arched but is straight in Agosia, some Chrosomus, Hesperoleucus, some Macrhybopsis, Meda, Moapa, some Notropis, Opsopoeodus, some Pimephales, Rhinichthys, and Yuriria. The bar is intraspecifically variable in width. In large Platygobio it is spread widely over the inner skull roof and does not form a discrete bar.

OTIC REGION

Supraoccipital

The supraoccipital is generally similar in the species examines. There are variations in size and shape of the crest but these are size related in some if not all species.

Parietals

The parietals suture with each other and the frontal simply or with moderate flexures. The suture with the supra-temporal-intertemporal is usually simple or slightly wavy. Iotichthys is unique in that a sub-rectangular portion of the parietals and frontals tapering posteriorly is not ossified.

Medial extrascapulars

These are dealt with separately under the section on head canals.

Autosphenotics

The autosphenotic has a large square or round tipped lateral process posterior to the orbital wing of the frontal. The process is always present and well developed.

Autopterotics

The autopterotic process is usually well developed and pointed except in Ericymba, Iotichthys and Opsopoeodus where it is weak.

Prootics

The prootics are similar to those observed in Notemigonus but were not examined in detail.

Tecta synotica and epiotics

These were not examined in detail.

Opisthotics

The opisthotic is best developed in large fish and is weak to absent in small fish. It generally overlies the autopterotic-exoccipital suture but may be restricted to the autopterotic in small fish. Its presence and position seem to be size related and these characters were not pursued further.

Exoccipitals

The exoccipital bears a thin spiky or rounded process projecting mesially over the vagal foramen in Acrocheilus, variably in Algansea, Chrosomus neogaeus, some Couesius, Dionda, Eremichthys, Exoglossum, weakly in Extrarius and Hespe-
roleucus, Lepidomeda, Moapa, Mylocheilus, Opsopoeodus, Phenacobius
uranops, Rhinichthys cataractae and Yuriria.

Supratemporal-intertemporal complexes

The anterior junction of each complex with the frontal has been discussed under the latter bone.

Bullae and semicircular canals

The semicircular canals were not examined. The bullae are present in the positions indicated for Notemigonus, although there are some variations in relative size which were not pursued.

Otoliths

The otoliths may prove to have useful characters but an adequate comparative survey could not be made since a large proportion of the available specimens lacked discernible otoliths (acidic formalin may have caused their disintegration). In those specimens with observable otoliths the basic structure of each one was similar to that described by Buhan (1970). The serrations of the margin of the asteriscus are intraspecifically variable.

Head canals

The supratemporal canal is usually complete or has a small gap at the mid-point. The presence or absence of this gap is intra- and inter-specifically variable. The canal is interrupted at various points in Chrosomus.

The preoperculomandibular canal usually terminates on the preopercle level with the lower half of the eye. In Agosia, Chrosomus, some Hemitremia, Iotichthys, Macrhybopsis, some Notropis, Opsopoeodus, Phenacobius, Pimephales vigilax, some large Platygobio, Rhinichthys, and Tiaroga it is below the lower edge of the eye while in Mylopharodon, Notemigonus and Orthodon it is level with the upper half of the eye. The position of the anterior end of this canal also varies. On the dentary it usually ends about half way from the ascending process to the tip but may be anterior or posterior to this point. The position is intra- and inter-specifically variable.

The infraorbital or suborbital canal ends at the antero-dorsal corner of the lachrymal but it is posterior to this on the dorsal edge in Erimystax and Phenacobius and is at the mid-point of the anterior edge in Hybognathus hayi and Xystrosus.

The supraorbital canal ends anteriorly near the anterior edge of the nostril as a free-lying nasal bone. It may be poorly ossified in small specimens. Posteriorly it may terminate on or near the posterior edge of the frontal, on the parietal with a weak lateral terminal flexure, or meet the

supratemporal canal. The extent of the canal varies between and within species and even a singular individual may have its left and right canals ending at different levels.

BASICRANIAL REGION

Basioccipital (Figure 55).

The basioccipital bears a flat or concave masticatory plate which is usually pitted. In Phenacobius the plate is convex in some individuals. Anteriorly a process is developed from the plate ventral to the aortic canal in some Acrocheilus, weakly in Agosia, rarely in Algansea, in Campostoma, Chrosomus oreas, Dionda, Eremichthys, Hybognathus (not in a single specimen of H. hayi), Lavinia, Moapa, Mylocheilus, Mylopharodon, a few Notemigonus, Notropis umbratilis and Orthodon (curling dorsally). The pharyngeal process of the basioccipital is parallel to the body axis and its posterior end is rounded or angular. In Lavinia the process is noticeably slim and pointed.

Parasphenoid (Figure 54).

The parasphenoid has wings on its shaft at a right angle or obtusely, or more rarely at an acute angle to the shaft. Examples of the latter are Erimystax, Exoglossum, Mylopharodon, and Orthodon. Fusions are not seen but the wings are delicate and closely associated with the prootic such that they are easily torn when the parasphenoid is detached from the skull. Some fusion may occur in this region. There is usually a

dorsal ridge between the parasphenoid wings often with a dorsally-directed spike. The spike is absent and the ridge weak to absent in Agosia, Erimystax, Extrarius, Macrhybopsis, Meda, some Notropis, Opsopoeodus, Plagopterus, Platygobio, Relictus, and Xystrosus and a ridge is present without a spike in Acrocheilus and Hybopsis. A ventral keel is well developed in Campostoma, Dionda, Erimystax, Hybognathus, Iotichthys, Lavinia, some Notropis, Orthodon, some Pimephales, Pogonichthys, Xystrosus and Yuriria between the wings but other genera show ridges in this region and keel development may well be independent. In some specimens of Dionda and Exoglossum, in Macrhybopsis, Moapa, some Opsopoeodus, Phenacobius, Pimephales a small foramen is seen near the anterior edge of the wings. (? for the pseudobranchial artery). Other genera may have a notch in this position but both the foramen or notch are not present in all individuals of a species.

OROMANDIBULAR REGION

Premaxillaries

The premaxillaries are similar in all the genera. Variation is limited to its length and the height of the ascending process. Such features are at least interspecifically variable, e.g. in Notropis and the height of the ascending process is intraspecifically variable in Agosia. The symphysis

is simple except in large specimens, e.g. Orthodon where some thickening or a jagged surface is apparent. The ascending process may be straight or curved anteriorly a little at the tip. These conditions are intra- and inter-specifically variable. In species where the anterior head region is compressed antero-posteriorly the premaxilla is shortened and the horizontal arm flexes dorsally at its mid-point e.g. in Phenacobius. Phenacobius also has a jagged margin to the antero-ventral portion of the horizontal arm.

Maxillaries

The ascending process of the maxillary is positioned about mid-way along the bone although in some genera it may be obviously posterior e.g. Acrocheilus. The antero-dorsal corner of the process usually projects anteriorly, with the anterior edge concave, such that the process is slightly antorse. Alternatively this projection is absent or there is a slight posterior projection so that the process is retrorse. The process is slightly retrorse in Campostoma, Erimystax, Extrarius, and some Rhinichthys. The dorsal margin of the processes is rounded, sloped posteriorly and directly to the posterior dorsal edge of the maxillary or has a posterior slope which then falls abruptly or concavely to the posterior dorsal edge of the maxillary. These conditions are intra- and inter-specifically variable, e.g. in Orthodon and Nocomis respectively. Posterior to the ascending process

the maxillary is less deep than anteriorly.

The relative lengths of the antero-lateral plate and the mesial rod in dorsal view vary. The rod is slightly to markedly longer in most genera (intraspecifically variable), rod and plate are equal in Erimystax, Exoglossum, Hybopsis, Nocomis, Paréxoglossum, some Phenacobius and the plate is longer in Extrarius. The angle of the rod is interspecifically variable, e.g. in Macrhybopsis gelida it is almost ventrally directed while in M. meeki it is almost horizontal.

On the ventral edge of the maxillary bone just posterior to the antero-lateral plate a small process is developed for ligament attachment. The process projects ventrally or is slightly above the ventral edge of the maxillary and projects laterally. The process is connected via a ridge to another process on or about the middle of the antero-lateral plate in Erimystax, Hybopsis, Macrhybopsis gelida, Oregonichthys, Tiaroga, and Xystrosus.

Mentomeckelians

The mentomeckelians are always present with a shape similar to that reported for Notemigonus.

Coronomeckelians

This bone is not too dissimilar in most genera from the condition reported for Notemigonus. Its shape is generally variable. In Dionda the vertical plate of the bone rises

above the angular anteriorly. This is also seen in the Asian genus Tribolodon but is not regarded as evidence for relationship. Many other genera of N. American cyprinids show varying development of this vertical plate and that it should rise above the angular in at least one genus is not unexpected.

Dentaries (Figure 46).

The dentaries bear an ascending process about the mid-point of the lower jaw. The arm of the dentary anterior to this process is short in Campostoma so the process is anterior to the mid-point. Conversely in Eremichthys, Exoglossum, Lepidomeda, Macrhybopsis, Meda, Parexoglossum, and Plagopterus the process is located posterior to the mid-point. The process may be vertical (in relation to the long axis of the lower jaw), slope anteriorly or posteriorly and this is intraspecifically variable, e.g. in Acrocheilus and Algansea. The posterior edge of the process is often concave so the process appears retrorse. In Phenacobius the process overlaps the angular posteriorly as this area of the jaw is much compressed and the posterior bones of the jaw are very short.

The preoperculomandibular canal is evident on the dentary and usually occurs on the angular also. It is poorly ossified on the angular in some specimens, e.g. Campostoma, Chrosomus, Oregonichthys, Parexoglossum or it is absent, e.g. in some Chrosomus, Dionda, Iotichthys (also absent from dentary), some Macrhybopsis, Opsopoeodus and Phenacobius (also absent from dentary), but this may be related to specimen size. In

Rhinichthys and partly in Extrarius the canal is on the retroarticular rather than the angular.

The anterior arm of the dentary is strongly curved mesiad and is plate-like and horizontal in genera with short lower jaws like Acrocheilus and Eremichthys. In Exoglossum and Parexoglossum the dentary and associated lower jaw bones are positioned ventrally on the head rather than laterally. The dorsal edge of the anterior arm is notched in certain genera, e.g. Notemigonus and Xystrosus but similar notches are variably present in other genera, e.g. Notropis. An antero-lateral foramen is present for the truncus mandibularis of nerve VII in the anterior arm. It is usually less than half way along the arm from the process to the dentary tip but is anterior to the mid-point in Chrosomus, Hybognathus hayi, Moapa, Mylopharodon, Nocomis, some Oregonichthys, Parexoglossum, Relictus and Tiaroga and is about mid-way in Ericymba, Hesperoleucus and Lepidomeda. The foramen position was variable in Eremichthys, Iotichthys, Notemigonus, Notropis, and Rhinichthys.

Articulars

The articulars are enclosed by the angulars and were not examined.

Retroarticulars

Each retroarticular is an irregular shaped bone ventral to the angular and posterior to the dentary. In small specimens

it may lie free but is usually closely associated with the neighbouring bones, though not fused. It may bear part of the preoperculomandibular sensory canal (see above).

Angulars (Figure 46).

The dorsal edge of the angular may be low posterior to the ascending process of the dentary, e.g. in Algansea, Hybognathus hankinsoni, Hybognathus nuchalis and Lavinia or it may be high, e.g. in Eremichthys, Exoglossum, Parexoglossum, and Phenacobius. It can be rounded or pointed, the latter particularly if it is high. Height of this dorsal edge is size dependent in Notemigonus and probably other genera.

The articulation for the quadrate is unique in some Exoglossum since it is orientated in a dorsal rather than a posterior position because the dorsal lip is weak to absent. In other genera the ventral lip is produced posteriorly and the dorsal lip is vertical or slopes slightly anteriorly sometimes with a slight posterior curl to the tip.

Autopalatines (Figure 45).

The autopalatine is a short bone with dorsal, mesial and lateral processes at its anterior end. Its size varies with the individual and also with the degree of compression of the snout region. The mesial process is reduced in Exoglossum and Parexoglossum and is located at the mid-point of the bone. There is a dorsal depression and/or spike in

all genera on the posterior half of the bone and it is best developed as a strong spike in Eremichthys.

Endopterygoids

The shape of the endopterygoid is variable both intra- and inter-specifically but adheres to the general form outlined under Notemigonus. The bone may be perforated behind the socket in e.g. Acrocheilus, Hemitremia, and Moapa and it may project over the posterior end of the autopalatine in e.g. Chrosomus, Hesperoleucus, Phenacobius and variably in Pimephales. The bone is compressed antero-posteriorly in Exoglossum being a vertical sub-oval shape in large fish but a horizontal sub-oval shape in small fish. The size of the endopterygoid relative to the metapterygoid is usually the same or larger. It is the same or smaller in Algansea, Dionda, Eremichthys, Erimystax, Hybognathus (not H. hayi), Moapa, Oregonichthys, Orthodon, Relictus, Rhinichthys and Tiaroga.

Ectopterygoids

The ectopterygoid is usually oval in shape but may approach a triangular or rectangular shape. It projects under the autopalatine in e.g. Campostoma, Erimystax, and some Rhinichthys, and is often weakly developed i.e. the anterior part is not ossified, in Chrosomus neogaeus, Eremichthys, Exoglossum and Hemitremia. In Mylopharodon much of the ventral half the bone lies mesial to the quadrate,

more than in any other genus.

Quadrates

The quadrate is usually smaller than the endopterygoid and larger than the ectopterygoid. In Algansea and Nocomis it may be larger or smaller than the ectopterygoid and in Exoglossum it is almost as large as the endopterygoid. The dorsal and posterior edge of the quadrate is usually a curve but in e.g. Algansea and Xystrosus there is an evident postero-dorsal angle and in Macrhybopsis meeki it is notched along the posterior edge. There is also great variation in the form of this edge in Notropis where it may be curved, vertical or even concave. Rarely the quadrate may fuse with the symplectic e.g. in Rhinichthys atratulus.

Metapterygoids (Figure 54).

The metapterygoid is characterised by two dorsal wings a weak postero-lateral one and a more dorsally elongate antero-mesial one. The former often appears as a continuation of the dorsal strut. There is a smaller ventral or ventro-posterior strut. In Acrocheilus these struts are not clearly defined and there could be a single large strut extending over much of the posterior edge of the metapterygoid. A single postero-ventral strut is the only one seen in Campostoma, Eremichthys, Extrarius, Macrhybopsis, Nocomis, Pimephales, Platygobio, Rhinichthys and Tiaroga. The struts in, e.g.

Ericymba, are close together and almost parallel horizontally, while in Parexoglossum the struts are directed ventrally at the postero-ventral corner. The mesial wing may be pointed or rounded but this is intra- and inter-specifically variable along with the height e.g. in Pimephales. The lateral wing is weak to absent in Chrosomus and the mesial wing may be low and bear a jagged edge. The lateral wing is also weak in Couesius and it may be continuous with the mesial wing without the normal cleft between them. It is also continuous in some Notemigonus. In Platygobio the lateral wing is a strong spike directed antero-dorsally and the mesial wing is low and hardly developed.

HYOID REGION

Opercula

The operculum is very similar in all the genera studied. Proportional differences in breadth and depth are evident but these were not examined in detail. The shape of the operculum in Notropis species for example varied from deep and narrow to shallow and square. Larger specimens show more elaborate strengthening struts radiating from the point of articulation with hyomandibular. The operculum normally possesses a produced antero-dorsal corner, a convex or more rarely straight anterior edge, a sharp antero-ventral corner, a convex ventral edge, a rounded postero-ventral corner

(usually greater than 90°), a dorsally concave posterior edge, a rounded or sharp postero-dorsal corner and a straight or concave dorsal edge. The latter is individually variable and may rarely be convex, e.g. in Hybognathus hayi. The postero-ventral corner may be less than 90° , e.g. in Algansea monticola, Chrosomus, Hemitremia, Hesperoleucus, Hybognathus. In Iotichthys the antero-dorsal corner is only moderately produced and is square cut.

The most significant character of the operculum was the presence or absence of a tubular canal through the antero-dorsal corner for the preoperculomandibular canal. This was found in Notemigonus only and is discussed further in the character analysis.

Preopercula

The relative lengths of the vertical and horizontal rami of each preoperculum vary from equal to vertical or horizontal longer. These conditions are intra- and inter-specifically variable. The preoperculomandibular sensory canal is always present and usually fused to the preopercle. It extends to or almost to the tip of the vertical arm or ramus in most genera while in Agosia, Campostoma, Chrosomus, Dionda, some Iotichthys, some Notropis and Opsopoeodus it extends half way or less up the vertical arm. In Hemitremia, Hybognathus (not H. hayi), Phenacobius, Pimephales and Rhinichthys, the extent is one half to three quarters up the vertical arm. Occasionally the canal is not fused to the

preopercle, e.g. in some Chrosomus eos, Relictus and young Tiaroga. The unusual and unique canal system of Ericymba has been described by Hoyt (1972). The interior angle between the two arms of the preopercle is often expanded by a sheet of bone but this is interspecifically variable, e.g. Erimystax.

Subopercula

The suboperculum also shows proportional differences between species as with the operculum but these are not considered in detail here. The dorsal edge is usually straight or concave, rarely convex, e.g. in some Extrarius, and the ventral edge is convex curving up to a rounded posterior end. A rounded antero-ventral corner is usually found and the antero-dorsal corner is produced as a slim rounded or pointed process. This process is intraspecifically present or absent, e.g. in Algansea, Eremichthys, Pimephales. In Exoglossum it can be orientated vertically or postero-dorsally, with or without a forked tip. In addition the posterior end of the suboperculum is notched in Exoglossum.

Interopercula

The relative lengths of the interopercle and subopercle can be equal or either can be longer. Relative lengths were very variable, e.g. in Pimephales, both intra- and inter-specifically. The dorsal arm was weak to absent in Agosia, Campostoma, Ericymba, Erimystax, Macrhybopsis, Meda and particularly in Phenacobius where the bone was straight.

Branchiostegals

There are almost invariably three branchiostegals on each side of the head, rarely four in, e.g. a population of Notropis heterolepis (Scott and Crossman, 1973). The branchiostegals are most often widest at their mid-point and may taper abruptly distally. Occasionally the proximal ends are widest and more rarely the distal tip, e.g. the first branchiostegal of Platygobio. Position of maximum width is intra- and inter-specifically variable e.g. in Notropis, Pimephales, and Relictus. The distal tip of the first branchiostegal is usually pointed while the tips of the first and second are more rounded. They may all be pointed, e.g. in Dionda and Hybognathus, or all rounded, e.g. in Eremichthys, Exoglossum and Hesperoleucus. The tips may also be jagged in some genera, e.g. Moapa, and there is a tendency to this condition in the Plagopterini. Various combinations of rounded, pointed or jagged tips is seen in Notropis and such variation is also seen in other genera, some of it size dependent.

The length of the branchiostegals increases posteriorly such that the first was longest except in e.g. Agosia, variably in Lepidomeda, Notropis, Platygobio, and Tiaroga where the lengths are the same and in e.g. Eremichthys, Exoglossum where the first and second are about equal in length.

The second and third branchiostegals articulate with the ceratohyal and the first variously with the ceratohyal-epihyal

junction and the epihyal. The third branchiostegal may fork at its tip but this varies with the individual.

Hyomandibulars (Figure 49).

The general shape of each hyomandibular bone seems to be influenced by the head depth. In addition there are strong proportional differences between young and adult fish. A search was made for structural variations rather than proportional differences without much success. The anterior projection noted by Uyeno (1961) in Ptychocheilus and Gila robusta is not found elsewhere. The anterior wing of the hyomandibular is produced anteriorly at the point where it intersects in Eremichthys, Nocomis platyrhynchus, N. asper, N. leptcephalus, N. micropogon and Yuriria. In Platygobio the process is dorsal and just below the anterior condyle but may be regarded as the antero-ventral corner of the anterior wing since the hyomandibular is much curved in this genus.

The lateral ridge is usually weak or absent but it is strongly developed in Acrocheilus, Eremichthys, Exoglossum, Mylopharodon, variably in Notropis, Parexoglossum, Pimephales notatus, Platygobio, some Rhinichthys, and Xystrosus, and moderately in Erimystax, Hesperoleucus, Lavinia, and Nocomis. This character shows size variation in some genera, but not in small Parexoglossum where it is well developed, as well as interspecific variability.

The form and extent of the anterior wing is subject to

much size and individual variability. It may fall vertically and curve in sharply to the main shaft or it may curve gently from the anterior condyle to the shaft.

The posterior ridge is usually well developed postero-laterally and intersects a line drawn from the posterior tip of the opercular condyle to the posterior base of the shaft. (not in Hybognathus hayi, variably in Iotichthys, Macrhybopsis, Mylopharodon, Oregonichthys and Orthodon). Ventrally the ridge may form the posterior wall of the lateral hyomandibular foramen, e.g. in Chrosomus, Erimystax, Hybopsis, Notropis, or even the anterior wall in Parexoglossum, Platygobio and Xystrosus. Dorsally the ridge is developed as a dorsally directed spike level with the opercular condyle. It may be weak or ridge-like in some genera, e.g. Macrhybopsis, Plagopterus. The ridge is very well developed in Exoglossum and overlies the interopercle markedly.

The depth in width of the hyomandibular is usually about 2 in 1; 2-3 in 1 for Chrosomus, Erimystax, Hesperoleucus, Hybopsis, Moapa, some Notropis, Orthodon, Rimephales, and Xystrosus; and less than 2 in 1 for Eremichthys, Exoglossum, some Macrhybopsis, some Meda, some Nocomis, Parexoglossum, Plagopterus, Platygobio, Rhinichthys, and Tiaroga.

The lateral hyomandibular foramen is found low on the shaft at or about the level of intersection of the anterior wing or shaft i.e. about two thirds to three quarters down the shaft from the opercular condyle. In some individuals it

is elongate e.g. specimens of Coúsius, Hemitremia and Hesperoleucus. The mesial dorsal opening of the foramen is usually at the lower level of the opercular condyle in the middle of the hyomandibular. There are two mesial openings in e.g. Agosia, Lepidomeda, some Orthodon, separated by a strut and there may be several struts in Notemigonus. The foramen in Oregonichthys is overlain by a strut but there is no additional opening. In Ericymba the foramen opening is one third down from the opercular condyle and is noticeably lower than the condyle in e.g. Mylocheilus, Parexoglossum, and Yuriria.

The edge of the hyomandibular between the postero-dorsal condyle and the opercular condyle is incurved and is 1 in 3 to 4 of the depth of the hyomandibular. This proportion is 1 in 4 to 5 for Eremichthys, Macrhybopsis, Moapa, Mylocheilus, Nocomis and Yuriria and the lateral foramen is only one half to two thirds down the shaft from the opercular condyle (also in Lavinia, Macrhybopsis, Nocomis, Oregonichthys, Plagopterus, and Xystrosus). In some Hybognathus the foramen is almost one third down the shaft.

Symplectics

The symplectic may be arched or straight but this proved to be individually variable as did the presence or absence of notches and processes associated with complementary structures on the metapterygoid dorsal to the symplectic. In certain cases notches or processes on the symplectic are not matched

by complementary metapterygoid structures and the ventral edge of the metapterygoid is smooth. The length of the symplectic also varies intraspecifically and seems to be related to specimen size, e.g. in Platygobio.

Interhyals

Each interhyal is always present as a small rod either squarish, rectangular or rarely triangular in lateral view. These three shapes grade one into another.

Epihyals

Each epihyal is ventrally notched along with the ceratohyal at their junction but this notch is weak in e.g. Algansea, Chrosomus, Couesius, Erimystax, Meda, and Oregonichthys and is present or absent in e.g. Dionda, Macrhybopsis, Notropis, and Phenacobius.

Ceratohyals and upper and lower hypohyals (Figure 51).

The junction of the ceratohyal with the upper and lower hypohyals encloses a foramen in ventral view. A given species may possess only one or as many as three types of foramen in different individuals (see Uyeno, 1961 also). The foramen is not strongly evident in Hybognathus and Phenacobius where there are various small perforations in this region. The foramen may be present or absent in Oregonichthys.

Basihyal (Figure 50).

In dorsal view the basihyal is an elongate rectangle with a slightly to greatly expanded anterior end. The posterior end is rarely forked in some Acrocheilus. The anterior end may be expanded to a width up to five times that of the shaft in, e.g. Macrhybopsis, Meda, and other genera show varying degrees of expansion. However there is obvious individual and interspecific variation, e.g. in Chrosomus.

Urohyal (Figure 52).

The urohyal has two anterior processes which vary from short, e.g. in Mylopharodon and Nocomis, to long, e.g. some Notropis and Xystrosus with all intermediates. The most striking modification is found in Exoglossum and Parexoglossum where these processes are absent and a dorso-ventral foramen perforates the anterior end of the urohyal. In Phenacobius the anterior processes are short and stubby and almost meet in large P. mirabilis.

Ventrally the urohyal is weakly concave or flat. The concavity is most evident in Acrocheilus, Lepidomeda, Moapa, Mylopharodon, Plagopterus, Pogonichthys, some Relictus, Tiaroga, and Xystrosus usually because the sides of the horizontal plate are ventrally decurved.

The slope of the posterior edge of the vertical plate is variable. It may be rounded or square cut and vertical, e.g. some Chrosomus, some Eremichthys, but usually it is rounded dorsally and slopes anteriorly to the base such that

a ventral notch is formed. There is considerable individual variation. An unusual form is seen in Macrhybopsis where the vertical plate tapers to a smooth or jagged point posteriorly. The ventral notch is not seen in Nocomis where the plate also tapers to a point or rounded projection. In Parexoglossum the plate slopes posteriorly.

The sides of the horizontal plate may be parallel posteriorly, converge in to the base of the vertical plate or diverge. This character is mostly consistent within a genus except for Phenacobius and Pimephales where all three types are found and for Chrosomus and Platygobio where both parallel and convergent types are seen. Parallel or diverging sides may project posteriorly beyond the base of the vertical plate or even beyond the posteriormost dorsal part of the plate. This character is intraspecifically variable, e.g. in Erimystax.

In dorsal view the urohyal may be short and/or broad, e.g. in Erimystax and Phenacobius or elongate and/or thin, e.g. in Lepidomeda, Meda, Oregonichthys, and Plagopterus, but this is intra- or inter-specifically variable e.g. in Notropis and Xystrosus, and all intermediates are found.

BRANCHIAL REGION

Pharyngobranchials

Two pairs of pharyngobranchials are always present. Mahy (1975a) reported three pairs for Chrosomus neogaeus but

there are only two pairs in fourteen specimens examined for this study.

Epibranchials

The epibranchials number four on each side. Traces of a fifth cartilaginous epibranchial are seen in several genera but these are difficult to distinguish without adequate cartilage staining. A survey of cartilaginous elements in the cyprinid skeleton may reveal useful characters but was not undertaken here. The third and fourth epibranchials bear spikes as in Notemigonus but their presence or absence is individually variable.

Ceratobranchials

These are generally similar in all species and were not examined in detail.

Pharyngeal arch and teeth

The number of tooth rows and tooth counts are given in the character analysis. As trophic characters the gross form of the teeth varies with feeding niche occupied by the species and may not prove useful characters in relating genera. In addition some of the structural variation in pharyngeal arches can be attributed to differences between genera with one and two rows of teeth (which are no longer considered an adequate basis for generic separation (see Bailey et al., 1970)). Much of the variation seen in pharyngeal arches is of a proportional nature and not readily susceptible to analysis on the basis

of the available specimens (see also Eastman, 1970). Detailed studies involving also the pharyngeal musculature may reveal useful characters but this was not attempted here.

Hypobranchials

The hypobranchials are generally similar to *Notemigonus* except in Exoglossum and Parexoglossum where the first hypobranchials are large and plate-like rather than irregular.

Basibranchials

The first basibranchial is shorter than the following two and their shape is an elongate rectangle as in Notemigonus. In Exoglossum these bones are much compressed antero-posteriorly and the three bones are fused in large specimens.

Gill rakers (Figure 53).

The ossified portion of the gill rakers is usually a small triangle or cone with a small expanded base and a rounded or pointed tip. In large Nocomis they become more rod-like and the tip may fork. The rakers of Orthodon are peculiar with a circular base and a short shaft splitting into numerous distal branches. Gila bicolor also has branched tips but these are not numerous. The rakers of Xystrosus are also unique being slender, elongate and having a distinctive basal flexure.

VERTEBRAL COLUMN

Weberian region

The bones of the Weberian region were examined cursorily and are generally similar to those of Notemigonus. The second lateral process is invariably longer than the first process although relative lengths vary between species and within certain species. The first process is very weak in Campostoma and Dionda. The fourth neural spine may slope anteriorly or posteriorly but in Macrhybopsis both conditions are found. The intercalarium varies from a 'Y'-shape to almost triangular both within and between species. The tip of the fourth rib is expanded in Agosia, slightly in Ericymba where it may fork distally, in Exoglossum, slightly in Macrhybopsis, some Notropis and Phenacobius.

Abdominal, transitional and caudal regions

These are generally similar in all genera and were not examined in detail. Abdominal neural and caudal neural haemal foramina are open or closed and the condition is individually variable. Caudal fin bones are dealt with below and total vertebral numbers are assessed in the character analysis.

Interneural and intermuscular bones

These were not examined in detail but are generally similar in all genera.

MEDIAN FINS

Dorsal and anal fin bones

These fins received only a cursory examination and seem to be generally similar in all the species except the dorsal fin rays of Plagopterini which are modified as spines (Miller and Hubbs, 1960). Usually the first three proximal and intermediate pterygiophores of both the dorsal and anal fins are fused but occasionally this is two or four in either fin. There are evident differences in position of the dorsal fin relative to the pelvic fin and an attempt to analyse such data showed intra- and inter-specific differences. Modal counts of dorsal and anal fin rays are given in the character analysis.

Caudal fin bones (Figures

The caudal fin bones are generally similar among North American cyprinid genera. However certain species lack a sixth hypural and/or a third urodermal (Table). These characters are variable between individuals of a species and between species of a genus. Uyeno (1961) in his study on the osteology of Gila, Ptychocheilus, Richardsonius and Clinoostomus did not mention the third urodermal and gave the number of hypurals as 6 or 7 (i.e. 5 or 6 see p. present study) without specifying further which species or genera had which count. Both the sixth hypural and the third urodermal can be present but reduced to an irregularly shaped speck of bone in some individuals. This probably represents

an intermediate stage between presence and loss. Only in one instance (Dionda episcopa) does the fifth hypural seem swollen dorsally as though the sixth hypural had fused indistinguishably with it. However another individual of this species has the sixth hypural present as a speck of bone suggesting that reduction precedes loss and fusion does not occur. It is possible in, e.g. Gila, where mostly immature specimens were examined that development of a sixth hypural and a third urodermal is an adult trait. However mature G. alvordensis lack a third urodermal. Conversely Buhan (1972) has suggested that in Notemigonus crysoleucas the sixth hypural regresses with size and age. In examining 25 specimens for the present study 2 were found to have a normal-sized sixth hypural (43 and 94 mm. S.L.), 14 had a sixth hypural reduced to a speck of bone (18 - 109 mm. S.L.) and in 9 specimens it was absent (33 - 82 mm. S.L.). Larger and older specimens must be examined before it can be determined if regression occurs as this limited data shows considerable variation.

Loss of bones, especially small ones like the sixth hypural and third urodermal, is a poor indicator of relationship and may well have occurred independently in the various genera. The variability in expression of these two characters at the individual level also mitigate against their general use. However it appears that the third urodermal is consistently absent in Semotilus atromaculatus and S. corporalis but present in S. (Margariscus) margarita and it would seem to provide a

valid character for assessing the relationships of these three species. Despite their intraspecific and interspecific variability the sixth hypural and third urodermal are used as characters in the character analysis albeit with reservations.

Several other potential characters of the caudal skeleton were investigated. These are the shape and orientation of the hypurapophysis (Nursall, 1963), the diastema width, shape and size of the hypural and parhypural foramina (Monod, 1968), splitting and median expansions of neural and haemal spines (Buhan, 1970, 1972), angle of inclination to the vertebral column of the fifth and tenth preural centra neural spines and the general arrangement of the caudal bones.

The shape and orientation of the hypurapophysis is found to be intraspecifically variable, e.g. in Hybopsis (Extrarius) aestivalis it may be rounded, pointed or forked distally; in Hybopsis (Macrhybopsis) spp. it may curve dorsally or ventrally. In general it is a rounded or pointed process directed latero-ventrally and posteriorly.

The diastema width is also intraspecifically variable, e.g. in Acrocheilus alutaceus the second and third hypurals are closely associated with each other or in contrast they are well separated and the diastema is larger in both vertical and horizontal extent.

The hypural and parhypural foramina vary in shape and size and species or genera could not readily be characterised

by these structures. Size disparities between individuals and between species may account for some of the observed variation.

The neural, and less frequently the haemal, spines are often split vertically either to the base or restricted to the distal part of the spine. Occasionally the split is sagittal. In certain cases the split extends into the neural arch giving the "doubled" condition of Buhan (1972). Vertical splitting is of general occurrence though not as common as the normal condition. Median expansions of spines are better developed on the neural spines (up to the sixth preural spine) than on the haemal spines (up to the fourth preural spine). There is considerable variation in expansion size and extent at the individual level, e.g. in Relictus solitarius they could be large or absent. Extent of expansions does not seem to be correlated with size of fish or caudal peduncle depth.

The angle of inclination of neural (and haemal) spines to the vertebral column is variable between young and adult specimens in some species, e.g. in Lavinia exilicauda at the tenth preural centrum in a small fish (81 mm. S.L.) the angle is 59° while in a larger specimen (233 mm. S.L.) it is only 24°. Intrageneric variation is also observed, e.g. in Rhinicnthus species the approximate angles are: -

Species	Size (mm. S.L.)	Angle °	
		at 5th spine	at 10th spine
<u>atratalus</u>	53 - 62	45	55
<u>cataractae</u>	71 - 105	45	45
<u>evermanni</u>	57 - 84	35	45
<u>falcatus</u>	51 - 81	35	55
<u>osculus</u>	48 - 64	45	45

The anteriormost spines, at the tenth preural centrum, are generally the least depressed (at the tenth preural centrum the angle is centred about 45° and at the fifth centrum around 35°). These values must be regarded as approximate since the angle is difficult to measure (the spine is almost perfectly straight in some individuals, curved in others) and, as noted above, it is subject to size and specific variations. In addition it is not unusual for measurements on 5 individuals to be identical while the sixth differs markedly. The inclination of neural and haemal caudal spines has been related to the depth of the caudal peduncle, fishes adapted to swift water and having a slim peduncle possessing depressed spines (Uyeno, 1961; Buhan, 1972). This is most apparent in large species where body depth and caudal peduncle depth are markedly different.

The caudal bones are loosely arranged in most species but were closely packed in, e.g. Acrocheilus alutaceus, Orthodon microlepidotus, Gila robusta, Phenacobius uranops, Rhinichthys evermanni, Lavinia exilicauda and Pogonichthys macrolepidotus.

This is not intimately associated with large size since the above specimens ranged from 54 to 233 mm. S.L. but larger individuals and species tend to have more closely packed caudal bones as a result of growth and for better support of the caudal fin.

Fusions are rare anomalies, e.g. fusion of hypurals 2 and 3 at their bases in one specimen of Chrosomus eos and one Nocomis biguttatus; fusion of the epural to the neural arch in one Chrosomus neogaeus; partial fusion of the first hypural and the haemal spine in one specimen of Moapa coriacea; fusion of some hypurals in large Semotilus atromaculatus (Buhan, 1970); etc.. Differences of a proportional nature are noted between species but many of these were subject to individual and size related variation and could not be readily assessed for systematic significance. The number of branched caudal rays is 17, 9 articulating in the upper lobe and 8 in the lower. Occasional aberrant specimens are noted, e.g. 2 specimens of Rhinichthys atratulus had only 8 upper lobe rays and a single Phenacobius mirabilis had only 7 rays; a specimen of Pimephales notatus possessed a supernumerary ray at the diastema level. Minor caudal rays extend anteriorly on the caudal peduncle to a maximum level opposite the fifth preural neural and haemal spine. The level attained is intraspecifically and interspecifically variable. The most usual extent is to the level of the third or fourth spine.

In contrast to the variations noted in the preceding

pages Schlueter and Thomerson (1971) in examining caudal skeletons of 217 cyprinids representing 20 species found no noteworthy variation.

The caudal skeletons of North American cyprinids are generally similar and the minimal variation observed is of only limited value in assessing relationships.

PAIRED FINS

PECTORAL GIRDLE

Posttemporals

Each posttemporal bone is a tear-drop shape, with a rounded or square cut ventral base tapering dorsally. In Exoglossum the bone is rounded both dorsally and ventrally and approaches a rectangle in shape. The lateral line ossification or extrascapular passes diagonally across the base from the antero-dorsal to the postero-ventral corner. In the small genus Iotichthys the canal may be almost absent. The posttemporal is invariably shorter than the supracleithrum varying from one third to almost equal in length. Specimen size is an important factor affecting the relative lengths of these bones and obscured differences which might be of use in comparing genera.

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Supracleithra

The supracleithrum may bear a short length of ossified

lateral line canal dorsally on its posterior margin. The canal was absent from Ericymba, Exoglossum, Iotichthys, Opsopoeodus, Orthodon, Pimephales (but present in P. vigilax), Relictus, and Tiaroga (present or absent) or only just touches the supracleithrum as in Campostoma. The supracleithrum is an elongate bone often with an antrorse dorsal tip which narrow from a small anterior wing. The antero-dorsal corner of this wing is sometimes produced as a short process in Erimcymba, Nocomis and weakly in Exoglossum as a sharp or blunt point. The presence of the dorsal tip is intraspecifically variable in Chrosomus, Dionda, Hybognathus, Notropis and is only weakly developed in certain genera e.g. Lepidomeda, Meda, Notropis, Plagopterus, Pogonichthys, Tiaroga, and Yuriria. There is a mesial hook below the dorsal tip in Orthodon, some Dionda and very weakly in Notemigonus. The large lateral tube (not the sensory canal) seen in certain Abramidini is not found in N. American cyprinids except some Notemigonus and weakly in Agosia. A slender tube is present in most genera although even this may be absent.

Cleithra

The anterior arm of the cleithrum is usually longer than the dorsal arm. In Dionda, Orthodon and some Lavinia the two arms are about equal while in Eremichthys, Pimephales promelas and Tiaroga the dorsal arm is longer. The dorsal arm is very short in Phenacobius, a dorso-ventrally depressed species. The angle enclosed by the dorsal and anterior arms is intraspecifically variable and is usually 90° or a little more. The

angle is greatest in Parexoglossum and Xystrosus. The lateral ridge of the dorsal arm curls anteriorly or posteriorly. In some genera the curl is consistently in one direction; in others it is intra- or inter-specifically variable or absent. The dorsal tip of the cleithrum is a short, rounded or pointed, process angled posteriorly. This posterior angulation is most marked in Hybognathus. The anterior arm of the cleithrum is usually notched on its ventral edge posteriorly. The notch could be strong, weak or absent and is both intra- and inter-specifically variable, e.g. in Erimystax, Notropis, Relictus. The postero-ventral corner of the cleithrum is usually a rounded right angle produced a little posteriorly. In Dionda it is markedly produced, in other genera hardly at all and all intermediate conditions are found. In some genera the postero-ventral corner is elevated along the posterior edge of the dorsal arm. The angle in such cases is much more than 90°. This condition is seen in Agosia, some Extrarius, Macrhybopsis gelida, Meda, Phenacobius, Plagopterus, variably developed in Rhinichthys, and Tiaroga. The dorsal arm of the cleithrum has a mesial ridge or wing which expands anteriorly as a small wing just below the dorsal tip of the arm. The presence of this small wing is interspecifically variable, e.g. in Hybognathus, and in Plagopterus it could be hooked. The mesial wing is very large in Phenacobius but its development in other genera varies with the individual specimens. The lateral wing of the anterior arm could

curve in gradually, at 90° or at an acute angle to the tip of the anterior arm. There is some indication that this is size dependent in some genera, certainly the angle is variable between individuals of Mylocheilus, and the angle is variable between species of the genus Pimephales. A recurved ridge with or without a foramen, within or without its boundaries, is often present along the mesial edge of the lateral wing. Its presence is intra- and inter-specifically variable, e.g. in Relictus and Notropis respectively. The slope of the lateral wing also varies between species, e.g. in Notropis from horizontal to almost ventral. It is also strongly ventro-laterally orientated in Exoglossum and Parexoglossum, particularly anteriorly. The dorsal edge of the anterior arm is normally a free structure of varying height but in Xystrosus the mesial wing merges posteriorly with it in some specimens and in Hybopsis amblops and Mylocheilus it is interrupted with the anterior part merging with the mesial wing of the anterior arm and the posterior part beginning lateral to this merger and ascending the dorsal arm. No cleithrum approaches the shape seen in Evomus navaho, a Middle Pliocene cyprinid with a modified mesial wing (Uyeno and Miller, 1965).

Postcleithra

Each postcleithrum is usually present as an elongate, slim, S-shaped bone with rounded or pointed ends. In larger specimens, the body of the bone is flattened, expanded or

angulate and produced a little where it passes mesial to the cleithrum. As noted previously the postcleithrum is much reduced in Notemigonus. In Extrarius it is elongate or quite short but not as short as in Notemigonus. Development of this bone is also moderate in Plagopterus and it is absent in Meda, Tiaroga and most Rhinichthys cataractae (see also Nelson, 1973). Rhinichthys evermanni has a weakly developed postcleithrum in some specimens, in others it is absent. In Rhinichthys atratulus the bone is small while in Rhinichthys falcatus and Rhinichthys osculus (including lariversi) development is normal. Reduction and loss in these species and genera may be independent.

Coracoids

The development of the anterior end of the coracoid where it meets the cleithrum and the size of the foramen between these two bones are intra- and inter-specifically variable, and at least in part, size related. The anterior end is thin and pointed or broad and square or jagged. The foramen varies from large to small, and occasionally is open anteriorly because the coracoid and cleithrum do not meet. There is usually a small foramen posteriorly on the coracoid close to the articulation with the mesocoracoid. A similar but smaller foramen is occasionally present on the mesial wing of the cleithrum opposite this posterior coracoid foramen, e.g. in Hemitremia, some Lavinia, Orthodon.

Mesocoracoids

The mesocoracoid is a slim to broad bone, dorsally recurved where it articulates with the cleithrum and with a slight S-shape or straight in mesial view. The S-shape is most evident in, e.g. Eremichthys but its development is intra- and inter-specifically variable in, e.g. Erimystax, Hybognathus and Notropis. Breadth of the mesocoracoid often increases with size of the fish and is also intra- and inter-specifically variable, e.g. in Pimephales and Notropis.

Scapulae

The scapula shows only minor variations in shape although the ridge for articulation with the mesocoracoid is weakly developed in some specimens.

Pectoral radials

Four radials are always present with some accessory ossifications in larger fish. The first radial bears one or two heads posteriorly for dorsal ray articulations but this is intraspecifically variable in Notemigonus, for example, and interspecifically in e.g. Notropis, Pimephales, and Rhinichthys.

PELVIC GIRDLE

The pelvic girdle does not show any good characters for use at the generic level with the exception of spiny fin

rays in Plagopterini and modal ray counts (see character analysis). The basipterygium width in length varies from 1 in 2 to almost 1 in 3 and is size dependent. The relative lengths of the anterior processes vary intra- and inter-specifically and are equal, or the mesial or lateral process longer relative to its partner, e.g. in Notropis. The end of these processes is blunt or sharp and the mesial process is weakly or strongly expanded as an almost horizontal plate. These characters also vary at the individual specimen level. The posterior medial processes are closely approximated or meet anteriorly and usually diverge laterally caudad. In some species and individuals they parallel one another for much of their length, e.g. in Hybognathus, Lepidomeda, Meda, Notemigonus, Orthodon, some Pimephales, some Plagopterus, Pogonichthys. This is particularly evident in Plagopterini but even here is individually variable. The processes are rod-shaped to triangular with a rounded, pointed or square-cut posterior tip but these features show individual variation.

DISCUSSION

This osteological survey at the generic level revealed few characters of widespread use. Certain characters are assessed in the character analysis. Synapomorphy was difficult to establish because a general pattern of cyprinid osteology is adhered to by Nearctic cyprinids. Variations on this pattern were mainly of a proportional nature or showed evident intra- and inter-specific variation. These variations might prove useful in interpreting generic relationships but large series of adult specimens would be required to place such work on a rigorous comparative basis. Convergence would be difficult to detect since distantly related species adapted to similar modes of life might show the same modifications of the general pattern.

Figure 44. Posterior views of the ethmoid complex (prevomer and lateral ethmoids removed), A- Orthodon microlepidotus, B- Nocomis asper, C- Hybopsis (Extrarius) aestivalis. Scales: 0.5 cm., 1 mm. and 1 mm. respectively.

E: ethmoid, SE: supraethmoid.

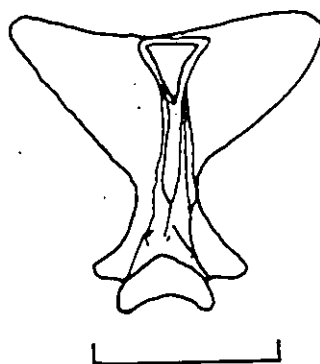
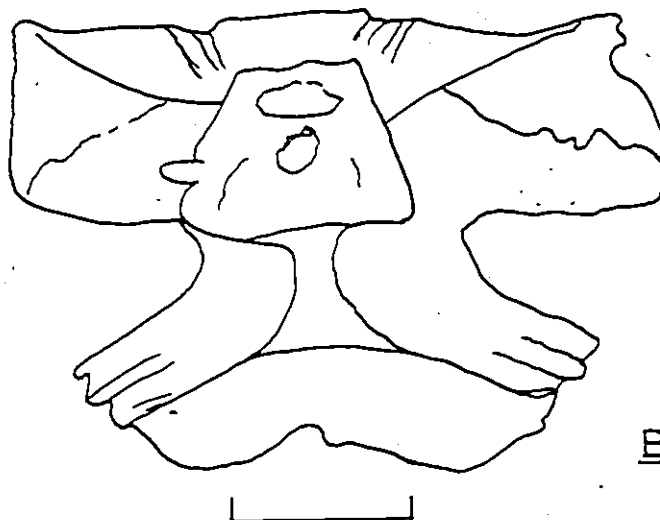
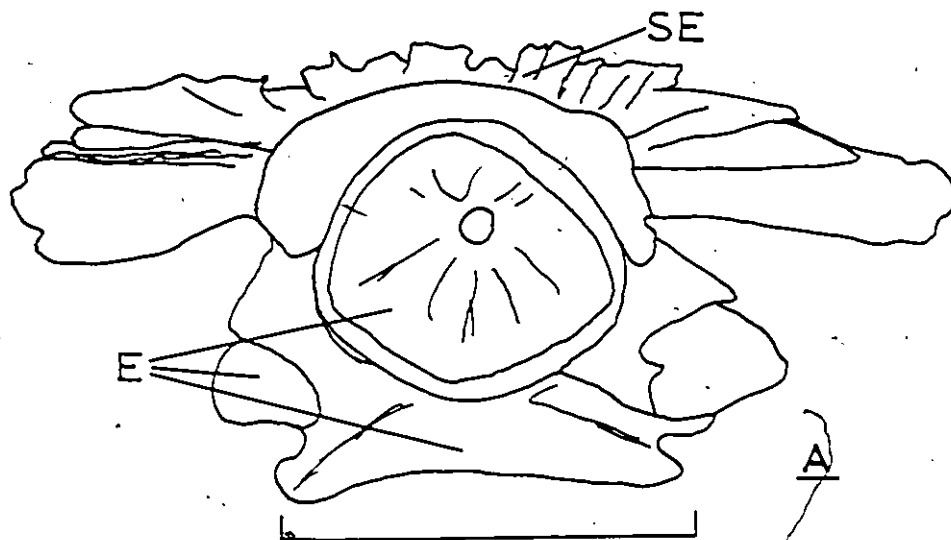
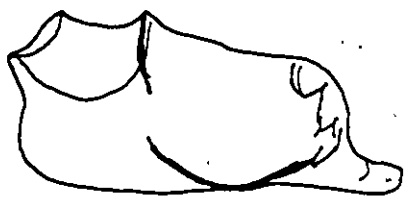
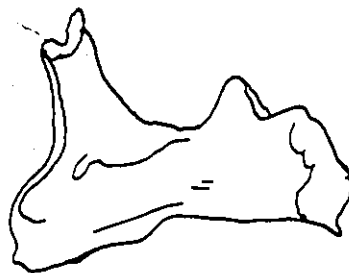


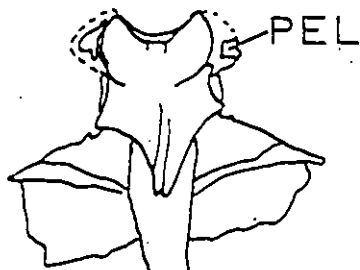
Figure 45. A- Dorso-mesial view of left autopalatine of Exoglossum maxilllingua, B- lateral view of left autopalatine of Eremichthys acros, C, D and E- ventral views of the prevomer and associated bones of Hybognathus nuchalis, Plagopterus argentissimus, and Dionda episcopa respectively. All scales: 1 mm. LE: lateral ethmoid, PEC: preethmoid cornua, PEL: lateral preethmoid, PS: parasphenoid, PV: prevomer.



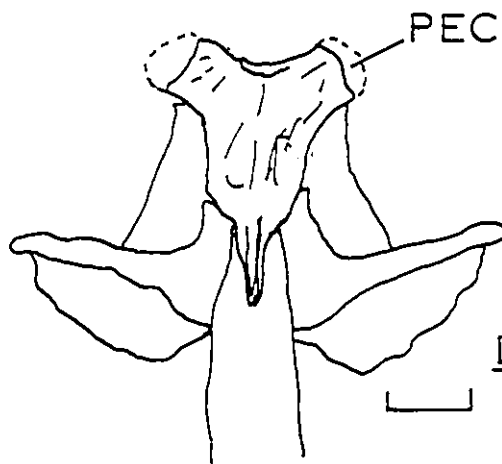
A



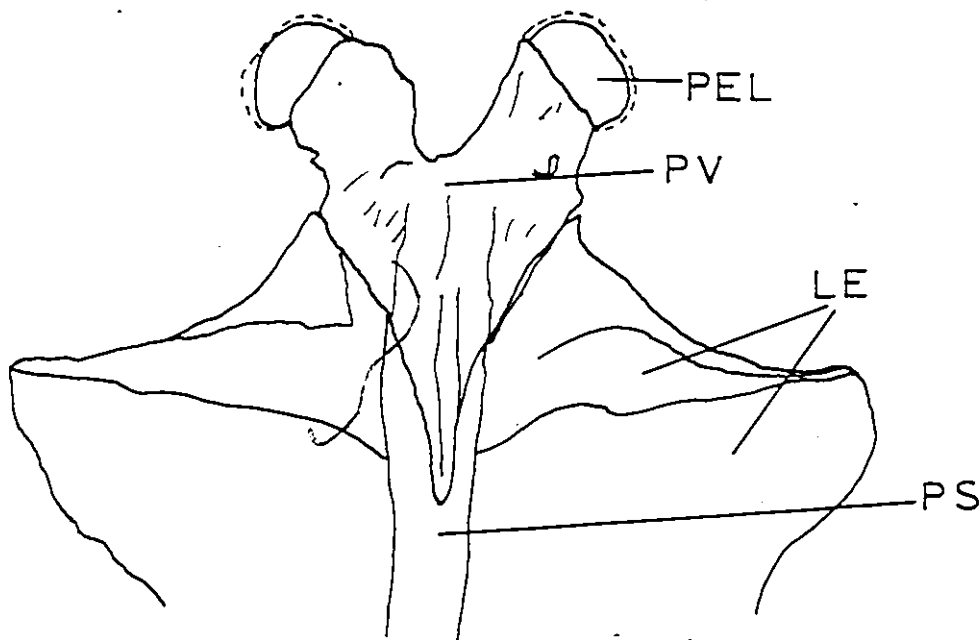
B



C



D



E

Figure 46. A and B- Mesial views of right dentaries of Parexoglossum laurae and Exoglossum maxilllingua, C- mesial view of right lower jaw of Acrocheilus alutaceus, D- lateral view of left lower jaw of Phenacobius mirabilis. All scales: 1 mm.

A: angular, CM: coronomeckelian, D: dentary, M: mentomeckelian, RA: retroarticular.

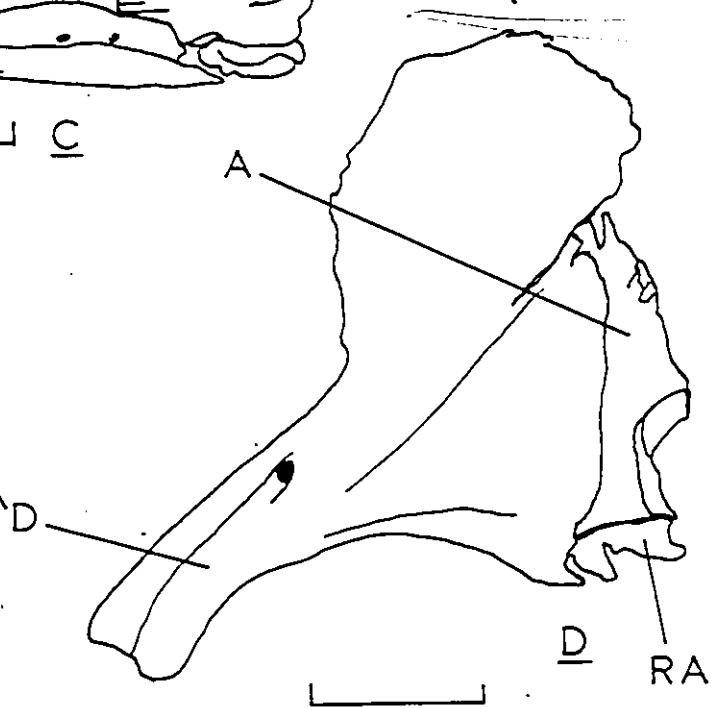
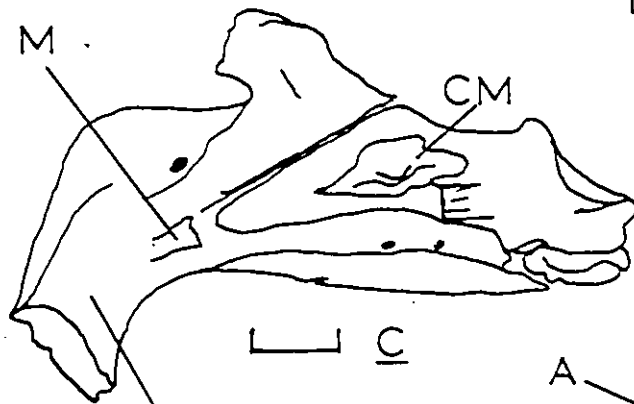
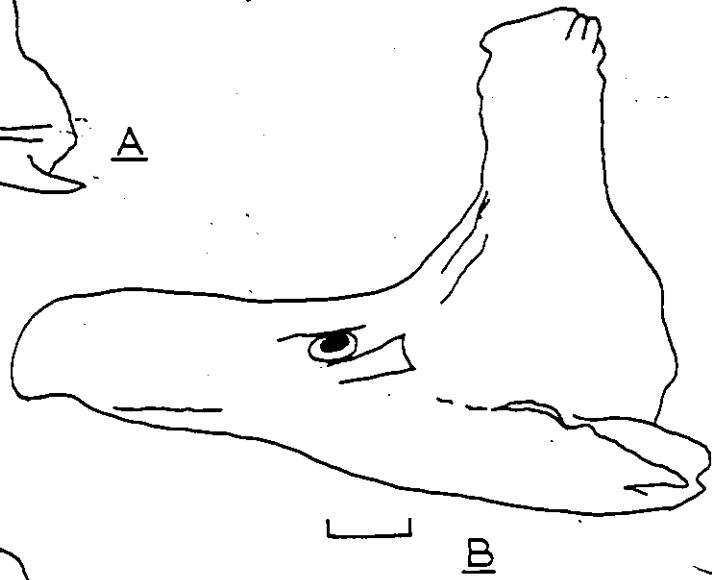
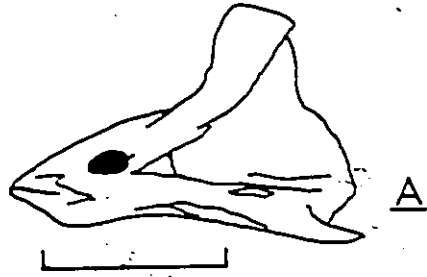


Figure 47. Suborbital series of Xystrosus popoche (above) and Algansea tincella (below). Scales: 1.0 cm. and 0.5 cm. respectively.

F: frontal, L: lachrymal, SI: supratemporal-inter-temporal, SO₃₋₆: suborbital bones, SP: supraorbital.

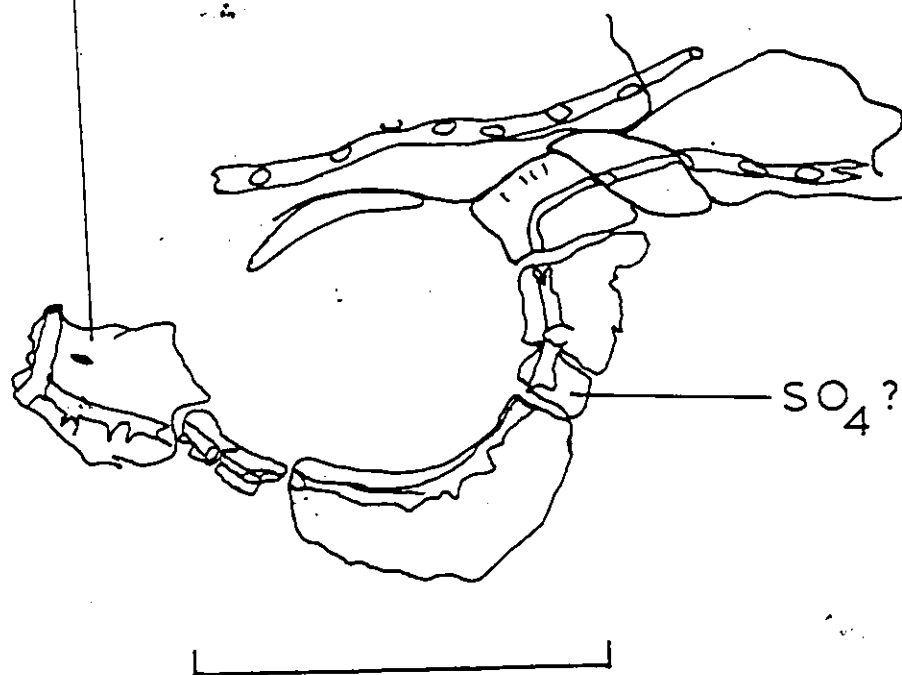
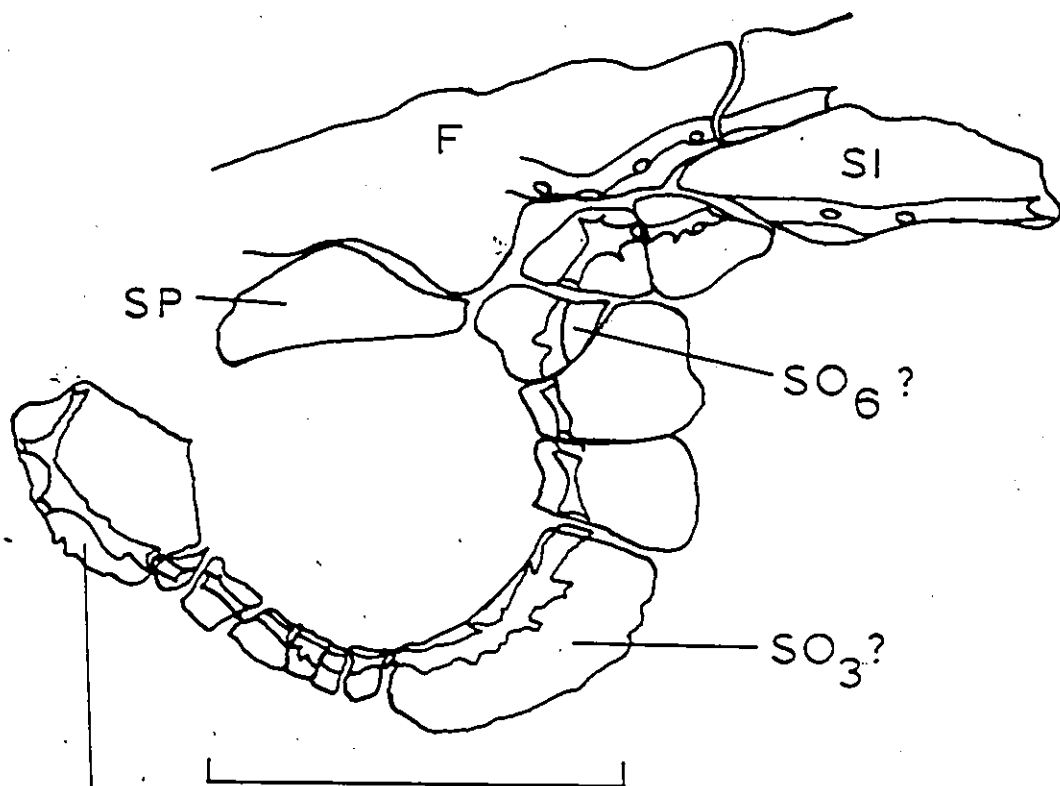
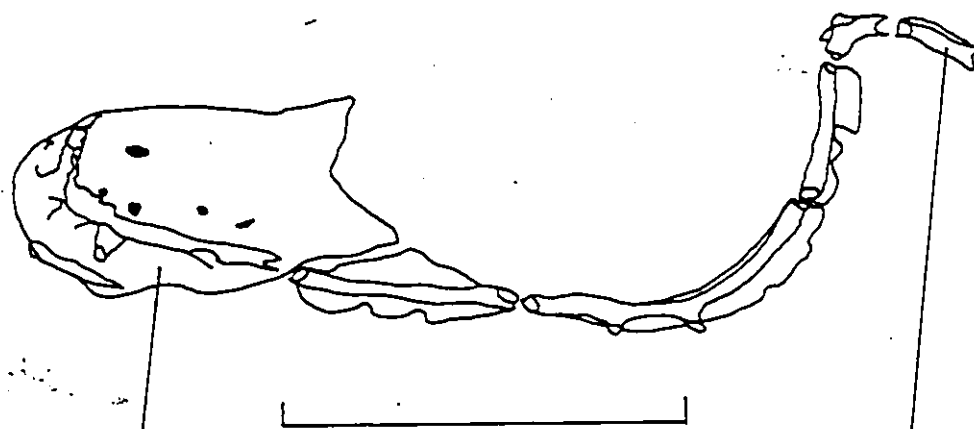


Figure 48. Suborbital series of Hybopsis (Erimystax) dissimilis
(above) and Acrocheilus alutaceus (below). Scales:
0.5 cm.
DS: dermosphenotic, L: lachrymal, SO₂₋₅: suborbital
bones.



DS

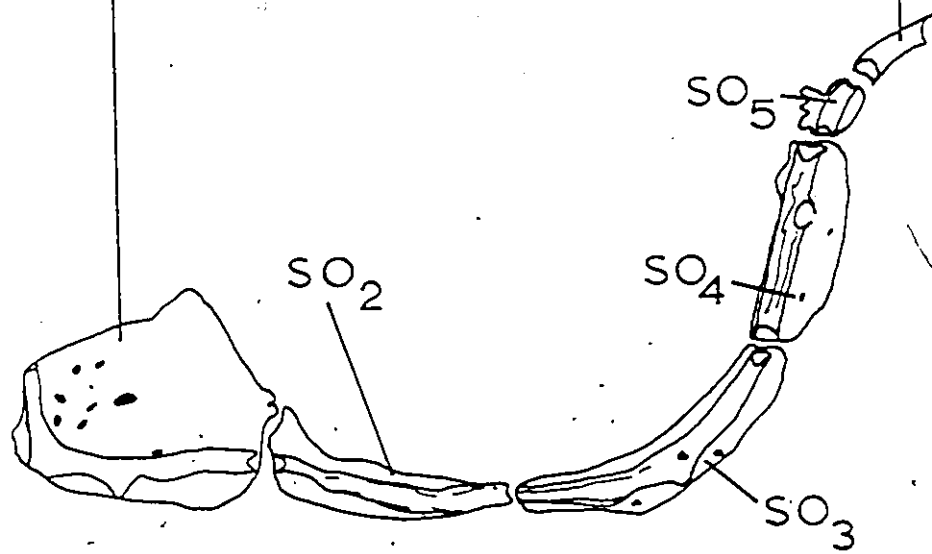


Figure 49. Lateral views of left hyomandibulars of A-
Platygobio gracilis, B- Eremichthys acros, C-
Lavinia exilicauda, D- Hemitremia flammea. Scales:
0.5 cm., 0.1 cm., 0.5 cm. and 0.1 cm. respectively.

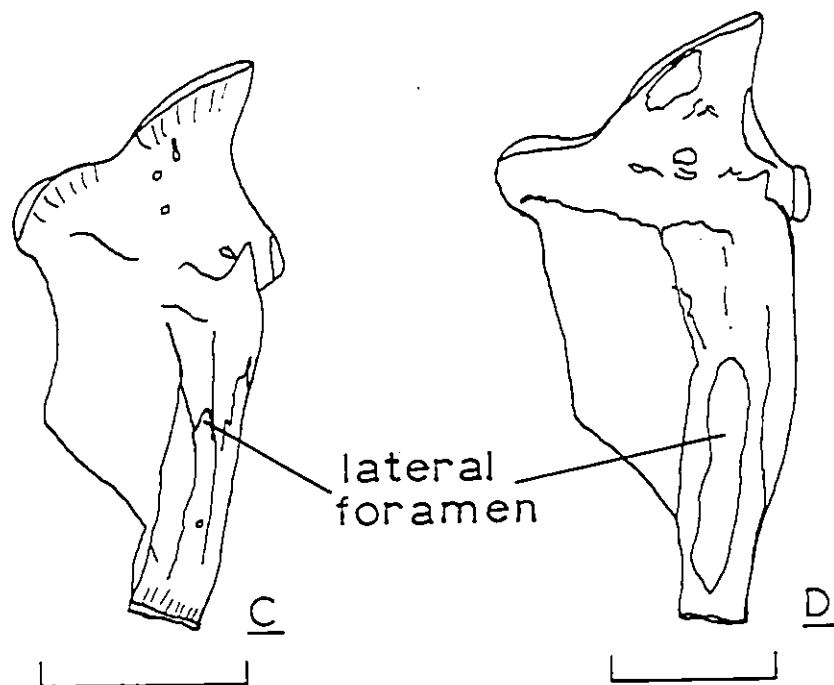
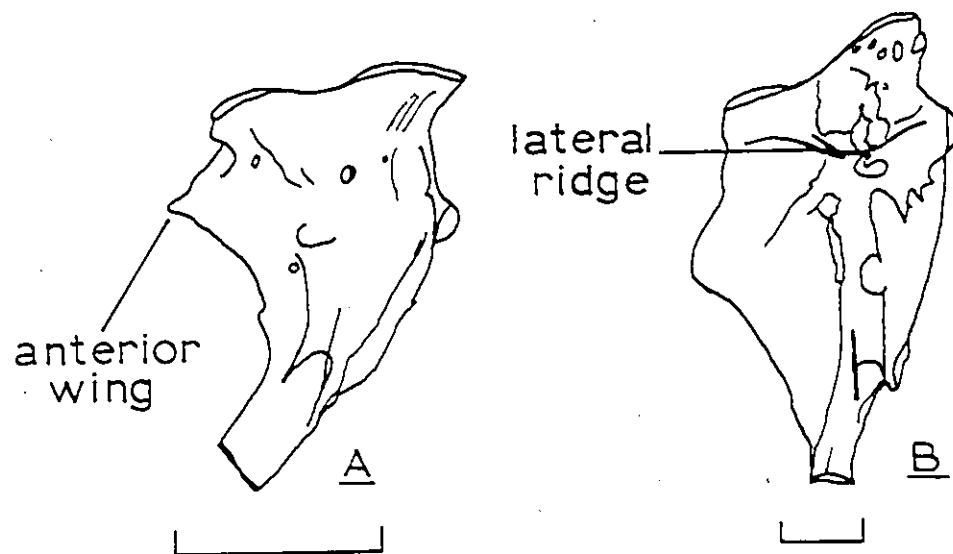


Figure 50. A-and B- Dorsal views of right posterior part of cranium to show autosphenotic intervening between frontal and supratemporal-intertemporal in Nocomis biguttatus and Hybognathus placitus respectively. Scales: 1 mm. and 0.5 cm. C, D and E- Dorsal views of basihyals of Phenacobius mirabilis, Meda fulgida and Rhinichthys evermanni. Scales: 1 mm. AS: autosphenotic, F: frontal, P: parietal, SI: supratemporal-intertemporal.

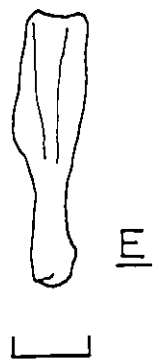
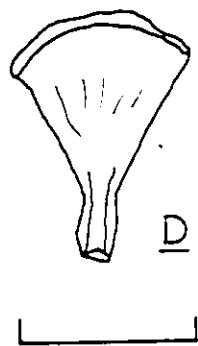
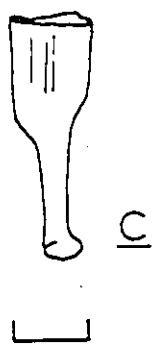
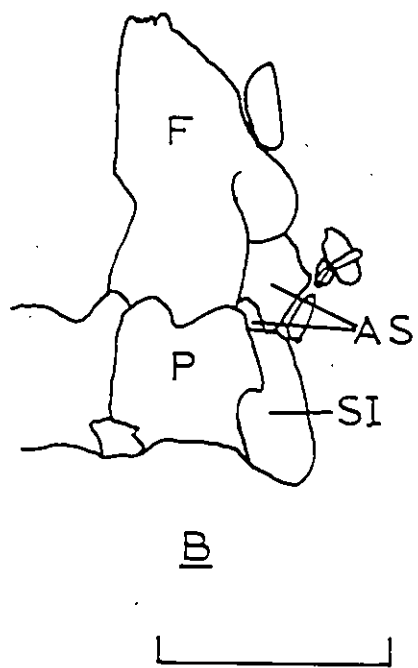
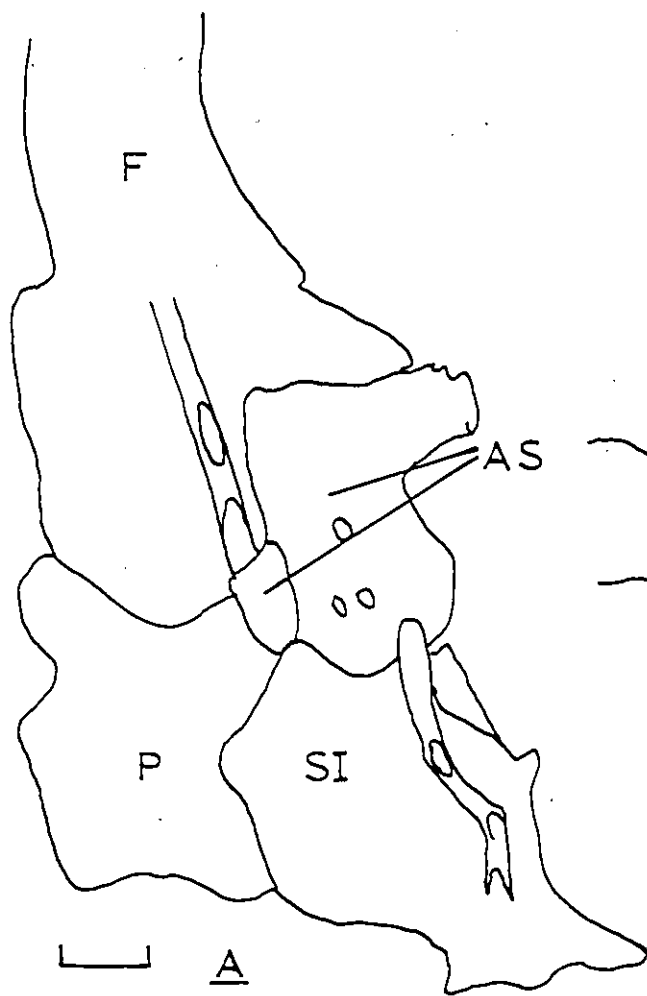
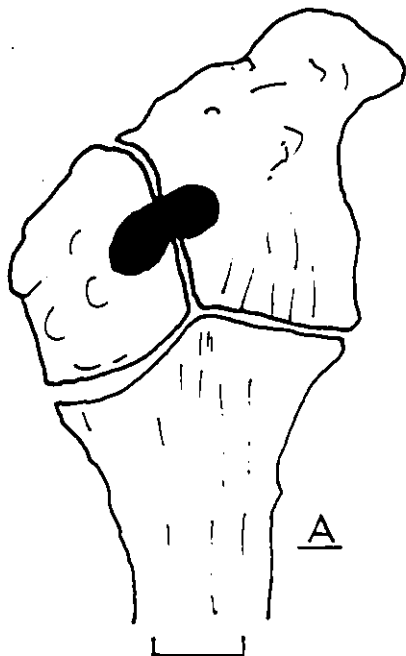
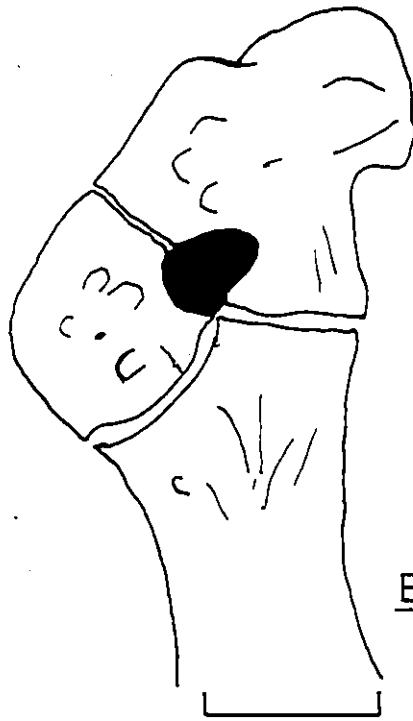




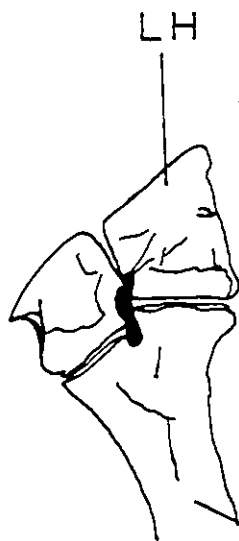
Figure 51. Variation in foramen position at junction of upper and lower hypohyals: A- Nocomis leptcephalus, B- Acrocheilus alutaceus, C- Opsopoeodus emiliae, D- Tiaroga cobitis. Scales: 1 mm.
CH: ceratohyal, LH: lower hypohyal, UH: upper hypohyal.



A



B



C



D

CH



Figure 52. Urohyals of A- Exoglossum maxilllingua, B- Barexo-
glossum laurae, C- Nocomis leptocephalus, D- Agosia
chrysogaster, E- Xystrosus popoche, F- Ericymba
buccata. Scales: 1 mm.

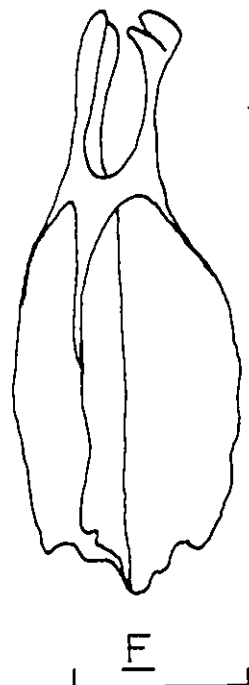
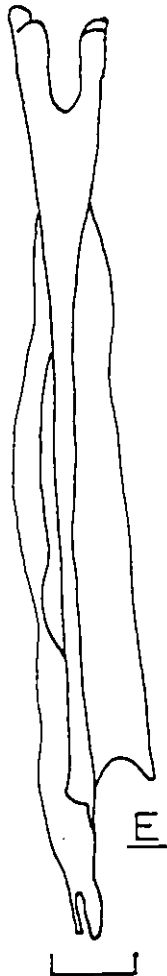
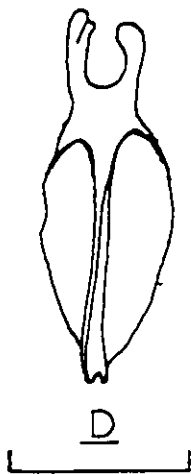
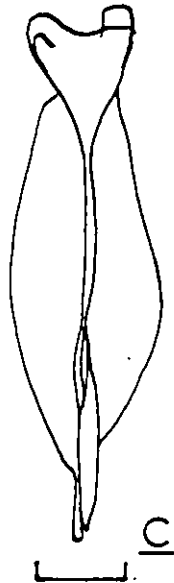
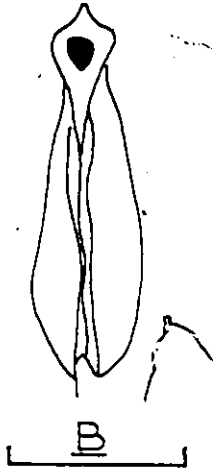




Figure 53. Antero-lateral views of gill rakers (from middle of the outer row on the first left arch) of A- Xystrosus popoche, B- Orthodon microlepidotus, C- Nocomis leptcephalus, D- Eremichthys acros, E- Gila bicolor. Scales: 1 mm.

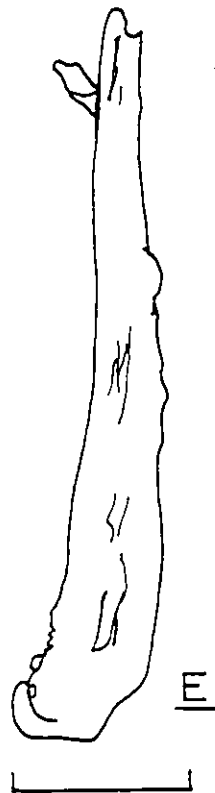
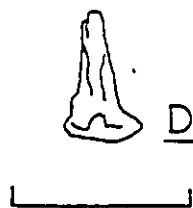
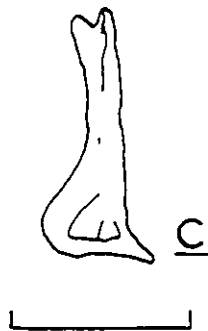
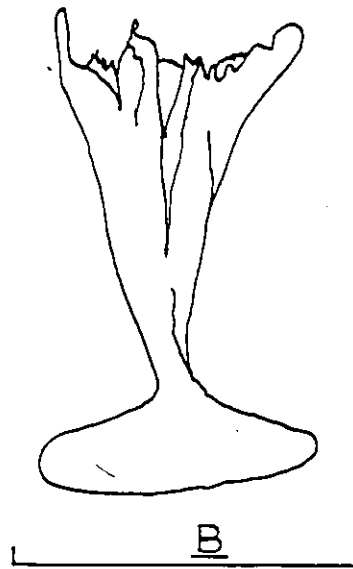
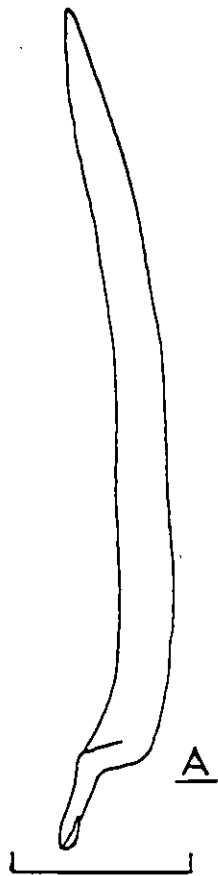


Figure 54. A and B - Dorsal views of parasphenoids of Dionda episcopa and Nocomis micropogon. Scales: 1 mm. and 0.5 cm. C - Lateral view of parasphenoid of Campostoma anomalum. Scale: 1 mm. D and E - Lateral views of metapterygoids of Hybopsis (Erimystax) dissimilis and Couesius plumbeus. Scales: 1 mm.

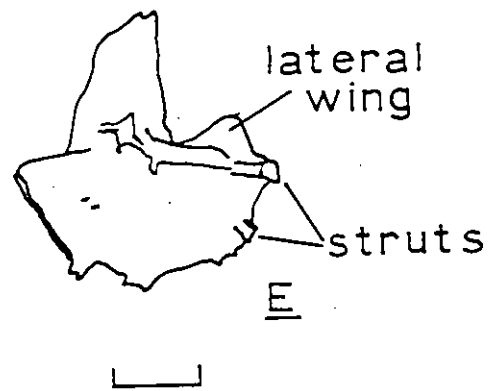
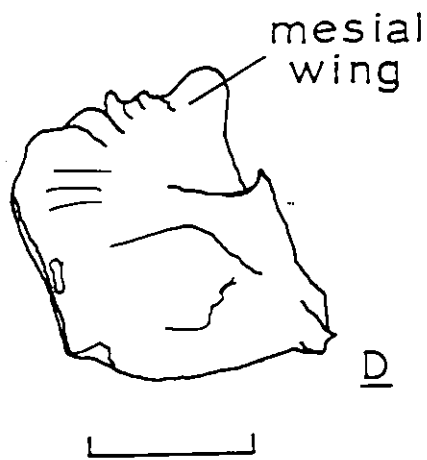
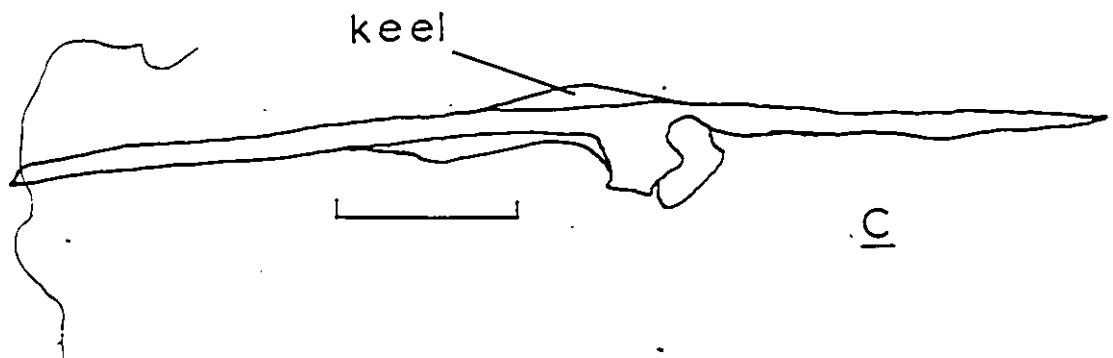
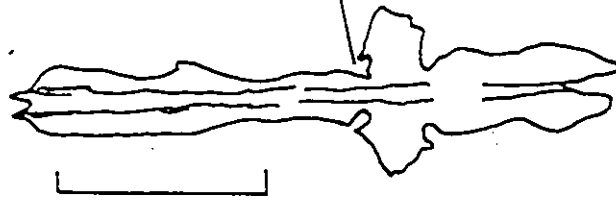
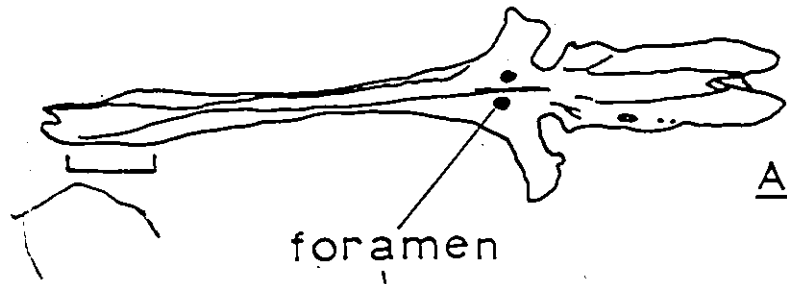


Figure 55. A and B - Ventral views of basioccipitals of Hybognathus placitus and Lavinia exilicauda. Scale: 0.5 cm. C - Lateral view of basioccipital of Orthodon microlepidotus. Scale: 0.5 cm.
ACP: process ventral to aortic canal.

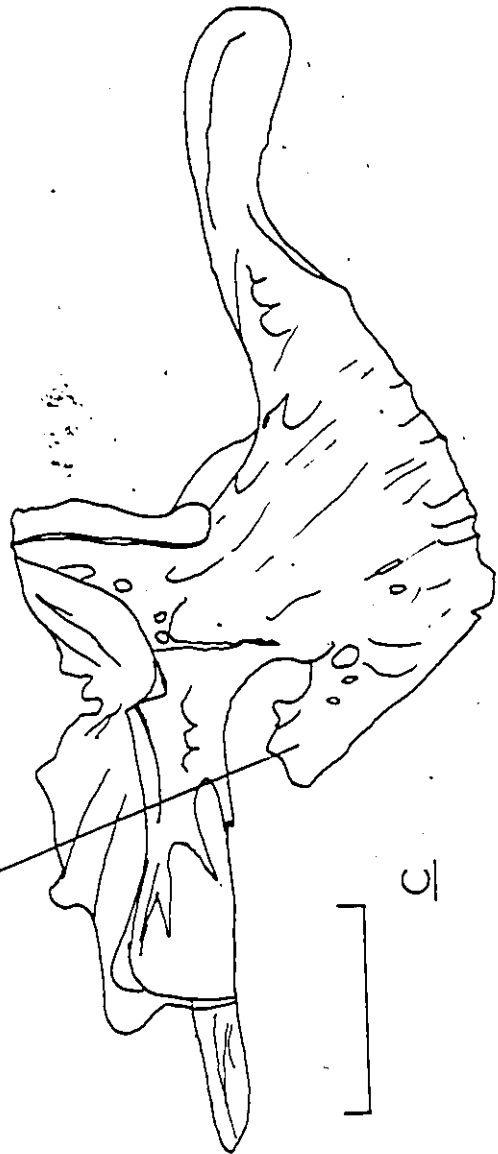
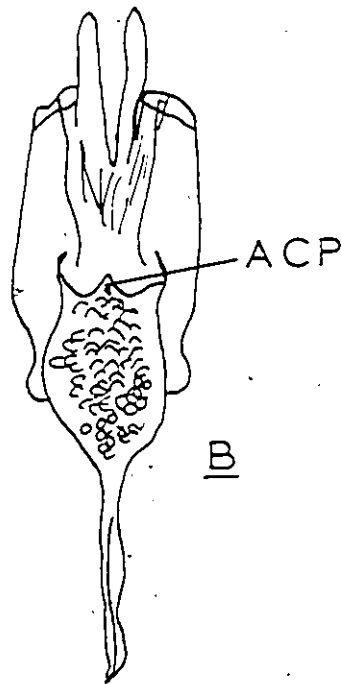
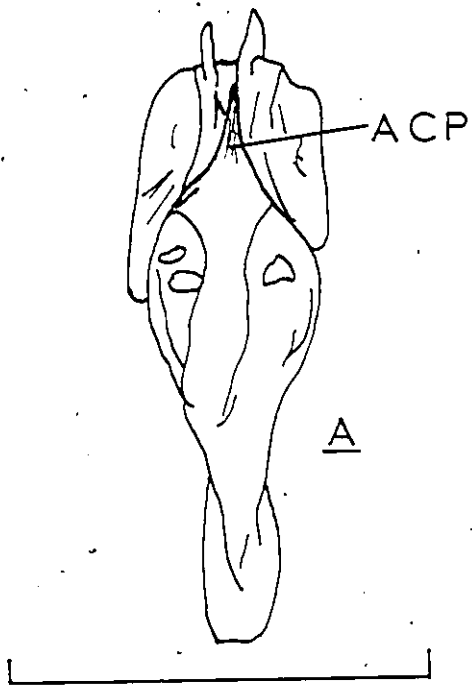




Figure 56. A- Dorsal view of anterior arm of left pectoral girdle of Notropis venustus, B- Mesial view of left pectoral girdle of Phenacobius mirabilis, C- Mesial view of right pectoral girdle of Tiaroga cobitis (pectoral radials and fin rays removed in B and C). Scales: 1 mm.

CC: coracoid, CL: cleithrum, MC: mesocoracoid,
PCL: postcleithrum, SC: scapula.

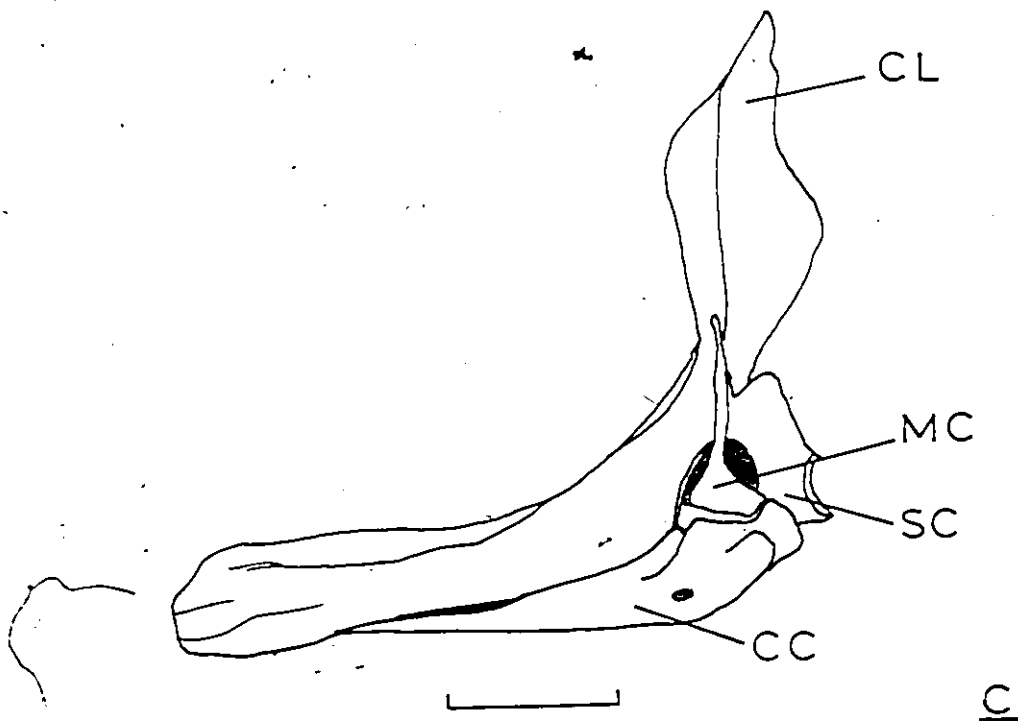
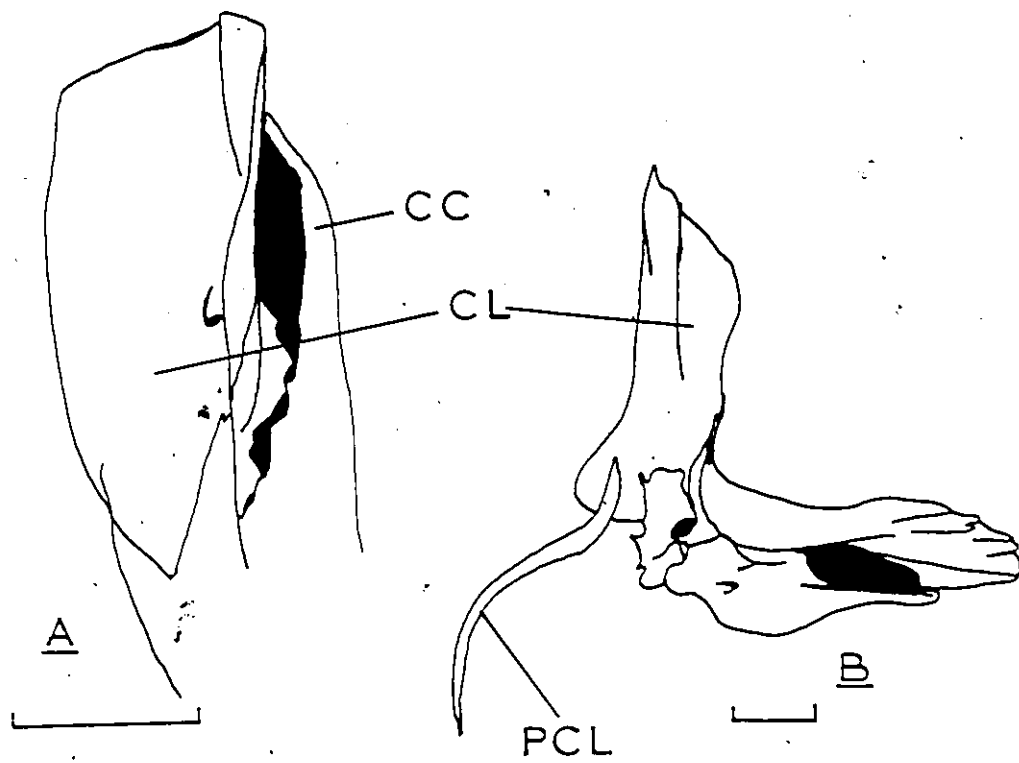
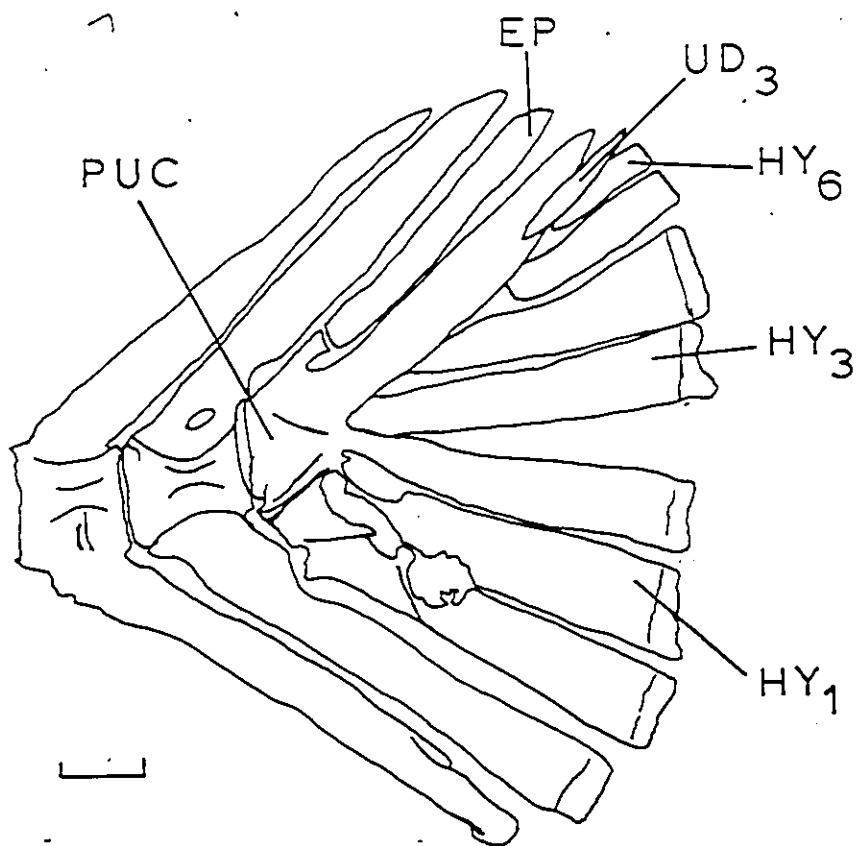
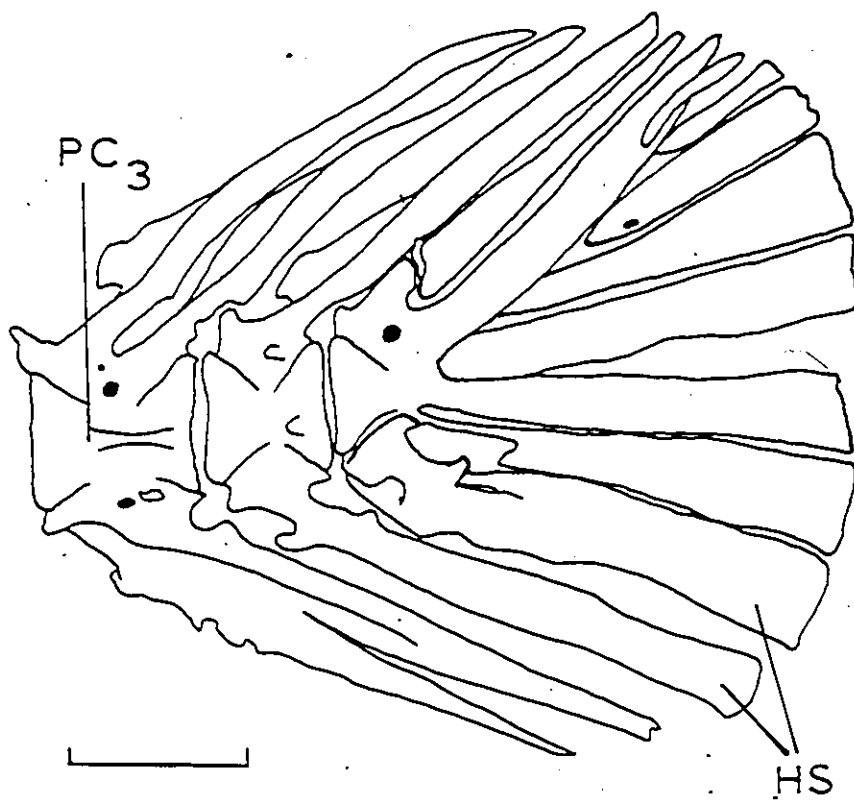


Figure 57. Lateral views of caudal skeleton of Phenacobius
uranops (above) and Acrocheilus alutaceus (below):

Scales: 1 mm.

EP: epural, HS: haemal spine, HY₁, HY₃, and HY₆:
first, third and sixth hypurals, PC₃: third preural
centrum, PUC: fused first preural centrum and first
and second ural centra, UD₃: third urodermal.



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Character analyses for North American
cyprinid genera

INTRODUCTION

This section describes and attempts to analyse from a phyletic viewpoint various characters of North American cyprinid genera. The limits of these genera have, in several cases, been variously interpreted and the listing used here is in some ways arbitrary and idiosyncratic. It includes most of the sub-genera which have had a fairly recent chequered history at the generic level. Thus, the troubled genus Hybopsis s.l. is split into the sub-genera Couesius, Erimystax, Extrarius, Hybopsis, Macrhybopsis, Nocomis, Oregonichthys, Platygobio and Yuriria while Gila, which seems to have gained acceptance as a cohesive taxon since Uyeno's osteological study in 1961, is not split into sub-genera. In addition, Opsopoeodus was separated from Notropis, Margariscus from Semotilus, Clinostomus from Richardsonius, Parexoglossum from Exoglossum and Xystrosus from Algansea.

Each character is described and analysed and the character states resulting are summarised in Table 10. Choice of characters was governed in part by the availability of information. Certain characters such as chromosome number were included, although not all genera have been examined, because some light is cast on certain generic relationships.



Skeletal and scale data were based on information generated in this thesis. Sources for other information are cited below and where literature reports were contradictory the relevant specimens were examined.

MATERIALS AND METHODS

The general literature sources used were Jordan and Evermann (1896), Meek (1902), Snyder (1918), Forbes and Richardson (1920), Blatchley (1938), Kuhne (1939), Eddy and Surber (1947), Simon (1951), Beckman (1953), Alvarez and Navarro (1957), Koster (1957), Trautman (1957), Slastenenko (1958), Carr and Goin (1959), Cook (1959), Legendre (1960), Bond (1961), Clay (1962), Bailey and Allum (1962), LaRivers (1962), Sigler and Miller (1963), Cross (1967), Moore (1968), Smith-Vaniz (1968), Whitworth et al. (1968), Carlander (1969), Eddy (1969), Harlan and Speaker (1969), Alvarez del Villar (1970), Baxter and Simon (1970), McPhail and Lindsey (1970), Paetz and Nelson (1970), Brown (1971), Buchanan (1973), Hopkirk (1973), Miller and Robison (1973), Minckley (1973), Scarola (1973), Scott and Crossman (1973), Douglas (1974), McAllister and Coad (1974).

In addition several original species descriptions, synoptic and revisionary works, and other descriptions were used such as Jordan (1879), Garman (1881), Hubbs and Ortenburger (1929a, 1929b), Hubbs (1931), Trautman (1931), Schultz (1936), Schultz and Schaeffer (1936), Hubbs and Kuhne (1937), Buen (1941), Hubbs (1942), Miller (1945a, 1945b), Hubbs and Miller (1943),

Hubbs and Black (1947), Hubbs and Raney (1947), Gosline (1948), Hubbs and Miller (1948a, 1948b), Hubbs and Raney (1948), Hubbs and Bonham (1951), Hubbs and Raney (1951), Suttikus (1951), Bailey and Suttikus (1952), Hubbs and Bailey (1952), Miller (1952), Bailey, Winn and Smith (1954), Weisel (1954, 1955), Navarro (1955), Raney (1955a, 1955b, 1955c), Bailey and Gibbs (1956), Hubbs and Brown (1956), Hubbs and Crowe (1956), Gibbs (1957a, 1957b, 1957c), Howell (1957), Hubbs and Hubbs (1958), Suttikus (1959), Miller and Hubbs (1960), Kimsey and Fisk (1960), Patten (1960), Fingerman and Suttikus (1961), Gibbs (1961), Gilbert (1961), Gilbert and Bailey (1962), Minckley and Craddock (1962), New (1962), Gibbs (1963), Miller (1963a, 1973b), Alvarez and Cortes (1964), Gilbert (1964), Romero (1965), Nelson (1966), Stewart (1966), Lachner and Jenkins (1967), Aspinwall (1968), Barbour and Contreras (1968), Cortes (1968), Hill and Jenssen (1968), Snelson (1968), Suttikus and Clemmer (1968), Holden (1968), Gilbert (1969), Philipps (1969), Rinne (1969), Tsai and Zeisel (1969), Holden and Stalnaker (1970), Legendre (1970a, 1970b), Swift (1970), Clemmer (1971), Clemmer and Suttikus (1971), Howell and Williams (1971), Lachner and Jenkins (1971a, 1971b), Lachner and Wiley (1971), Snelson (1971), Gilbert and Bailey (1972), Hubbs and Miller (1972), Lugaski (1972), Robison and Miller (1972), Snelson (1972), Greenfield et al. (1973), Snelson (1973), Hubbs and Miller (1974), and Hubbs, Miller and Hubbs (1974).

Further sources are listed and discussed under certain character descriptions and in Appendix 2.

Criteria for character analyses

The criteria used in this study follow Marx and Rabb (1970, 1972) and their reasoning is reproduced below.

a) Designation of character states.

Characters are described by character states which indicate the relative variation of the character. At its simplest a qualitative character may have two states, e.g. scales present versus scales absent, although it may be manifested in several states. Quantitative characters, such as meristic data, represented by a few generic modes, could be assigned directly to character states, e.g. dorsal fin ray counts. In certain cases a generic modal value was not immediately apparent because of evolutionary trend(s) within the genus had given a wide range of modes. If two-thirds or more of the species were at a given mode then this was considered to represent the mode of the genus. Where two modal values were evenly split between species of a genus, the primitive mode, based on a comparison with other genera particularly the ancestral genus, was chosen. Where data was only available as ranges the following procedure was used. Non-overlapping classes were defined and each genus was assigned to its appropriate class. Where a generic range bridges the gap between two non-overlapping classes an additional intermediate class was erected unless the range fell into either adjacent class by two-thirds or more, e.g. Class 1 = 5-10, Class 3 = 11-16, then character range 8-13 would be

placed in the intermediate class 2 but character range 9-16 has two-thirds of its range in Class 3 and so is placed there. Character states may now be determined by observing major breaks in the frequency distribution of genera in the various classes. Several classes may be lumped into a few states if the frequency distributions warrant it.

- b) Determination of derived and primitive character states.

It is necessary to choose a genus to represent the ancestral characters so that characters in other genera may be analysed relative to it. Marx and Rabb (1972) consider this to be equivalent to "out-group" comparative analysis (Throckmorton, 1968). Whether the choice is logical or arbitrary it unequivocally determines a direction of change in any character having a state unique to "descendent" genera (see criterion 1 below).

The genus Notropis is designated as the "ancestral" group. It contains a majority of species of North American Cyprinidae and is to some extent heterogeneous. This is particularly true if species presently included in Hybopsis and Dionda are considered to belong to Notropis (see species list for comments). Most other genera are more restricted in abundance, distribution and phenetic variation. It seems probable that the members of this genus are more likely to have arisen from the same ancestors as other cyprinid genera, even if they are not directly on the evolutionary path to them.

1) Uniqueness

A character state is derived if it is unique to a descendent group. Other states occurring in both ancestors and descendents may be derived or primitive and it is necessary to examine them in the light of other criteria.

2) Relative abundance

A character state widely distributed in the ancestral group is primitive for descendent groups because such a state has a greater probability of having had its genotype transferred to various descendent stocks than does a rare state. It also follows that any other state of the same character that is rare in the ancestral group is a derived state in reference to the ancestral stock.

These two criteria and their application have been summarised by Marx and Rabb (1970) in tabular form:-

	<u>Character states</u>		<u>Interpretation of states in descendent</u>
	<u>Ancestor</u>	<u>Descendent</u>	
1.	a > b	a > b or a < b	a is primitive, b is derived
2.	a > b	a	a is primitive
3.	a > b	b	b is derived
4.	a	b > c or b < c	b and c are derived
5.	a > b	b > c or b < c	b and c are derived, b is more primitive than c
6.	a > b	a > c or a < c	a is primitive, c is derived

3) Correlation of derived states

A character state is derived if its occurrence is positively correlated with derived states of other characters. Such correlation probably results from a common genetic history of taxa but pleiotropy should be eliminated if recognised. Care was taken to eliminate potential states correlated by reasons of morphology, e.g. obviously fish lacking scales could not be correlated with a character such as absence of scale radii. When data is unavailable for reasons of logical necessity 999 is placed in the appropriate section of Table 10.

4) Morphological specialisation

A character state is derived if it is predominant in some adaptive specialisation. Within a given stock several morphological structures may be used to accomplish the same function e.g. character 2. Within a homogeneous group a specialised function is usually accomplished with the same structure. A state representing such a structure was probably selected from among the generalised states in the ancestral phenetic pool. The state may have arisen several times in parallel, but the direction of change would probably be the same in each instance; the common ancestral gene pool makes a similar response to similar selection pressure more likely.

5) Ecological specialisation

A character state is derived when it is relatively more abundant in taxa with a particular mode of life.

6) Geographic restriction

A character state is derived if it is predominant in taxa from a particular geographic area.

7) Closely related taxa

A character state is derived if it is chiefly abundant in a numerically restricted morphologically homogenous group of taxa since that state probably has common origin in these taxa. The tribe Plagopterini of the Colorado River system is an example.

8) Correlation of applied criteria

A character state is more probably derived if two or more of the above criteria agree in indicating phyletic direction. The more criteria which can be applied to a character's states, the more confidence can be attached to the character phyletics.

9) Genetic structure

Information is, at present, too limited to enable a general treatment of genetic structure. Some data on chromosome number is discussed (character 8).

10) Fossil record

The fossil record provides details of the phenetics of the actual lineage. Unfortunately cyprinid fossils to date have been ascribed to extant genera or seem to be products of local evolution and extinction. Intergeneric relationships have not been clarified by any fossil finds.

These criteria do not all have equal value. Criteria 1 and 6 are considered better than criterion 8, for example.

c) Directional sequence criteria

In characters with only two states determination of the derived state will give directional sequence. When more states occur the sequence may be unidirectional or multidirectional. Criteria indicating a single directional sequence of different states of a particular character are:-

- 1) A derived state represents intraspecific or intrageneric variation between two other states.
- 2) Derived states are correlated mostly with derived states of the same characters.
- 3) Taxa in the different states are predominantly abundant in the same habitat zones.
- 4) The states perform the same function.
- 5) A derived state is a logical intermediate condition between other states in a single gradient morphological continuum.

Criteria indicating different directional sequences of states of a particular character are:-

- 1) Derived states correlate mostly with derived states of different other characters.
- 2) Taxa in the derived states are predominantly abundant in different habitat zones.
- 3) Derived states perform different functions.

- 4) The primitive state has a logically intermediate relation to other states.
- 5) Derived states are overwhelmingly abundant in different unrelated taxa.
- 6) Derived states are abundant in taxa from different major geographic areas.

d) Character state trees and characters

The phyletic character analyses are presented in the form of character state trees. Types of trees found are given below with letters nearer the beginning of the alphabet indicating more primitive states. The coded values assigned in each character tree are given in parentheses.

<u>Number of States</u>	<u>Character Tree</u>	<u>Number of Characters</u>	<u>Characters</u>
<u>Unidirectional</u>			
2	A → B (0) (100)	9	4, 5, 6, 7, 24, 25, 26, 27, 28
3	A → B → C (0) (50) (100)	6	3, 9, 10, 11, 12, 23
4	A → B → C → D (0) (33) (67) (100)	1	14
5	A → B → C → D → E (0) (25) (50) (75) (100)	1	21
6	A → B → C → D → E → F (0) (20) (40) (60) (80) (100)	1	22
<u>Multidirectional</u>			
3	B → A → C (50) (0) (100)	1	2
4	B → A → C → D (33) (0) (67) (100)	4	16, 17, 19, 20
5	E → D → A → B → C (50) (25) (0) (75) (100)	1	8
5	B → A → C → D → E (25) (0) (50) (75) (100)	2	13, 18
6	B → A → C → D → E → F (20) (0) (40) (60) (80) (100)	1	15

Procedure for analysis of character states

Two state characters are scored 0 (primitive) or 100 (derived). Multiple state characters are assigned scores by sub-division of the 0 to 100 range, e.g. a four state character would be scored 0, 33, 67 and 100. Where the character state is unknown for a genus either because of lack of data or logical necessity, the character is scored as 999. These scores are necessitated by the computer program and hardware used. For program listings see Appendix 5.

Hennig's coefficient was calculated for each pair of taxa using the formula:-

$$\text{Hennig's coefficient} = \frac{\text{Number of derived characters shared by both taxa.}}{\text{Number of characters which are derived in one or both taxa.}}$$

Hennig's coefficient was devised by D.E. McAllister to measure relationships between taxa in the sense of Hennig (1966). A computer program written by McAllister run on a Hewlett-Packard 9830 minicomputer was used to calculate the Hennig's coefficients for this study. The coefficient can vary between 0 and 100 (or between 0 and 1 if desired). The coefficients will only be a good a measure of relationship as the set of characters selected and the correctness with which the derivedness of character states is assigned. Coefficients of 0 indicate that the pair of taxa are completely unrelated. Higher values indicate closer degrees of relationships.

If the number of taxa and characters are few phylogenies can be worked out by hand. When the taxa are numerous it is much more difficult to disentangle the web of possible relationships. The program has the advantage that the number of characters can be increased, e.g. see section on Nearctic - Palaearctic relationships.

After Hennig's coefficients have been calculated, each genus is then paired with that genus with which it shares the highest coefficient, e.g. Acrocheilus had its highest coefficient with Mylocheilus. Since Mylocheilus had its highest coefficient with Acrocheilus these two genera can be linked and the available character states recoded for the linked group. Recoding is carried out as follows. The same states of a character in each genus remain the same in the new linked group. Where the states differ the least advanced is chosen to represent the linked group, e.g. the pair 100 - 0 becomes 0, 50-25 becomes 25 etc. State 999 (data not available) is always retained in the new group.

In cases where the second member of a pair of genera did not have its highest coefficient with the first member but with a third genus, the pair of the trio with the highest coefficient is grouped (but only where the difference in coefficients exceeds 0.010, otherwise the coefficients are deemed to be equal; the difference was less than 0.010 in only one instance when Meda was grouped with the pair Lepidomeda - Plagopterus and the coefficient for Lepidomeda - Meda was 0.462 and Plagopterus - Meda was 0.467 - a difference of

0.005) e.g. Ericymba had its highest coefficient (0.400) with Hybognathus but Hybognathus paired at a higher level (0.600) with Dionda (and Dionda had its highest coefficient with Hybognathus). Ericymba therefore could not be grouped with another genus in this cycle and entered the next cycle unpaired. Where the highest coefficient between a given genus and another genus is matched by an equal coefficient between the latter and a third genus, degree of advancement scores (Table 11) are calculated according to the formula:-

$$\text{Degree of advancement} = \frac{\text{Total of character codes}}{\text{Number of available characters}}$$

Characters coded 999 (data not available) are omitted in the numerator and denominator. An example of this pairing procedure follows, e.g. Oregonichthys and Algansea had a coefficient of 0.500 but so did Oregonichthys and Nocomis. Degree of advancement scores were 33.1 for Algansea, 19.8 for Nocomis and 17.1 for Oregonichthys. The latter two genera were paired because their degree of advancement scores are closest. Algansea's higher score indicates it possesses more derived characters than either Nocomis or Oregonichthys.

After all possible links in this cycle have been made, Hennig's coefficients are recalculated on the recoded data. The linking is repeated with the new coefficients and the process continued until no further coefficients exist between groups or all groups are linked.

RESULTS

A total of 28 characters were used in the analysis of the 49 North American genera and the types of character trees found are summarised above. Marx and Rabb (1972) list several other types of trees. The maximum number of states in the present study for a character was 6, and the mean number of states per character was 3.3. There was a total of 1372 states, 895 primitive and 402 derived (75 states were unknown).

Three other types of characters were encountered but these could not be used in this survey. Single state characters are not susceptible to phyletic analysis within the group, e.g. possession of a Weberian apparatus. Non-directional characters are those with more than one state whose direction cannot be determined because no criteria are applicable.

A third type of character cannot be used in relating genera but is included in the survey. This type is the derived character unique to a genus. Such characters can be used to determine degree of advancement or derivativeness of a genus:-

Campostoma

An elongate intestine is coiled around the gas bladder.

Eremichthys

Horny sheaths are present on both the upper and lower jaws. Both Acrocheilus and Rhinichthys have lower jaw sheaths, the latter genus only occasionally. A detailed examination of these sheaths was not undertaken.

Ericymba

Reno (1971) has described the unique cavernous expansions of the infraorbital and preoperculomandibular canals of this monotypic genus.

Iotichthys

Portions of the frontal and parietal bones on the dorsal head surface do not ossify in this genus leaving a large fontanelle in alizarin stained specimens. (see osteology section of this study).

Notemigonus

This genus is unique within N. America in its possession of a naked ventral keel (see scale descriptions).

Orthodon and Xystrosus

Both these genera have unique gill raker structures as described in the osteology section.

Phenacobius, Exoglossum and Perexoglossum

These genera have modified lower jaws figured by Moore (1968). Osteology of these jaws is discussed elsewhere in this thesis.

Pimephales

The first dorsal ray in adult males is short, blunt, thickened and separated by a membrane from the second ray.

Pogonichthys

The upper caudal fin lobe is longer than the lower lobe in adults.

Ptychocheilus

The body is long and pike-like with a long and pointed snout.

There are doubtless many other more subtle unique characters which could be revealed by diligent searching. In addition tubercle patterns are often unique to a genus, e.g. in Notemigonus (see Nearctic-Palaeartic relationships section).

Character correlation coefficients

Correlation coefficients were determined for all character pairs. It is suggested that any character showing no significant correlation ($P > 0.05$) with any other character should be discarded since it contributes no useful information. Only character 8 (chromosome number) showed no correlation with any other character and this may be accounted for by the lack of data for many taxa. Conversely characters showing very high correlations with other characters indicate an element of redundancy (perhaps through pleiotropy) and should also be discarded. It is difficult to draw the line

between correlation due to redundancy and correlation due to a common descent. Certainly, all characters having a correlation above $r=0.900$ should be discarded. The highest positive correlation coefficient was between characters 4 and 5 ($r=0.808$). The range in positive correlation coefficients was $0.292-0.808$, mean 0.476 . Significant negative correlation coefficients were comparatively rare (8 out of 76 or 10.5%, range -0.302 to -0.541 , mean -0.370). It is suggested that a predominately negative series of significant correlation coefficients for a character indicates that it was coded in the wrong direction. Character 2 (presence or absence of barbels) had its only significant correlation, a negative one, with character 11 (three other correlations of character 11 with other characters were positive). It is not considered that character 2 was coded in the wrong direction (barbels primitive, absence of barbels derived) as there is evidence to show that possession of barbels is a derived condition, albeit independently derived in several North American genera (see Jenkins and Lachner, 1971; Gilbert and Bailey, 1972).

Matching coefficients

The data accumulated for this study were analysed by Hennigian methods and the data were scored appropriately. Not all the data were therefore suitable for numerical analysis although all unidirectional characters were. Nevertheless calculation of matching coefficients was undertaken to give a rough comparison of numerical and

Hennigian methods. At the first clustering cycle 6 out of 10 linkages in the numerical method were the same as those found for the Hennigian method (there were 13 initial linkages in the latter method). Also a correlation coefficient based on 86 pairs of matching and Hennig's coefficients gave a correlation coefficient of 0.713 ($P < 0.001$). Numerical methods therefore show a moderate degree of similarity to Hennigian methods which suggests that they might be used to some extent in assessing relationships where complex derived characters are hard to find.

The following pages describe the various characters and give phyletic conclusions for these characters. Character states are summarised in Table 10. The phylogenetic trees resulting from analysis of characters states are presented as Figures 58-63. The genera Evarra and Stypodon, on which adequate data were lacking, were eliminated from consideration when compiling the trees.

Character 1 - Distribution and Zoogeography

Character description

There are two principal drainage basins for cyprinid genera within North America, the Atlantic - Gulf of Mexico drainage and the Pacific drainage. The North American Cordillera formed during the late Cretaceous, effectively separates these two basins. In both areas species, and in some cases genera, may be restricted to certain smaller drainages but this is particularly marked on the Pacific slope which has more monotypic genera and endemic species of cyprinids than in the east (Miller, 1959).

Cyprinids are generally believed to have entered North America via a Bering land (and water) bridge from Asia (Darlington, 1957; Miller 1965). Fossils have been recovered from middle - Miocene and Oligocene beds in Montana (Uyeno and Miller, 1963; M. Wilson, pers. com. 1974) and entry may have occurred in the early Oligocene. Certainly a land bridge existed through most of early and middle Tertiary time (Hopkins, 1967). A tranatlantic or transarctic land

connection has been suggested by Banareseu (1965) and Leippman and Hubbs (1969) as a dispersal route from Europe to North America. Such a connection may have existed in the early Tertiary (Hopkins, 1967), but on the evidence of the North American fossil record this is too early to be of interest here. However White (1931) reported an Eocene cyprinid from England and Orlov (1964) and Romer (1966) listed several records of Palaeogene (possibly Palaeocene) cyprinids from Eurasia. It should also be noted that the majority of Eurasian and North American fossil cyprinids have been assigned to extant genera, or represent genera of local distribution and probably evolution which became extinct because of climatic changes (Miller, 1965; Uyeno and Miller, 1965). Hallam (1973) and Romer (1973) suggest that a land connection between North America and Europe lasted until the early Eocene on the evidence of a close similarity in mammal faunas up to this time followed by a sharp divergence. The possibility that this route was used by cyprinids cannot be ruled out but its vindication depends on the discovery of Palaeogene American cyprinids.

The entry route(s), the specie(s) entering and exact time of entry are unknown and the possibility of multiple entries cannot be excluded at present. The Pleistocene glaciations have been a major influence on the distribution of cyprinids but have also obscured pre-Pleistocene drainage patterns. It is possible that a Pacific coastal dispersal took place to populate river systems draining west from the

North American Cordillera. Although cyprinids are regarded as primary division fishes (Darlington, 1957) certain species are tolerant of saltwater in varying degrees e.g. the sea-run Japanese genus Tribolodon suggested by Miller (1959) to be related to the western American genus Gila; Mylocheilus caurinus (Clark and McInerney, 1973) and Pogonichthys macrolepidotus (Moore, 1968) of western American rivers and Hybognathus nuchalis, Notemigonus crysoleucas, Notropis bifrenatus and Notropis hudsonius (Mansueti and Hardy, 1967; Musick, 1972) and Notropis petersoni (Bailey, Winn and Smith, 1954) of eastern North America. A second route into North America utilizing major river systems similar to the present day Yukon, Mackenzie and Missouri would have given access to the eastern lowlands for truly primary division fishes. Alternatively eastern genera may have entered from Europe (see above). Banarescu (1969) suggests that immigrants from Siberia reached western North America (and presumably dispersed eastwards over the Cordillera) and were replaced in eastern North America by more modern genera. Subsequent colonisation of western North America by immigrants from the east is also advocated but these movements are not clearly defined at the generic level.

Variation within a genus

Certain species in some genera e.g. Gila, Notropis Rhinichthys, occur on both slopes of the Cordillera but the majority of species and probable centre of origin of the

genus can be allocated to western or eastern drainages. Gila is thus regarded as a western genus and Notropis as an eastern genus. The genus Rhinichthys presently contains five species, three in western drainages, one in eastern drainages and one distributed across northern North America. This genus is somewhat arbitrarily assigned to the western drainage where most species and subspecies occur (Hubbs and Miller, 1972; Hubbs, Miller and Hubbs, 1974).

Character states

State 0 - Atlantic - Gulf of Mexico drainages

State 100 - Pacific drainages

The close relationship of Lepidomeda, Meda and Plagopterus which are restricted to the Colorado River basin is acknowledged but this derivation from State 100 is not separately codified here.

Phyletics

Both states may be regarded as derived relative to the unknown Eurasian ancestor(s). With reference to the "ancestral" genus Notropis, an eastern taxa, western genera are derived. However the states are mutually exclusive and a directional sequence between them is not implied.

Character 2 - Barbels

Character description

Certain North American species of cyprinids possess barbels, others lack them. Possession of a terminal maxillary barbel has been used as a key character for separating

Hybopsis s.l. from Notropis and in defining other genera. However, the character is variable and labile (Jenkins and Lachner, 1971; Gilbert and Bailey, 1972; Cortes, 1968) but it is still possible to characterise genera as barbeled or non-barbeled - "the capacity to develop a barbel..... is of more significance than its actual presence or absence" (Hubbs and Miller, 1948a). A second type of barbel is found in the groove between the upper lip and the flesh covering the edge of the lachrymal bone. The barbel is a flap of tissue positioned well anterior to the mouth angle and not produced.

Variation within a genus

Only three genera are listed here as non-barbeled but contain some barbeled species or individuals. These are Notropis (see Cortes, 1968), Diionda (see Hubbs and Miller, 1974) and Pimephales in which nuptial males of P. notatus develop a barbel-like protuberance from the posterior angle of the lips. In these genera the majority of species lack barbels and the barbel-like structure in P. notatus is a transient phenomenon. The genus Phenacobius is regarded here as barbeled since Phenacobius catostomus, crassilabrum, teretulus, and uranops have a flap-like structure in the upper lip groove similar to that in Semotilus and Margariscus. It is absent from Phenacobius mirabilis (Gilbert and Bailey, 1972). Most genera have a fold of skin in this groove but development into a barbel is restricted to the above species and possibly to some species of Hybopsis.

sub-genus Erimystax as noted by Jenkins and Lachner (1971) and Branson (1962). However the latter also possess a terminal maxillary barbel and a single specimen of Hybopsis x-punctata examined for the present study showed a structure similar to that depicted by Branson (1962), and unlike Semotilus, Margariscus and Phenacobius. A maxillary barbel is absent from two species of Algansea s.s. (lacustris, and tincella) and present in four species (barbata, monticola, avia MS and aphanea MS) according to R.R. Miller (pers. comm. 1975).

Further discussions on barbel variability may be found in the studies cited above.

Character states

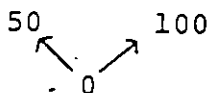
State 0 - Barbel absent

State 50 - Flap-like maxillary barbel in groove above upper lip well in advance of mouth angle.

State 100 - Terminal maxillary barbel present i.e. barbel is pendant from or very close to mouth angle or corner.

Phyletics

Possession of a barbel or capacity to develop one is regarded as a derived condition (criteria 2,3,4,5,8). The character path is bidirectional on gross morphological grounds but slight differences in position



and developmental complexity indicate that barbels of State

100 may be derived independently in many of the genera. The flap-like barbel (State 50) of Margariscus, Phenacobius and Semotilus is very similar but the presence of a skin fold in the upper lip groove of most genera of N. American cyprinids examined makes an independent evolution of this character a possibility not to be ignored..

Character 3 - Protrusion of premaxillae

Character description

The premaxillae may be protrusible (frenum absent) or not (frenum present).

Variation within a genus

The only recognized genus containing species with both protrusible and non-protrusible premaxillae is Rhinichthys. Premaxillae are protrusible in Rhinichthys falcatus, variably protrusible and non-protrusible in Rhinichthys osculus, and non-protrusible in Rhinichthys atratulus, cataractae, and evermanni.

Character states

State 0 - Protrusible premaxillae

State 50 - Species with states 0 and 100

State 100 - Non-protrusible premaxillae

Phylogenetics

Character state 100 is considered to be derived (criteria 1,3,4,8) and character state 50 is transitional between 0 and 100, i.e. 0 50 100.

Character 4 - Thickened pelvic rays

Character description

This character is restricted to members of the tribe Plagopterini in the Colorado River system. Miller and Hubbs (1960) furnish a description.

Character states

State 0 - Pelvic rays not thickened

State 100 - Pelvic rays thickened

Phylogenetics

Character state 100 is derived (criteria 1,3,4,6,7,8)

Character 5 - Scalation

Character description

Scales are absent (i.e. reduced to bony platelets) or present over most of the body. Reduction or absence is restricted to certain members of the tribe Plagopterini of the Colorado River system. The character is described more fully elsewhere in this thesis.

Character states

State 0 - Scales present

State 100 - Scales absent or reduced to bony platelets

Phylogenetics

Reduction or loss of scales is a derived condition (criteria 1,3,4,5,6,7,8).

Pharyngeal Tooth Count

Character description

Teeth in cyprinids are found only on the modified fifth ceratobranchial arches and are known as pharyngeal teeth. North American cyprinids have teeth in one or two rows (Vladykov, 1934) (and very rarely in three rows in Semotilus according to Moore (1968) but this instance was probably due to faulty tooth replacement). The inner row is called the major row and the outer row the minor row and counts are expressed thus 2,5-4,2 i.e. minor row teeth 2 left and right, major row teeth 5 left and 4 right. Eastman and Underhill (1973) and Gilbert and Bailey (1972) have suggested that trends in major row tooth gain and minor row tooth loss exist in some genera while others retain a static formula. A trend to reduction in major row teeth is only found in rare variants of Nocomis leptcephalus and certain Notropis species (Lachner and Jenkins, 1967; Eastman and Underhill, 1973). Presumably in Stypodon signifer (0,3-3,0) this trend finds its unique expression and other cases are examples of faulty development.

Similar rare cases of minor row tooth counts greater than 2 have been reported and these too may be due to faulty development, specifically tooth replacement (Eastman and Underhill, 1973).

Modal tooth counts were determined from literature reports and available specimens (Table 6). The two trends were analysed on the modal count and are codified separately

TABLE 6

Modal values for pharyngeal teeth and dorsal,
anal and pelvic fin rays.

GENUS	PHARYNGEAL TEETH	DORSAL RAYS	ANAL RAYS	PELVIC RAYS
<i>Acrocheilus</i>	0,5-4,0	10	9	9
<i>Agosia</i>	0,4-4,0	8	7	8
<i>Algansea</i>	0,4-4,0	8	7	8
<i>Camposoma</i>	0,4-4,0	8	7	8
<i>Chrosomus</i>	0,5-5,0	8	8	8
<i>Clinosomus</i>	2,5-4,2	8	8	8
<i>Couesius</i>	2,4-4,2	8	8	8
<i>Dianda</i>	0,4-4,0	8	8	8
<i>Eremichthys</i>	0,5-4,0	8	8	8
<i>Ericymba</i>	1,4-4,1	8	8	8
<i>Erismylax</i>	0,4-4,0	8	7	8
<i>Evarna</i>	0,4-4,0	8	7	-
<i>Exoglossum</i>	1,4-4,1	8	7	8
<i>Extharius</i>	0,4-4,0	8	7	8
<i>Gila</i>	2,5-4,2	8	8	8
<i>Hemistremia</i>	2,5-4,2	8	8	8
<i>Hesperoleucus</i>	0,5-4,0	8	7	8
<i>Hybognathus</i>	0,4-4,0	8	8	8
<i>Hybopsis</i>	1,4-4,1	8	8	8
<i>Iotichthys</i>	2,5-4,2	8	8	8
<i>Lavinia</i>	0,5-5,0	11	12	9
<i>Lepidomeda</i>	2,5-4,2	10	9	7
<i>Macrhybopsis</i>	1,4-4,1	8	8	8
<i>Margariscus</i>	2,5-4,2	8	8	8
<i>Meda</i>	1,4-4,1	9	9	7
<i>Moapa</i>	0,5-4,0	8	8	8
<i>Mylocheilus</i>	1,5-5,1	8	8	9
<i>Mylopharodon</i>	2,5-4,2	8	8	9
<i>Nocomis</i>	1,4-4,1	8	7	8
<i>Nolemigonus</i>	0,5-5,0	8	8-19	9
<i>Nothopsis</i>	2,4-4,2	8	8	8
<i>Opsopocodus</i>	0,5-5,0	9	8	8
<i>Oregonichthys</i>	1,4-4,1	8	7	8
<i>Orthodon</i>	0,6-6,0	10	8	10
<i>Panexoglossum</i>	1,4-4,1	8	7	8
<i>Phenacobius</i>	0,4-4,0	8	7	8
<i>Pimephales</i>	0,4-4,0	8	7	8
<i>Plagopterus</i>	1,5-4,1	10	10	7
<i>Platygobio</i>	2,4-4,2	8	8	8
<i>Pogonichthys</i>	2,5-5,2	9	8	9
<i>Ptychocheilus</i>	2,5-4,2	9	8	9
<i>Relictus</i>	0,4-4,0	8	7	8
<i>Rhinichthys</i>	2,4-4,2	8	7	8
<i>Richardsonius</i>	2,5-4,2	8	8-24	9
<i>Scmotelus</i>	2,5-4,2	8	8	8
<i>Scleropoda</i>	0,3-3,0	8	8	8
<i>Tetrago</i>	1,4-4,1	8	7	8
<i>Xystesius</i>	0,4-4,0	8	7	9
<i>Yunnan</i>	0,4-4,0	8	8	10

as Character 6 and Character 7.

Variation within a genus

There is often considerable variation in counts between individuals of certain species while others have remarkably consistent counts (Eastman and Underhill, 1973). One formula usually predominates and may be taken as the typical count.

Formulae may also vary between species of a genus and such differences have been used in separating genera in the past. Chrosomus (Pfrille) neogaeus, for example, has teeth in two rows while the other three species in Chrosomus have teeth in one row. The genus is characterised here as one rowed. In Gila the majority of genera have two rows but species with one row exist (G. bicolor, G. mohavensis) and at least a limited trend to reduction is evident. The genus is characterised as two rowed since the majority of species fall in this category. A trend to reduction in minor row teeth is apparent in Rhinichthys where the species osculus commonly has 1,4-4,1 variants typifying certain subspecies. The majority of species are 2,4,-4,2 however. Lepidomeda vittata is usually 2,4-4,2 while other species of this genus are modally 2,5-4,2. In Notropis minor row counts for 100 species were 2 (50%), 1 (24%) or 0 (26%) and a trend to reduction is obvious. It was, however, scored as 2,4-4,2 arbitrarily.

Character states

Character 6 - Major row pharyngeal teeth

State 0 - Major row tooth not gained (count
3 or 4)

State 100 - Major row tooth gained (count 5 or 6)

Character 7 - Minor row pharyngeal teeth

State 0 - Minor row tooth not lost (count 2)

State 100 - Minor row tooth lost (count 0 or 1)

Phyletics

It seems probable that the trends analysed as Characters 6 and 7 are independent in certain genera and do not indicate a close phylogenetic relationship, cf. Notemigonus and Opsopoeodus with identical counts but differing in other, trenchant characters.

Chu (1935) stated that 5 was the primitive major row count for Cyprinidae and that specializations occurred by increase or decrease. In considering Chu's work Gilbert and Bailey (1972) suggest that a reversal of this earlier phyletic trend to reduction in major row count may have occurred in certain North American cyprinids. Eastman and Underhill (1973) consider that "many" North American cyprinids were derived from ancestral stocks which possessed 4 major row teeth before populating North America.

Eastman and Underhill (1973) support Chu (1935) in believing that North American cyprinids have undergone reduction in number of tooth rows further to that of East Asian forms from which North American cyprinids are presumably derived. Minor row teeth, primitively 4 after Chu, have been gradually lost and are completely absent in some

genera. Apparently major row teeth possess a greater utility than minor row teeth because the latter are lateral to the main occlusal area. Selection favours loss of minor row teeth and gain in major row teeth, at least in species with a plastic tooth formula (Eastman and Underhill, 1973).

These trends are not necessarily universal although nearly all genera show at least one. The present treatment of a complex subject, not yet fully understood, presupposes an ancestral tooth formula of 2,4-4,2. Since it is possible that North American cyprinids are derived from several invading species, this may be an oversimplification but it does provide a starting point for comparison. The ancestral group Notropis is equivocal, 50% of species being 2,4-4,2 and 50% being 0 or 1,4-4,1 or 0.

Character 8 - Chromosome number (2n)

Character description

The chromosome number (2n) in North American cyprinids varies from 46 to 52 (Denton, 1973; Stewart, 1966; Greenfield et al, 1973; Greenfield and Greenfield, 1972; Uyeno and Miller, 1973):-

- 2n = 46 (Acrocheilus alutaceus)
- 2n = 48 (Opsopoeodus emiliae, Exoglossum maxillingua)
- 2n = 50 (Chrosomus eos, Chrosomus erythrogaster, Chrosomus eos x, C. naogoeus,
Coesius plumbeus, Gila ~~argentea~~ hesperoleucus symmetricus, Lepidomeda
molispinis, Lepidomeda vittata, Meda fulgida, Notemigonus crysoleucas,
Notropis callistius, Notropis cornutus, Notropis lutrensis, Notropis
texanus, Notropis venustus, Pimephales promelas, Plagopterus
argentissimus, Relictus solitarius, Rhinichthys evermanni, Semotilus
margarita)
- 2n = 52 (Pimephales notatus, Ptychocheilus oregonensis, Semotilus atromaculatus,
Semotilus corporalis)

Variation within a genus

The only variation within a genus is for Pimephales. Legendre and Steven (1969) report $2n = 52$ for Pimephales notatus while Levan et al. (1964) report $2n = 50$ for Pimephales promelas. Semotilus (Margariscus) margarita has a lower count than Semotilus corporalis and Semotilus atromaculatus. Campos and Hubbs (1973) remove Opsopoeodus from Notropis because of its lower chromosome number.

Character states

- State 0 - $2n = 50$
- State 25 - $2n = 50$ and 52 (variable between species of genus)
- State 50 - $2n = 52$
- State 75 - $2n = 48$
- State 100 - $2n = 46$

Phylogenetics

Character state 0 is regarded as the most primitive (criteria 1,8,9) and the other states are derived. $2n = 50$ is also the commonest chromosome number in Eurasian cyprinids (Denton, 1973; Chiarelli and Capanna, 1973; Berberovic and Sofradzija, 1972; Sofradzija and Berberovic, 1972; Berberovic et al., 1970; Itoh and Niiyama, 1972; Ojima, Hayashi and Ueno, 1972; Raicu, Taisescu and Banarescu, 1973; Rudek, 1974) although some tetraploids have also been reported (Ohno et al., 1967; Berberovic et al., 1973; Sofradzija and Berberovic, 1973).

It is evident that chromosome number alone is not sufficient for interpreting relationships between all North

American cyprinids because the range of variation is so limited. Its value in certain cases, eg. Opsopoeodus in relation to Notropis, Margariscus in relation to Semotilus, seems evident but Uyeno and Miller (1973) have observed that distinctly different karyotypes may develop between closely related species because of Robertsonian fusions whereas distinct species in different orders may show virtually identical karyotypes (see also Ohno, 1974).

The value of chromosome studies, therefore, lies in detailed comparative analyses of number, centromere position, size, D.N.A. content, banding etc. between supposedly related species or within small monophyletic groups.

Character 9 - Distribution of scale radii

Character description

Scales bear radii which may be distributed in all fields or restricted principally to the posterior field. A fuller description is given elsewhere in this thesis.

Character states

- State 0 - Radii on posterior scale field
- State 50 - Species or individuals varying between states 0 and 100
- State 100 - Radii on all fields

Phyletics

By reference to the ancestral group Notropis, state 100 is derived (criteria 1,3,6,8). State 100 may have been in-

dependently acquired in several western genera (Hubbs, Miller and Hubbs, 1974).

Character 10 - Third urodermal bone

Character description

The third urodermal bone in the caudal skeleton may be present, absent or variably present and absent within individuals of a species or between species of a genus. Further descriptions are given elsewhere in this thesis (see also p. 300).

Character states

State 0 - Third urodermal present

State 50 - Third urodermal present or absent

State 100 - Third urodermal absent

Phyletics

Character state 100 is derived (criteria 1,3,8) and character state 50 is regarded as a transitional stage leading to loss of the third urodermal.

Character 11 - Sixth hypural bone

Character description

The sixth hypural bone in the caudal skeleton may be present, absent or variably present and absent within individuals or species of a genus. Further descriptions are given elsewhere in this thesis (see also p. 300).

Character states

State 0 - Sixth hypural present

State 50 - Sixth hypural present or absent

State 100 - Sixth hypural absent

TABLE 7

Hypural numbers and presence of third urodermal

Genus	Number of hypurals	Presence (+)/ Absence (-) of third urodermal
<i>Achocheilus</i>	6	+
<i>Agosia</i>	6	+
<i>Algansea</i>	6	+ -
<i>Campostoma</i>	5-6	+
<i>Chrosomus</i>	6	+ -
<i>Clinostomus</i>	5-6	+
<i>Gobesius</i>	6	+
<i>Dionda</i>	5-6	-
<i>Eremichthys</i>	5-6	+ -
<i>Ericymba</i>	6	+
<i>Elimystax</i>	6	+
<i>Evarra</i>	SPECIMENS NOT AVAILABLE	
<i>Exoglossum</i>	6	+
<i>Extrarius</i>	6	+
<i>Gila</i>	5-6	+ -
<i>Hemistremia</i>	5-6	-
<i>Hesperoleucus</i>	6	+
<i>Hybognathus</i>	5-6	+
<i>Hybopsis</i>	6	+
<i>Isoichthys</i>	5-6	-
<i>Lavinia</i>	6	+
<i>Lepidomeda</i>	5-6	+
<i>Macrhybopsis</i>	6	+
<i>Margariscus</i>	6	+
<i>Neda</i>	5	-
<i>Noapa</i>	5-6	+ -
<i>Nylocheilus</i>	6	+
<i>Nylopharodon</i>	6	+
<i>Nocomis</i>	6	+ -
<i>Notemigonus</i>	5-6	-
<i>Notropis</i>	5-6	+
<i>Opsopocodus</i>	6	+
<i>Oregonichthys</i>	6	+ -
<i>Orthodon</i>	5-6	+ -
<i>Paraxoglossum</i>	6	+
<i>Phenacobius</i>	6	+
<i>Pimephales</i>	5-6	+
<i>Plagopterus</i>	6	+
<i>Platygobio</i>	6	+
<i>Pogonichthys</i>	6	+
<i>Psychocheilus</i>	6	+
<i>Relictus</i>	5-6	+
<i>Rhinichthys</i>	5-6	+
<i>Richardsonius</i>	5-6	+
<i>Semotilus</i>	6	-
<i>Stypodon</i>	SPECIMENS NOT AVAILABLE	
<i>Tiaroga</i>	6	+
<i>Xystesius</i>	6	+
<i>Yuriria</i>	6	+

Phyletics

Character state 100 is derived (criteria 2,3,8) and character state 50 is regarded as a transitional stage leading to loss of the sixth hypural.

Character 12 - Postcleithrum bone

Character description

The postcleithrum bone of the pectoral girdle may be present and elongate, present and reduced to a short splint, or absent. This character is described more fully elsewhere in this thesis.

Variation within a genus

One genus, Rhinichthys, contains species with an elongate postcleithrum (osculus and falcatus) and species with a reduced or absent postcleithrum (atratus, cataractae, evermanni). The latter conditions vary with the individual. Rhinichthys was arbitrarily scored as state 50.

Character states

State 0 - Postcleithrum present and elongate

State 50 - Postcleithrum present and reduced

State 100 - Postcleithrum absent

Phyletics

Reduction or loss of the postcleithrum is a derived condition (criteria 1,3,8). It seems probable that the reduction or loss is independent in Extrarius, Notemigonus, Rhinichthys, Tiaroga and in the Plagopterini (Meda and Plagopterus) as these genera are different in many other characters.

Character 13 - Modal anal ray count

Character description

The majority of genera have a characteristic modal, anal ray count. Counts were made on available specimens and derived from literature sources using the generally accepted method of Hubbs and Lagler (1964).

Variation within a genus

The species of certain genera have evolved several modal counts. In Notropis modes range from 7 to 12 for 107 species with frequencies at 7 of 21.5%, at 8 of 32.7%, at 9 of 20.6%, at 10 of 17.8%, at 11 of 6.5% and at 12 of 0.9%. The mode of the modes is 8 but substantial numbers are found at other modes. In Erimystax four species have modal counts of 7 and two have modal counts of 8 and the mode for the genus is taken as 7. In Hybopsis one species has 7 rays and six species have 8 rays so the modal count is regarded as being 8. In the genera Clinostomus and Ptychocheilus modes of 8 and 9 are evenly distributed between the species and an arbitrary choice of the lower count of 8 was made to characterise the genus. The genus Evarra is characterised by a modal count of 7 although one of its three species has 14 anal rays. This species, Evarra tlahuacensis Meek, is represented by a single apparently normal, type specimen in the Field Museum of Natural History, Chicago. In Gila modal counts range from 7 to 10 but 8 is the most frequent.

In Dionda erimyzonops the modal number is 9 in contrast to the other 4 species which have 8. Two genera Richardsonius

and Notemigonus have evolved a wide range in anal ray counts, 8-24 and 8-19 respectively. These genera differ in many other respects and this character evolved independently. These genera both share a deep body, decurved lateral line and a tendency towards numerous anal fin rays. The latter two features may be adaptive responses to a deep body. No attempt was made to determine a mean or modal value in these two genera since these vary with the population examined and these genera were scored as 999 (data not available).

Character states

- State 0 - Modal count of 8 anal rays
- State 25 - Modal count of 7 anal rays
- State 50 - Modal count of 9 anal rays
- State 75 - Modal count of 10 anal rays
- State 100 - Modal count of 12 anal rays

Phyletics

A modal count of 8 anal rays is regarded as primitive (criteria 2,3,8) and other counts are derived (see Table 6) by reduction (7) or increase (9-12 and wide ranging).

Character 14 - Modal dorsal ray count

Character description

A modal dorsal ray count may be determined for each genus as with anal ray counts. Ossified rays in the Plagopterini were each counted as one ray both here and in the anal and pelvic fins. Counts are given in Table 6.

Variation⁵ within a genus

Modal counts for species of Notropis range from 7 to 9 but 8 is by far the most frequent (approximately 90%). In Clinostomus and Richardsonius modal counts of 8 and 9 were evenly distributed between the included species. The genus Rhinichthys contains three species with modes at 8 and two species with modes at 9. In these three genera a mode of 8 was chosen with reference to the ancestral genus Notropis. In Ptychocheilus the mode is 8 for one species and 9 for three others and the latter value was taken as the generic mode. Algansea species have modes at 7 and 8 but 8 is the most frequent (R.R. Miller, pers. comm. 1975). Modal values for 15 species of Gila were 7 (1), 8 (9), 9 (4), 10 (1) and a mode at 8 was chosen to represent the genus.

Character states

- State 0 - Modal dorsal ray count 8
- State 33 - Modal dorsal ray count 9
- State 67 - Modal dorsal ray count 10
- State 100 - Modal dorsal ray count 11

Phyletics

A modal dorsal ray count of 8 is regarded as primitive (criteria 2,3,8) with other counts derived.

Character 15 - Total vertebral number

Character description

Total vertebral number as a range was determined from radiographs, alizarin preparations and literature reports.

The count included the Weberian apparatus as four vertebrae and the hypural plate as one vertebra. Literature counts were modified to be consistent with this method.

Comparisons of caudal and pre-caudal counts may also prove fruitful but such information was not readily available. Variation within a genus

Attempts to use modal counts as characteristic of a genus were frustrated by poor information in the literature but more especially by marked variation interspecifically and intraspecifically within a genus. Macrhybopsis gelida has a modal count of 39 while in M. meeki it is 43. Platygobio gracilis gracilis has a modal count of 45 but in Platygobio gracilis gulonella it is 40. Modal values for 46 Notropis species ranged from 35-41 though the majority of modes were less than 40. Other examples of modal variation are common in speciose genera. (Table 8). Notropis was placed in class 3 and Gila in class 5. Knowledge of additional modes may necessitate re-allocation of these genera.

Character states

Genera were assigned to classes based on their range in total vertebral number except for Notropis and Gila:-

Class	Range in vertebral number	Number of genera
1	30-34	0
2	Intermediate	1
3	35-39	19
4	Intermediate	9
5	40-44	13
6	Intermediate	3
7	45-49	2

TABLE 8

Total vertebral number

Genus	Range	Species Mode(s)
<i>Acrocheilus</i>	44-46	45
<i>Agosia</i>	36-39	37
<i>Algansca</i>	33-42	36, 38, 41
<i>Camposoma</i>	40-42	?
<i>Chasomus</i>	35-40	?
<i>Clinostomus</i>	38-42	40, 42
<i>Coesius</i>	39-44	42
<i>Diorda</i>	33-39	34, -
<i>Exemichthys</i>	34-36	35
<i>Exicymba</i>	34-36	35
<i>Eximysax</i>	36-43	37, 38, 39, 40, 42
<i>Evanna</i>	NOT AVAILABLE	
<i>Exoglossum</i>	37-40	38
<i>Extrarius</i>	34-39	36
<i>Gila</i>	35-50	37, 42, 44, -
<i>Hemistremia</i>	36-38	37
<i>Hesperoleucus</i>	37-41	38
<i>Hybognathus</i>	35-39	?
<i>Hybopsis</i>	35-41	36, 37, 38, 39, 40
<i>Isoichthys</i>	34-35	35
<i>Lavinia</i>	40-44	42
<i>Lepidomeda</i>	41-44	41, 42, 43
<i>Macrhybopsis</i>	39-43	39, 43
<i>Margariscus</i>	37-42	41
<i>Meda</i>	39-42	40
<i>Moapa</i>	36-37	37
<i>Mylocheilus</i>	42-48	45
<i>Mylopharodon</i>	46-47	47
<i>Nocomis</i>	37-44	39, 40, 41
<i>Nosemionus</i>	36-39	38
<i>Nolopis</i>	32-44	35 to 41
<i>Opsopoeodus</i>	36-39	38
<i>Oregonichthys</i>	35-36	36
<i>Orichodon</i>	42-45	43
<i>Parexoglossum</i>	39-40	40
<i>Phenacobius</i>	38-44	?
<i>Pimephales</i>	35-39	?
<i>Plagepterus</i>	39-41	40
<i>Platygebi</i>	40-47	40, 45 *
<i>Pogonichthys</i>	41-45	43
<i>Psychocheilus</i>	40-47	?
<i>Relictus</i>	35-39	36
<i>Rhenichthys</i>	35-44	?
<i>Richardsonius</i>	38-43	40
<i>Semotilus</i>	39-46	43, 44
<i>Scypodon</i>	NOT AVAILABLE	
<i>Tiaroga</i>	36-40	37
<i>Xystosus</i>	39-40	39
<i>Yurania</i>	38-41	39

* Sub-species modes.

- Other modes, not given in literature sources.

States were determined by examining the frequency distributions of the classes and by reference to the ancestral genus Notropis:-

State 0 - Class 3

State 20 - Class 2

State 40 - Class 4

State 60 - Class 5

State 80 - Class 6

State 100 - Class 7

Phyletics

By reference to the ancestral genus state 0 is primitive and other states derived (criteria 2,3,8). Intra- and interspecific variability is apparent and trends to increase in vertebral number are probably independent in different genera, and in many instances related to body size.

Cephalic lateral line canal pores

Character description

Cephalic lateral line canals are pored and the pore count is characteristic of certain species and genera. The infra-orbital, preoperculo-mandibular, supraorbital and supratemporal pore counts are defined as in Illick (1956). Note that the infraorbital canal count included that for the post-ocular commissure of Reno (1966, 1969b, 1971). The addition of these two counts which Reno gave as ranges was performed by taking the lowest figures for each range and adding them and similarly for the highest counts. The range for the combined count may

exceed by one or two pores the count existing in the specimens but this did not affect the allocation of genera to classes.

Principal sources for the counts were Illick (1956), Reno (1966, 1969b, 1971), Suttkus and Raney (1955a, 1955b, 1955c), Snelson (1968, 1971, 1972, 1973), Miller (1963), Barbour and Contreras (1968) and Hubbs, Miller and Hubbs (1974). Additional counts were made on certain genera, notably Eremichthys, Hybognathus, Margariscus, Moapa, Relictus, Semotilus and Yuriria. Counts are summarised in Table 9.

Variation within a genus

Specific differences are apparent in some counts for certain genera but usually ranges overlap (Reno, 1969b).

Character states

Classes based on range in counts were erected but this led to multi-state characters where many states were representing overlap ranges. An alternative analysis was carried out using the central value of each range to characterise the genus. The following classes and states were determined:-

Character 16 - Infraorbital canal pore count

		Number of genera	
Class 1	0 - 9	1	State 33
Class 2	10 - 19	32	State 0
Class 3	20 - 29	12	State 67
Class 4	40 - 49	2	State 100

TABLE 9

Cephalic lateral line canal pore counts (median in parentheses.)

(IO = infraorbital canal; PM = preoperculo-mandibular canal;
SO = supraorbital canal; ST = supratemporal canal).

Genus	IO	PM	SO	ST
<i>Acrocheilus</i>	21-28 (25)	13-18 (16)	10-15 (13)	7-15 (11)
<i>Agosia</i>	14-16 (15)	9-10 (10)	7-10 (9)	5-7 (6)
<i>Algansea</i>	11-30 (21)	8-25 (17)	7-17 (12)	4-18 (11)
<i>Camposoma</i>	12-19 (16)	9-13 (11)	8-10 (9)	5-9 (7)
<i>Chasomus</i>	14-21 (18)	11-15 (13)	7-11 (9)	2-6 (4)
<i>Clinostomus</i>	12-17 (15)	11-17 (14)	8-9 (9)	4-8 (6)
<i>Couesius</i>	13-20 (17)	9-12 (11)	7-11 (9)	4-9 (7)
<i>Dionda</i>	13-14 (14)	10-11 (11)	8-11 (10)	4-7 (6)
<i>Exemichthys</i>	13-17 (15)	10-15 (13)	8-11 (10)	6-9 (8)
<i>Exicymba</i>	12-19 (16)	7-9 (8)	7-10 (9)	4-6 (5)
<i>Eximystax</i>	9-18 (14)	7-11 (9)	5-11 (8)	1-7 (4)
<i>Evarra</i>	NOT AVAILABLE			
<i>Exoglossum</i>	15-18 (17)	9-12 (11)	8-11 (10)	4-8 (6)
<i>Exocoetis</i>	11-23 (17)	10-15 (13)	6-11 (9)	3-7 (5)
<i>Gila</i>	17-40 (29)	13-30 (22)	9-22 (16)	6-15 (11)
<i>Hemilacania</i>	13-17 (15)	10-12 (11)	6-9 (8)	2-6 (4)
<i>Hesperoleucis</i>	14-21 (18)	10-14 (12)	7-12 (10)	4-8 (6)
<i>Hybognathus</i>	13-17 (15)	9-13 (11)	7-10 (9)	3-6 (5)
<i>Hybopsis</i>	9-21 (15)	8-17 (13)	5-12 (9)	1-7 (4)
<i>Isoichthys</i>	3-12 (8)	4-10 (7)	3-6 (5)	1-7 (4)
<i>Invinia</i>	20-26 (23)	20-24 (22)	11-15 (13)	7-11 (9)
<i>Lepidomeda</i>	14-21 (18)	9-16 (13)	7-10 (9)	5-8 (7)
<i>Macrhybopsis</i>	11-19 (15)	7-12 (10)	5-12 (9)	3-6 (5)
<i>Margariscus</i>	16-19 (18)	11-15 (13)	11-12 (12)	5-9 (7)
<i>Meda</i>	14-21 (18)	11-14 (13)	8-11 (10)	3-9 (6)
<i>Neopa</i>	17-22 (20)	11-17 (14)	10-12 (11)	9-14 (12)
<i>Nylocheilus</i>	23-29 (26)	14-20 (17)	13-16 (15)	9-11 (10)
<i>Nylopharodon</i>	24-30 (27)	18-21 (20)	14-18 (16)	10-13 (12)
<i>Nocomis</i>	11-20 (16)	7-12 (10)	6-12 (9)	3-9 (6)
<i>Nothemigonus</i>	18-23 (21)	16-23 (20)	10-14 (12)	7-11 (9)
<i>Nothopis</i>	10-19 (15)	6-15 (11)	7-12 (10)	0-10 (5)
<i>Opsopocodus</i>	14-18 (16)	9-12 (11)	7-12 (10)	2-7 (5)
<i>Oregonichthys</i>	15-23 (19)	13-18 (16)	4-13 (9)	6-13 (10)
<i>Orthodon</i>	31-48 (40)	27-34 (31)	16-22 (19)	12-21 (17)
<i>Parexoglossum</i>	13-17 (15)	9-11 (10)	9-10 (10)	5-7 (6)
<i>Phenacobius</i>	12-16 (14)	6-7 (7)	8-10 (9)	5-8 (7)
<i>Pimphales</i>	14-17 (16)	7-11 (9)	6-11 (9)	2-6 (4)
<i>Plagopterus</i>	18-21 (20)	10-14 (12)	8-11 (10)	5-7 (6)
<i>Platygobio</i>	13-21 (17)	11-16 (14)	6-10 (8)	4-9 (7)
<i>Pogonichthys</i>	24-27 (26)	19-23 (21)	14-22 (18)	8-11 (10)
<i>Psychocheilus</i>	26-66 (46)	21-54 (38)	17-30 (24)	10-27 (19)
<i>Relictus</i>	16-20 (18)	11-19 (15)	8-9 (9)	6-8 (7)
<i>Rhinichthys</i>	15-19 (17)	8-13 (11)	8-10 (9)	4-7 (6)
<i>Richardsonius</i>	12-20 (16)	11-18 (15)	8-15 (12)	4-9 (7)
<i>Semotilus</i>	13-24 (19)	11-16 (14)	10-15 (13)	4-11 (8)
<i>Stygedon</i>	NOT AVAILABLE			
<i>Tintaga</i>	14-17 (16)	5-11 (8)	7-10 (9)	3-7 (5)
<i>Xystosus</i>	19-30 (25)	15-23 (19)	10-15 (13)	8-12 (10)
<i>Yurinia</i>	20-27 (24)	17-20 (19)	13-15 (14)	15-17 (16)

Character 17 - Preoperculomandibular canal
pore count

Number of genera			
Class 1	0 - 9	6	State 33
Class 2	10 - 19	34	State 0
Class 3	20 - 29	5	State 67
Class 4	30 - 39	2	State 100

Character 18 - Supraorbital canal pore count

Number of genera			
Class 1	4 - 7	1	State 25
Class 2	8 - 11	31	State 0
Class 3	12 - 15	10	State 50
Class 4	16 - 19	4	State 75
Class 5	> 20	1	State 100

Character 19 - Supratemporal canal pore count

Number of genera			
Class 1	0 - 4	6	State 33
Class 2	5 - 9	29	State 0
Class 3	10 - 14	9	State 67
Class 4	15 - 19	3	State 100

Phyletics

The states are derived relative to the ancestral genus Notropis. Trends to reduction and increase in pore count can be seen in small and large sized genera respectively. Such trends may not reflect phylogeny but perhaps are correlated with sensory coverage of the body surface. Trends to loss or gain of pores have also been correlated with such environ-

mental features as clear and turbid water. Secondary invasion of a clear-water environment by a turbid-water species can be reflected by an increase in pore count (Reno, 1969b), and thus obscure attempts to relate species and genera. Thus it is possible to characterise genera with strict environmental requirements by a relatively narrow range in pore counts. In other genera with species adapted to a variety of environments a wide range in pore counts may be seen.

Pore counts are here treated as four separate characters but high or low counts in one character are usually matched by high or low counts in the other characters.. This is not universally true but there is some redundancy.

Character 20 - Modal pelvic ray count

Character description

The modal pelvic ray count was determined from literature sources and, where these were contradictory, from the relevant specimens. Counts are given in Table 6.

Variation within a genus

Several genera contained species with differing modal pelvic ray counts. For Algansea data on four species were available and modes for two were 8 and for another two were 9. The former was chosen to represent the genus. In Gila pelvic ray counts ranged from 6-11 and for 14 species modal values were distributed 8 (6), 9 (7), 10 (1). Since no mode predominates the value chosen was that of the ancestral group, Notropis i.e. 8, as with Algansea.

Character states

State 0 - Modal pelvic ray count 8

State 33 - Modal pelvic ray count 7

State 67 - Modal pelvic ray count 9

State 1 - Modal pelvic ray count 10

Phyletics

A modal pelvic ray count of 8 is regarded as primitive and others counts are derived by loss (mode 7) or increase (9 or 10) (criteria 2,3,8).

Character 21 - Number of scales per vertebra

Character description

There are evident differences in lateral line scale counts which reflect relative scale size (see Table 2 in scale section). Ranges in counts are large in many genera and ready designation of classes is difficult. To circumvent this problem number of lateral line scales was expressed in terms of number of vertebrae as described previously. (see Table 4 in scale section).

Character states

Class 1 1.0 - 1.2 scales/vertebra (= State 0)

Class 2 1.3 - 1.5 scales/vertebra (= State 25)

Class 3 1.6 - 1.8 scales/vertebra (= State 50)

Class 4 1.9 - 2.1 scales/vertebra (= State 75)

Class 5 2.2 - 2.4 scales/vertebra (= State 100)

Character states were taken to correspond directly with these classes.

Phyletics

In relation to the ancestral genus Notropis state 0 is primitive and other states are derived (criteria 2,3, 8). There is probably some parallelism in these derived states since reduction in scale size may have occurred independently in several genera.

Character 22 - Lateral line decurvature

Character description

There are evident differences in decurvature of the lateral line but estimating these differences is difficult and subjective. Decurvature values were determined from the ratio of scale counts above and below the lateral line (see Table 3) as described previously.

Character states

	Ratio	Number of genera
Class 1	1.00 - 1.19	10
Class 2	1.20 - 1.39	12
Class 3	1.40 - 1.59	13
Class 4	1.60 - 1.79	7
Class 5	1.80 - 1.99	-
Class 6	2.00 - 2.19	1
Class 7	> 3.00	1

States were designated as follows:-

- State 0 - Class 1
- State 20 - Class 2
- State 40 - Class 3

State 60 - Class 4

State 80 - Class 6

State 100 - Class 7

Phyletics

By reference to the ancestral genus Notropis state 0 is primitive and other states are derived (criteria 2,3,8). As with character 24 parallelism probably occurs and the states are of only phenetic utility (see discussion of anal ray counts).

Character 23 - Paraphenoid ventral keel

Character description

A median ventral keel is found between the wings of the parasphenoid in Campostoma, Dionda, Erimystax, Hybognathus, Iotichthys, Lavinia, some Notropis, Orthodon, some Pimephales, Pogonichthys, Xystrosus, and Yuriria.

Character states

State 0 - Parasphenoid keel not present

State 50 - Parasphenoid keel present in some species

State 100 - Parasphenoid keel present

Phyletics

Character state 100 is derived and state 50 is regarded as an intermediate state (criteria 2,3,8). Ridges are commonly found on the ventral surface of the parasphenoid in other genera and an independent development of a keel in the above genera cannot be precluded.

Character 24 - Pelvic membrane

Character description

The pelvic fins usually lie free under the body being attached anteriorly. However in certain genera a membrane or membranes are found attaching the pelvic fins to the body. In Meda and Plagopterus the membrane extends about two-thirds the length of the inner-most pelvic ray while in Lepidomeda its extent is about half way. The pelvic fin of Rhinichthys falcatus is also attached to the body but by fleshy stays on the mesialmost rays rather than a single membrane.

Character states

State 0 - No pelvic membrane

State 100 - Pelvic membrane on inner-most ray

Phyletics

State 100 is derived in the Plagopterini (criteria 1, 4, 6, 7, 8). The condition in Rhinichthys falcatus is unique and independently derived on morphological grounds.

Character 25 - Nest building

Character description

In certain species and genera of eastern N. American cyprinids males construct nests out of pebbles during the spawning season. These genera are Campostoma, Couesius, Exoglossum, Nocomis, Parexoglossum and Semotilus. Further descriptions are given in works cited at the beginning of this section and in Raney (1939), Van Duzer (1939) and Balon (1975).

Variation within a genus

Nest building in Couesius plumbeus is poorly developed and restricted to certain populations (R.E. Jenkins, pers. comm. 1975) Notropis cornutus is reported to build nests of its own as well as using those of other species but this is not characteristic of the genus Notropis as a whole and this genus is scored as a non-nest builder.

Character states

State 0 - Nest not built during spawning season

State 100 - Nest built during spawning season

Phyletics

R.E. Jenkins (pers. comm. 1975) considers that the nest building habits restricted to six eastern N. American genera, could not have evolved six times and is evidence of relationship between these genera. E. K. Balon (pers. comm., 1975) disagrees citing such apparently independent evolution of an egg laying tube in Sarcocheilichthys (Gobioninae) and Acheilognathinae as evidence of the parallelism common in cyprinids. In relation to the ancestral genus, Notropis, nest building is a derived character, and parallelism is possible but unlikely (criteria 2,3,6,8). Nest building in Notropis cornutus may be evidence of its (and presumably through it other Notropis) relationship with other nest building genera. Certainly if it is regarded as an independent development, and nest building is rare in Notropis generally, then it may be argued that nest building could have developed independently in some of the other genera.

Character 26 - Urohyal arms

Character description

The urohyal has parallel anterior arms in most genera but these are absent and the anterior end of this bone is dorso-ventrally perforated by a foramen in Exoglossum and Parexoglossum (probably the anterior arms fused craniad enclosing the foramen). Other structural modifications of the jaw region of these two genera have been noted in the osteological survey and it would be redundant to encode all of them here.

Character states

State 0 - Two anterior arms to urohyal

State 100 - Anterior arms absent, foramen present.

Phyletics

State 100 is derived (criteria 1,7,8). It is interesting to note that in large Phenacobius mirabilis the anterior arms are short and almost meet to enclose a foramen. This may represent an intermediate state between States 0 and 100.

Character 27 - Enlarged posterior suborbital bones

Character description

The lateral temporal fossa is roofed over by enlarged posterior suborbital bones in Algansea, Xystrosus and in some Gila species (C.D. Barbour, pers. comm. 1975). Further descriptions are given on p. 208.

Character states

State 0 - Lateral temporal fossa not roofed over
by enlarged suborbital bones

State 100 - Lateral temporal fossa roofed over by
suborbital bones.

Phyletics

State 100 is derived by reference to the ancestral
genus (criteria 1,6,8).

Character 28 - Single postero-ventral metapterygoid
stout

Character description

The metapterygoid usually bears two struts on its posterior edge. A single postero-ventral strut is the only one seen in Campostoma, Clinostomus sp (see Buhan, 1970), Eremichthys, Extrarius, Macrhybopsis, Nocomis, Pimephales, Platygobio, Rhinichthys and Tiaroga.

Character states

State 0 - Two posterior metapterygoid struts present

State 100 - One postero-ventral metapterygoid strut
present

Phyletics

State 100 is derived (criteria 1,3,8) by reference to the ancestral genus. Loss of a structure may occur independently and is not as good a character as a shared complex derived structure.

TABLE 10

Character states of North American cyprinid genera

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Genus																												
Actinopterygii	100	0	0	0	0	100	100	100	50	0	0	0	50	67	100	67	0	50	67	67	75	40	0	0	0	0	0	0
Agosia	100	100	0	0	0	0	100	999	100	0	0	0	25	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0
Algansea	100	100	0	0	0	0	100	999	100	50	0	0	25	0	0	67	0	50	67	0	75	60	0	0	0	0	100	0
Camposoma	0	0	0	0	0	0	100	999	0	0	50	0	25	0	60	0	0	0	0	0	25	0	100	0	100	0	0	100
Chrosomus	0	0	0	0	0	100	100	0	100	50	0	0	0	0	0	0	0	0	33	0	75	60	0	0	0	0	0	0
Clinosomus	0	0	0	0	0	100	0	999	0	0	50	0	0	0	40	0	0	0	0	0	25	40	0	0	0	0	0	100
Couesius	0	100	0	0	0	0	0	0	0	0	0	0	0	0	60	0	0	0	0	0	50	40	0	0	100	0	0	0
Dionda	0	0	0	0	0	0	100	999	0	100	50	0	0	0	0	0	0	0	0	0	0	40	100	0	0	0	0	0
Emmichthys	100	0	0	0	0	100	100	999	100	50	50	0	0	0	0	0	0	0	0	0	75	40	0	0	0	0	0	100
Elacymba	0	0	0	0	0	0	100	999	0	0	0	0	0	0	0	0	0	33	0	0	0	20	0	0	0	0	0	0
Erismyzon	0	100	0	0	0	0	100	999	0	0	0	0	25	0	40	0	33	0	33	0	0	20	100	0	0	0	0	0
Evania	100	0	0	0	0	0	100	999	999	999	999	999	25	0	999	999	999	999	999	999	999	999	20	999	999	999	999	999
Eroglossum	0	0	100	0	0	0	100	75	0	0	0	0	25	0	0	0	0	0	0	0	25	20	0	0	100	100	0	0
Extremus	0	100	0	0	0	0	100	999	0	0	0	50	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
Gila	100	0	0	0	0	100	0	0	50	50	50	0	0	0	60	67	67	75	67	0	50	40	0	0	0	0	0	100
Hemichromis	0	0	0	0	0	100	0	999	0	100	50	0	0	0	0	0	0	0	33	0	0	0	0	0	0	0	0	0
Hesperoleucus	100	0	0	0	0	100	100	0	50	0	0	0	25	0	40	0	0	0	0	0	25	40	0	0	0	0	0	0
Hybognathus	0	0	0	0	0	0	100	999	0	0	50	0	0	0	0	0	0	0	0	0	0	20	100	0	0	0	0	0
Hybopsis	0	100	0	0	0	0	100	999	0	0	0	0	0	0	0	0	0	0	33	0	0	0	0	0	0	0	0	0
Isaichthys	100	0	0	0	0	100	0	999	0	100	50	0	0	0	20	33	33	25	33	0	0	999	100	0	0	0	0	0
Levinia	100	0	0	0	0	100	100	999	0	0	0	0	100	100	60	67	67	50	0	67	25	60	100	0	0	0	0	0
Lepidomeda	100	0	0	100	0	100	0	0	50	0	50	0	50	67	60	0	0	0	0	33	75	20	0	100	0	0	0	0
Macrhybopsis	0	100	0	0	0	0	100	999	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
Margariscus	0	50	0	0	0	100	0	0	0	0	0	0	0	0	40	0	0	50	0	0	50	20	0	0	0	0	0	0
Meda	100	0	0	100	100	0	100	0	999	100	100	100	50	33	60	0	0	0	0	33	999	999	0	100	0	0	0	0
Moapa	100	0	0	0	0	100	100	999	100	50	50	0	0	0	0	67	0	0	67	0	75	20	0	0	0	0	0	0
Mylocheilus	100	100	0	0	0	100	100	999	0	0	0	0	0	0	80	67	0	50	67	67	50	40	0	0	0	0	0	0
Mylopharodon	100	0	100	0	0	100	0	999	0	0	0	0	0	0	100	67	67	50	67	67	50	60	0	0	0	0	0	0
Nocomis	0	100	0	0	0	0	100	999	0	50	0	0	25	0	40	0	0	0	0	0	0	20	0	0	100	0	0	100
Noemigonus	0	0	0	0	0	100	100	0	0	100	50	50	999	0	0	67	67	50	0	67	0	100	0	0	0	0	0	0
Nothopis	0	0	0	0	0	0	0	0	0	0	50	0	0	0	0	0	0	0	0	0	0	50	0	0	0	0	0	0
Opsopoeodus	0	100	0	0	0	100	100	75	0	0	0	0	0	33	0	0	0	0	0	0	40	0	0	0	0	0	0	0
Oregonichthys	100	100	0	0	0	100	999	0	50	0	0	0	25	0	0	0	0	0	67	0	0	20	0	0	0	0	0	0
Oreochromis	100	0	0	0	0	100	100	999	50	50	50	0	0	67	60	100	100	75	100	100	100	60	100	0	0	0	0	0
Parexoglossum	0	50	100	0	0	0	100	999	0	0	0	0	25	0	40	0	0	0	0	0	25	40	0	0	100	100	0	0
Phenacobius	0	50	0	0	0	0	100	999	0	0	0	0	25	0	60	0	33	0	0	0	25	0	0	0	0	0	0	0
Pimephales	0	0	0	0	0	0	100	25	0	0	50	0	25	0	0	0	33	0	33	0	0	60	50	0	0	0	0	100
Plagopterus	100	100	0	100	100	100	100	0	999	0	0	50	75	67	60	67	0	0	0	33	999	999	0	100	0	0	0	0
Platygebius	0	100	0	0	0	0	0	999	0	0	0	0	0	0	60	0	0	0	0	0	0	40	0	0	0	0	0	100
Pogonichthys	100	100	0	0	0	100	0	999	0	0	0	0	0	33	50	67	67	75	67	67	25	20	100	0	0	0	0	0
Ptychocheilus	100	0	0	0	0	100	0	50	100	0	0	0	0	33	80	100	100	100	100	67	50	40	0	0	0	0	0	0
Refectus	100	0	0	0	0	100	0	100	0	50	0	25	0	0	0	0	0	0	0	0	50	0	0	0	0	0	0	0
Rhinichthys	100	100	50	0	0	0	0	0	50	0	50	50	25	0	40	0	0	0	0	0	50	0	0	0	0	0	0	100
Richardsonius	100	0	0	0	0	100	0	999	0	0	50	0	999	0	60	0	0	50	0	67	25	60	0	0	0	0	0	0
Scotichthys	0	50	0	0	0	100	0	50	0	100	0	0	0	0	60	0	0	50	0	0	0	20	0	0	100	0	0	0
Stypodon	100	0	0	0	0	0	100	999	999	999	999	999	0	0	50	999	999	999	999	999	0	999	999	999	999	999	999	999
Tetragodon	100	0	100	0	0	0	100	999	100	0	0	100	0	0	0	0	33	0	0	0	50	999	0	0	0	0	0	100
Xysticus	100	0	0	0	0	0	100	999	50	0	0	0	25	0	40	67	0	50	67	67	50	40	100	0	0	0	100	0
Yutisia	100	100	0	0	0	0	100	999	0	0	0	0	0	0	40	67	0	50	100	100	0	80	100	0	0	0	0	0

TABLE 11

Degree of advancement scores for cyprinid genera

Genus	Degree of advancement	Number of available characters
Acrocheilus	36.9	28
Agosia	19.4	27
Algansca	33.1	27
Camposoma	20.7	27
Chrosomus	18.5	28
Clinosomus	13.1	27
Couesius	12.5	28
Dionda	14.4	27
Eremichthys	26.5	27
Encymba	5.7	27
Enemystax	16.7	27
Evaxia	24.5	10
Exoglossum	19.5	28
Extrarius	13.9	27
Gila	31.3	28
Hemitemia	10.5	27
Hesperoleucus	17.1	28
Hybognathus	10.0	27
Hybopsis	8.6	27
Iotichthys	22.8	26
Lavinia	36.9	27
Lepidomeda	23.8	25
Macrhybopsis	13.3	27
Margariscus	11.1	28
Neda	39.0	25
Noapa	27.0	27
Nylocheilus	30.4	27
Nylopharodon	30.7	27
Nocomis	19.8	27
Notemigonus	27.8	27
Notoopsis	3.6	28
Opsopocodus	16.0	28
Oregonichthys	17.1	27
Orthodon	48.6	27
Parexoglossum	21.5	27
Phenacobius	10.9	27
Pimephales	17.0	28
Plagopterus	42.1	25
Platygobio	11.9	27
Pogonichthys	32.6	27
Psychrocheilus	36.4	28
Relictus	15.2	28
Rhinichthys	22.0	28
Richardsonius	19.7	26
Semotilus	18.9	28
Stypodon	20.0	10
Tiaroga	27.2	26
Xystosus	31.7	27
Yunzira	31.0	27

List of characters

- 1- Distribution
- 2- Barbels
- 3- Protrusion of premaxillae
- 4- Thickened pelvic rays
- 5- Scalation
- 6- Major row pharyngeal tooth count
- 7- Minor row pharyngeal tooth count
- 8- Chromosome number
- 9- Distribution of scale radii
- 10- Third urodermal bone
- 11- Sixth hypural bone
- 12- Postcleithrum bone
- 13- Modal anal ray count
- 14- Modal dorsal ray count
- 15- Total vertebral number
- 16- Infraorbital canal pore count
- 17- Preoperculomandibular canal pore count
- 18- Supraorbital canal pore count
- 19- Supratemporal canal pore count
- 20- Modal pelvic ray count
- 21- Number of scales per vertebra
- 22- Lateral line decurvature
- 23- Parasphenoid ventral keel
- 24- Pelvic membrane
- 25- Nest building
- 26- Urohyal arms
- 27- Enlarged posterior surborbital bones
- 28- Single postero-ventral metapterygoid strut.

Figure 58. Phylogenetic tree for the Plagopterini (at left) and for six other genera of North American cyprinids (at right). If character 7 (minor row pharyngeal tooth count) is scored as being shared between Pimephales and Notropis then Hennig's coefficient is adjusted to the point shown. 50 % of Notropis species have reduced numbers of teeth in the minor row as in Pimephales. In these and following trees derived characters shared between genera are indicated by their numbers (see character listing on page 321).

Hennig's Coefficient

0.1—

0.2—

0.3—

0.5—

0.5—

0.6—

0.7—

1,4,6,
14,15,
20,24

Lepidomeda

Plagopterus

1,4,13,15,
20,24

Meda

6,10
11,19

Hemitremia

6,10,11

Iotichthys

Notemigonus

11

Notropis

11,
23

Pimephales

11

Rhinichthys



Figure 59. Phylogenetic tree for 17 genera of cyprinids. (Campostoma and Phenacobius share characters 7, 13, 15 and 21; Nocomis and Oregonichthys share characters 2 and 7 and the linkages marked with a parenthesis are all at a Hennig's coefficient of 0.500 but assort as shown at successive clustering cycles; Extrarius and Macrhybopsis share character 28 in addition to characters 2 and 7).



Phylogenetic tree of the subgenus *Erythraeus* based on 18S rDNA. The tree shows relationships between 15 species, with bootstrap values at nodes. The scale bar represents 0.2 substitutions per site. The species listed are *Exoglossum*, *Parexoglossum*, *Phenacobius*, *Campostoma*, *Agosia*, *Relictus*, *Tiaroga*, *Erimystax*, *Nocomis*, *Oregonichthys*, *Extrarius*, *Macrhybopsis*, *Hybopsis*, *Opsopoeodus*, *Dionda*, *Hybognathus*, and *Ericymba*. Bootstrap values are shown at the nodes: 3,7,13,21,25,26 for the first split; 7,13,21 for the second; 13 for the third; 1,7,9,13 for the fourth; 1,7,9,13,21 for the fifth; 2,7,13,22 for the sixth; 28 for the seventh; 2,7 for the eighth; 7,11,23 for the ninth; and 7,22 for the tenth.

0.
2
1

Figure 60. Modified tree of Figure 59. It is assumed that characters 8 (chromosome number) and 15 (vertebral number) are shared between genera at the points shown.

Hennig's Coefficient

0.2—

0.3—

0.4—

0.5—

0.6—

0.7—

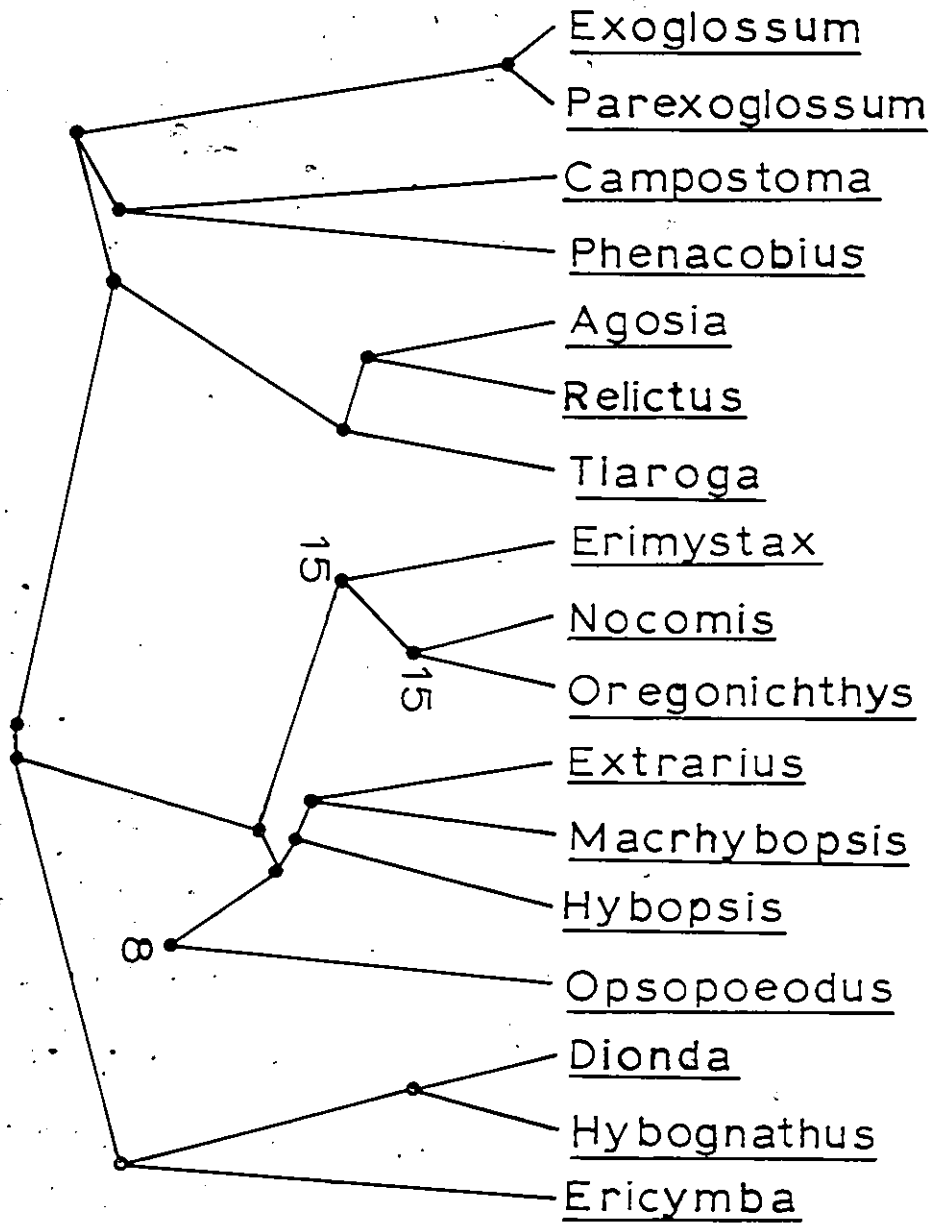


Figure 61. Phylogenetic tree for 11 genera of cyprinids.

0.7 Hennig's Coeff.

0.6

0.5

0.4

0.3

0.2

0.1

Acrocheilus

Mylocheilus

Xystrosus

Mylopharodon

Gila

Orthodon

Yuriria

Algansea

Ptychocheilus

Couesius

Platygobio

1,6,7,16,18,
19,20,22

1,7,16,18,
19,20,21,22

1,16,18,19,
20,21

1,16,19,
21,22

1,6,9,10,
11,15,18

1,15,
16,18

1,16,18,19

1,19,22

22

2,22

Figure 62. Phylogenetic tree for 10 genera of cyprinds

Hennig's Coefficient

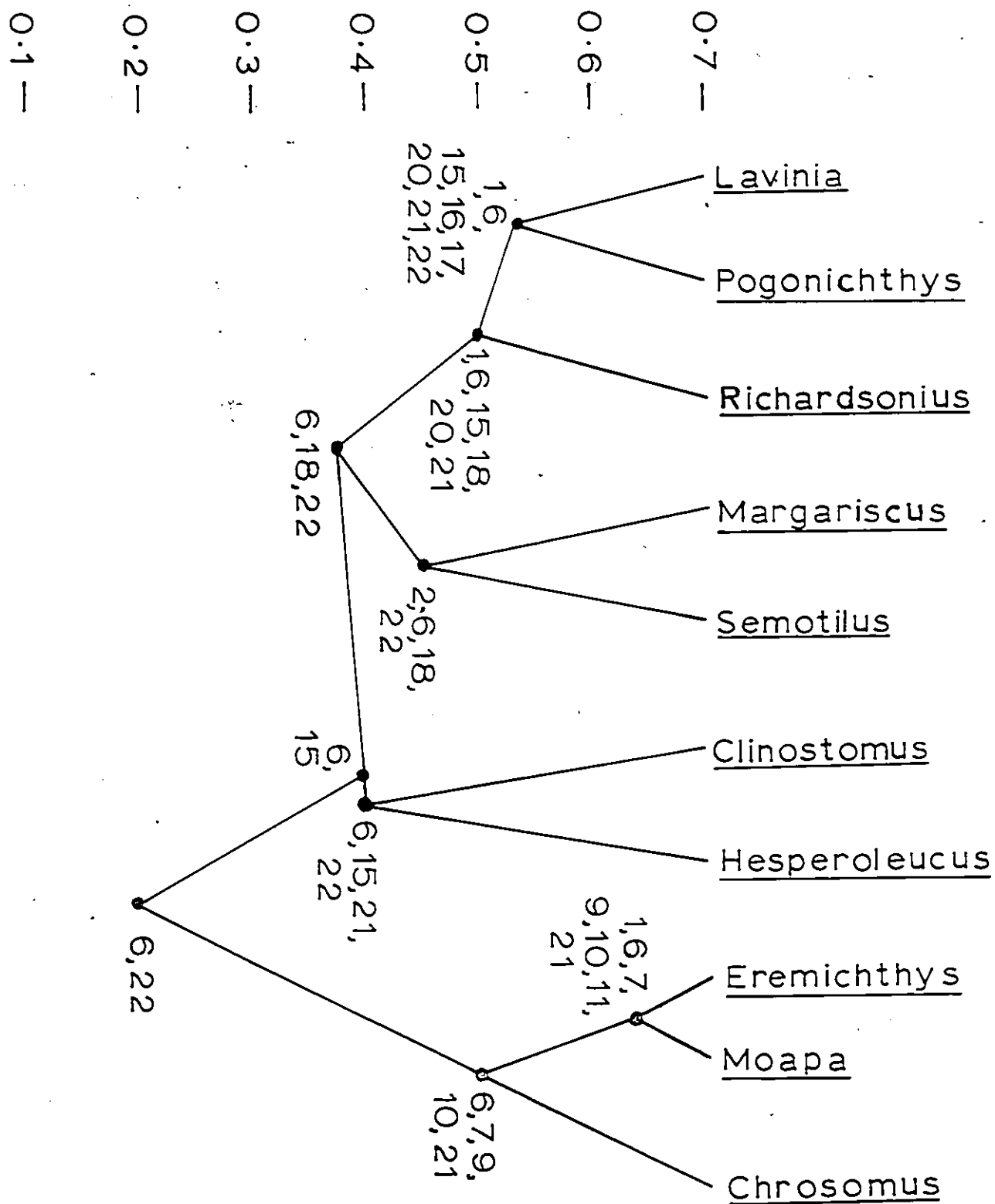


Figure 63. Modified tree of Figure 62. It is assumed that character 15 (vertebral number) is shared between genera at the point shown).

0.7—
0.6—
0.5—
0.4—
0.3—
0.2—
0.1—

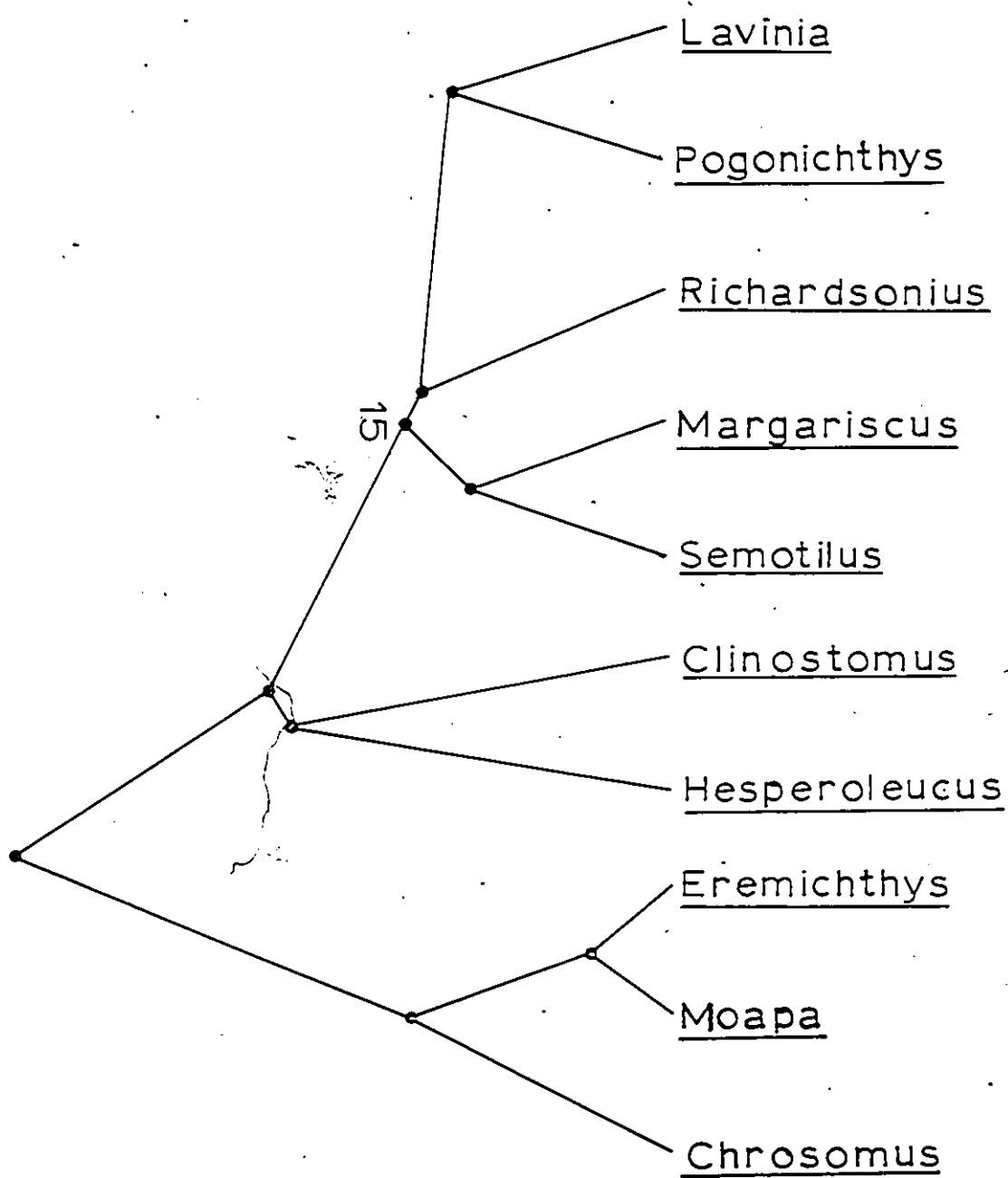


Figure 64. Hypothetical tree of eastern North American cyprinid genera (Hybopsis s. l. includes Erimystax, Extrarius, Hybopsis, Macrhybopsis and the western genus Oregonichthys but not Yuriria).

2 — Clinostomus

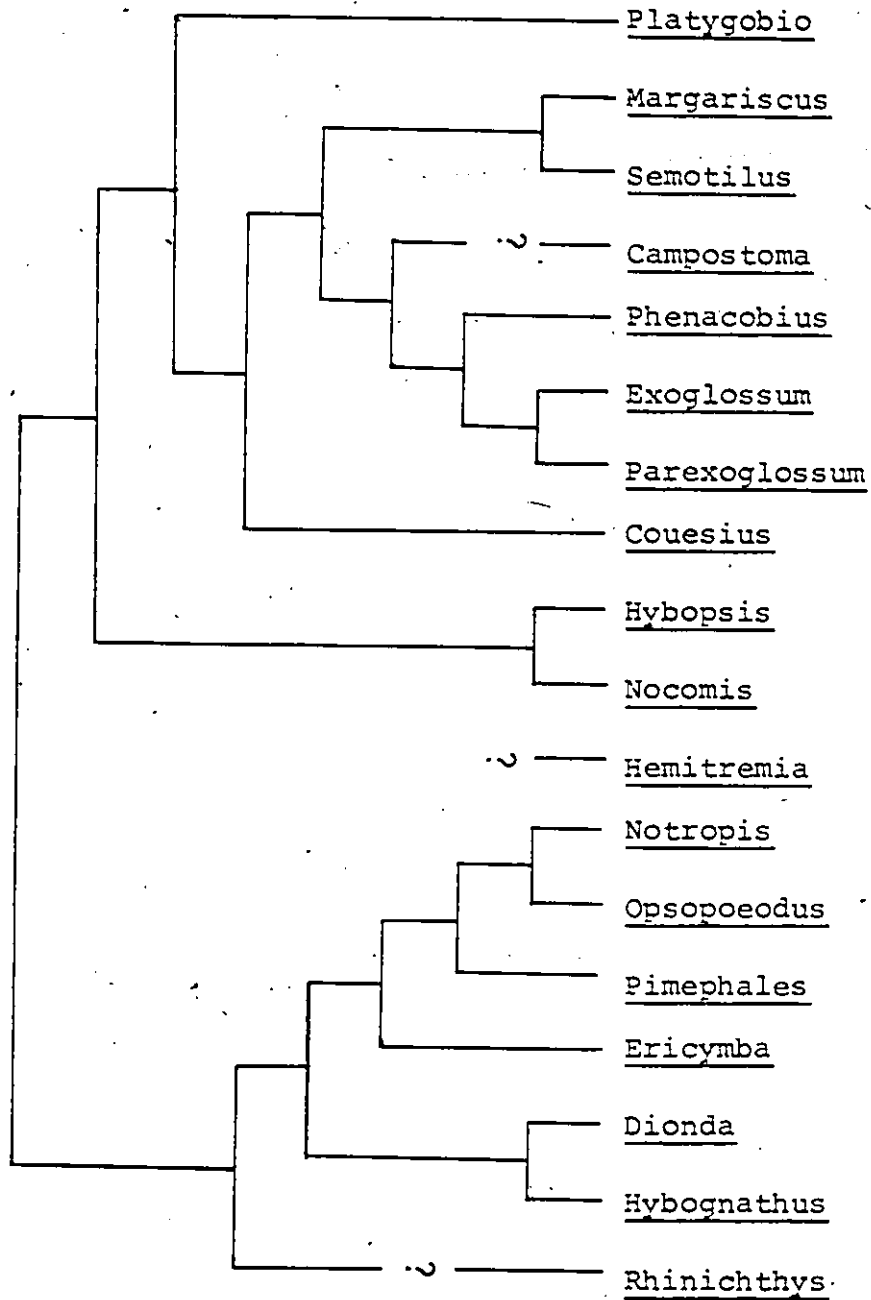
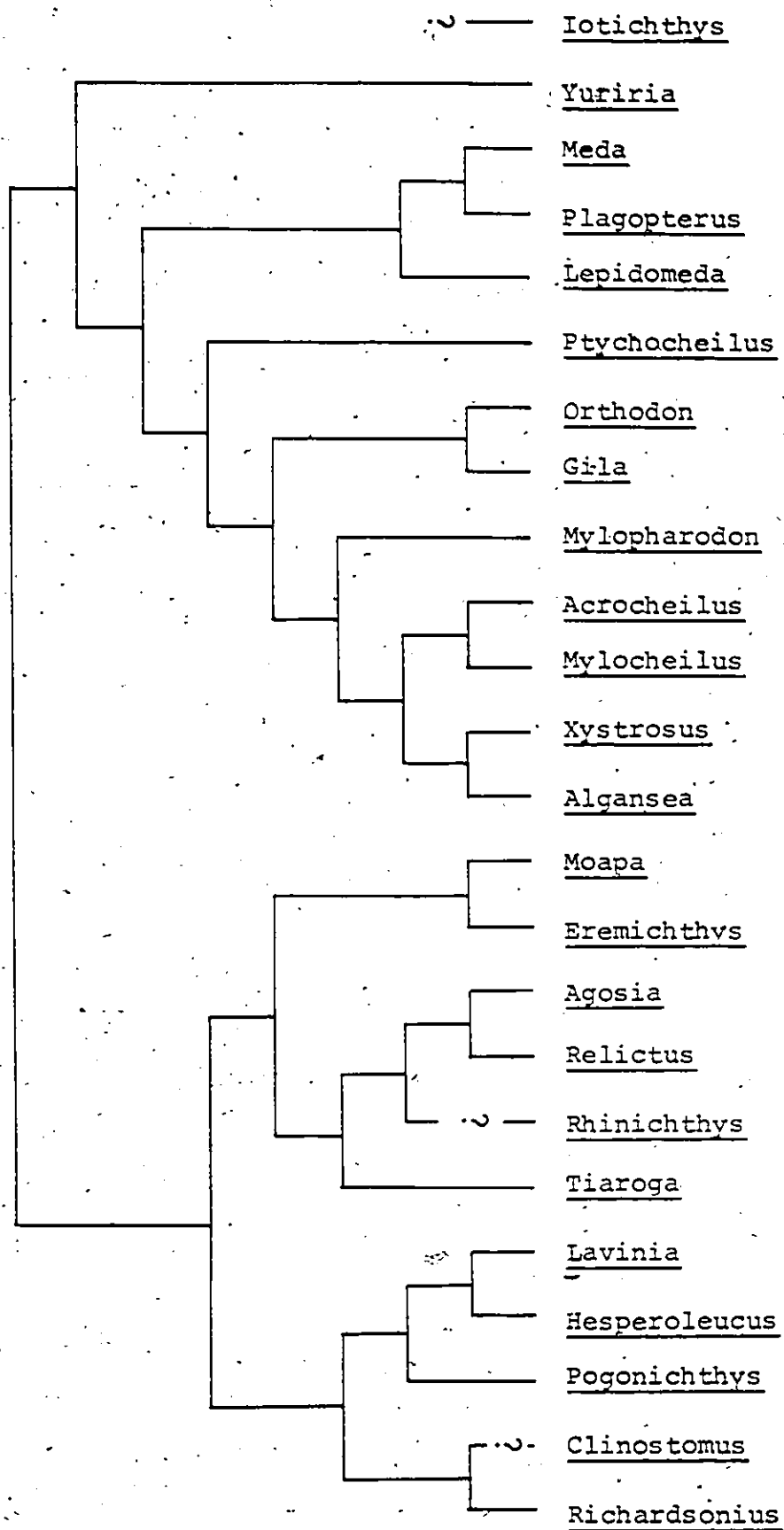


Figure 65. Hypothetical tree of western North American cyprinid genera (including also the eastern genus *Clinostomus*).



DISCUSSION

The five trees presented give an indication of phylogenetic relationship based on the suite of 28 characters examined. It is evident that more characters are needed both to link these trees and to clarify the phylogenies at the points where coefficients were the same. Some of the characters used can be regarded as good derived characters, e.g. 4, 5, 24, but their use is limited when considering all the North American genera because they refer to geographically restricted genera of evident close relationship. Qualifications about other characters have been discussed in the character analysis itself.

The five trees may now be compared to other studies, bearing in mind the reservations expressed above.

The relationships of Lepidomeda, Meda and Plagopterus have been discussed by Miller and Hubbs (1960) who regard them as a tribe, Plagopterini, of the Leuciscinae. Lepidomeda was considered to be the most generalised and Plagopterus the most highly modified. The tree given here (Figure 58) places Lepidomeda closer to Plagopterus than Meda because fewer derived characters are compared (14) than with Meda (15) and Hennig's coefficient is correspondingly changed. The closer relationship of Meda and Plagopterus is undeniable. They share a derived character in lack of scales unique among North American cyprinids and advanced trends in Meda are more advanced in Plagopterus (see character state table).

Neither Miller and Hubbs (1960) nor this study definitely relate this tribe to another North American genus but it appears to be close to other western genera such as Acrocheilus (Hennig's coefficient for this genus and Lepidomeda is 0.353), Richardsonius (0.333) Orthodon (0.316) and Moapa (0.313). Miller and Hubbs (1960) suggest Gila or some similar genus but the Hennig's coefficient for Lepidomeda and Gila is only 0.278.

Figure 59 shows a close relationship between Exoglossum and Parexoglossum. This agrees with the observations of Jenkins and Lachner (1971) and Gilbert and Bailey (1972) who have lumped these two genera as Exoglossum and they are regarded as congeneric here. Minckley and Craddock (1962) and Moore (1968) suggest that Phenacobius is related to Exoglossum and Parexoglossum and it appears close to these genera here. Campostoma is, however, closer on the basis of character 16 (vertebral number). Vertebral number may reflect similar trends in body form and size rather than phylogeny.

Opsopoeodus is placed close to the Hybopsis s.l. group. It has been regarded as a Notropis (Gilbert and Bailey, 1972; Campos and Hubbs, 1973). The relationships of Notropis and Hybopsis s.l. and their close allies such as Opsopoeodus, Ericymba, Dionda, Hybognathus and Pimephales is in need of detailed review. They are not readily susceptible to analysis at the present time because there are no good apomorphic characters known which can be used for

Hennigian studies on these taxa. It is however suggested that Dionda and Hybognathus are congeneric and very close to Notropis in which they could well be lumped.

The genera Nocomis, Oregonichthys, Erimystax, Extrarius, Macrhybopsis and Hybopsis (= Hybopsis s.l. in part) assort together. Couesius and Platygobio (Figure 61) have been assigned to Hybopsis s.l. by Bailey (1951) but are here grouped with several western genera on the basis of character 22 (lateral line decurvature). In view of the reservations expressed about the phylogenetic utility of this character the relationship of these two genera to the western genera is probably remote. Even the relationship of Couesius to Platygobio is only based on two additional shared derived characters, namely possession of a terminal maxillary barbel and similar vertebral counts. Qualifications about vertebral counts have been noted above and in this instance the position of the maxillary barbel differs slightly in the two genera which may indicate parallel evolution. Jenkins and Lachner (1971) consider that Couesius is closely related to Margariscus and Semotilus and that Platygobio is a close ally of Macrhybopsis and Erimystax. In the first clustering cycle Couesius is closest to Platygobio (Hennig's coefficient = 0.333) but Platygobio is closest to Macrhybopsis (0.400). Macrhybopsis however links with Extrarius at 0.500. Margariscus is evidently close to Semotilus (Figure 62) and is generally regarded as a species of Semotilus (Moore, 1968). However Semotilus s.l. in this study assort with three

western genera on the basis of characters 6 (major row pharyngeal tooth count), 18 (supraorbital head canal counts) and 22 (lateral line decurvature). These similarities can be attributed to parallelism as trends in these characters may have occurred independently. Character 7 (minor row pharyngeal tooth count) and character 13 (modal and ray number) also represent trends which may have occurred independently in separate genera, e.g. see Hubbs, Miller and Hubbs (1974) on anal rays. Characters 7 and 13 are the derived characters linking several groups of genera in Figure 60 including the western genera Agosia, Relictus and Tiaroga whose relationships to eastern genera is more probably remote.

In Figure 59 Dionda and Hybognathus are closely linked and Moore (1968) has suggested that these two genera are allied. Dionda shows evident affinities with Notropis (Hubbs and Miller, 1974) and Ericymba is said by Moore (1968) to be closely allied to Notropis also. Notropis assorts with Pimephales in Figure 58 and Hubbs and Black (1947) regard Pimephales as a specialised derivative of Notropis. However the placement of Pimephales and Notropis close to Hemitremia, Iotichthys and Notemigonus is erroneous. Notemigonus in particular has several unique characters for a North American genus which relate it to the Abramidini of Eurasia rather than to other North American genera. The relationships of Rhinichthys are obscured because it only links to other genera at the seventh clustering cycle after

recoding has eliminated all but one of its derived characters. In the first clustering cycle Rhinichthys has Hennig's coefficients of 0.364 with both Extrarius and Relictus. These genera link with other taxa at a higher level and so do not form a group with Rhinichthys. Rhinichthys may well find its closest relatives in Agosia and Relictus. This "loss" of characters by recoding is a major fault of this method of analysing relationships when relatively large numbers of taxa are studied. Hennigian methods applied to many taxa require a much greater number of characters than numerical techniques but are one way to establish phylogenetic relationships through similarity by descent rather than similarity by convergence or parallelism.

Figure 61 (excluding Couesius and Platygobio see above) relates nine western genera including Yuriria which is usually placed as a sub-genus of Hybopsis. Algansea and Xystrosus may be congeneric (R.R. Miller, pers. comm., 1975) but their relationship here is relatively distant. They do however share an unequivocal derived character (27, enlarged posterior suborbital bones) which was "lost" in the recoding when Xystrosus was linked with Acrocheilus and Mylocheilus. It is recommended that Xystrosus be lumped in Algansea.

Figure 62 (excluding Semotilus and Margariscus see above) relates several western genera and the eastern genus Clinostomus. Uyeno (1961) has included Richardsonius in Clinostomus on osteological similarities. In the present study

Clinostomus assorts more closely with Hesperoleucus.

Reservations expressed about independent derivation of certain characters also applies here and the relationship suggested by Uyeno has not been clarified. In this tree Moapa assorts with Eremichthys and these two genera with Chrosomus. Hubbs and Miller (1968) place Moapa with Agosia or derive these genera from a common ancestor. Eremichthys is said to be close to Siphateles (now a sub-genus of Gila) by these authors. Chrosomus is congeneric with the Eurasian genus Phoxinus (see Nearctic and Palaearctic relationships study) and its relationship with these western Nearctic genera is probably remote. Chrosomus or its ancestors may well have entered North America independent from the ancestors of other Nearctic cyprinids, as did Notemigonus or its ancestor. Notemigonus in particular seems to be only distantly related to other Nearctic cyprinids. Unlike Chrosomus, which hybridizes freely with other eastern North American genera, Notemigonus has not been recorded as hybridizing with sympatric genera. Legendre (1970b) placed Chrosomus in Margariscus on the basis of hybridization data but it differs in 8 of the characters examined here and cannot be considered congeneric.

In summarising the above and also taking into account other studies and character similarities between genera a provisional tree relating North American genera is given in Figures 64 and 65.

It is hoped that the data accumulated on North American

cyprinids in this thesis will form a basis for future studies on their intergeneric relationships. Hennigian methods require large numbers of derived characters to be effective with many taxa and it is essential that these characters be unequivocally derived. In the lower branches of a Hennigian tree a single derived character is often the only link between groups of taxa and it should be a firm link. The character analysis and resolution of the data matrix have therefore served to emphasize the need for further work to reveal adequate derived characters which may be incorporated to place the generic systematics of Nearctic cyprinids on a firm basis.

Relationships between Nearctic and
Palaeartic Cyprinidae

Many North American species of cyprinids were originally described under European genera (see Jordan and Evermann, 1896) but were later placed in genera peculiar to N. America. This section examines the supposed relationships between Chrosomus s.l. (Nearctic) and Phoxinus (Palaeartic), between Notemigonus (Nearctic) and the Palaeartic tribe Abramidini and between Gila (Nearctic) and the N. East Asian genus Tribolodon.

General information on characters of Eurasian genera was obtained from Bagenal (1973), Berg (1949), Harder (1964), Ladiges and Vogt (1965), Maitland (1972), Muus and Dahlstrom (1971), Okada (1959-1960), Oliva (1952), Spillman (1961), Vladykov (1931), Wheeler (1969), Wu (1964) and Zhukov (1960). Data sources for N. American genera may be found elsewhere in this thesis.

Chrosomus - Phoxinus

The N. American genus Chrosomus s.l. contains five species of which four have been described. These are C. eos, C. erythrogaster, C. neogaeus and C. oreas. The fifth species is referred to in Menhinick, Burton and Bailey (1974). The species neogaeus was originally described by Cope (1869) as a Phoxinus, was later placed in Pfrittle erected for it by Jordan (1924) because of its uncertain affinities (as Pfrittle neogaea), and in 1951 Bailey suggested it should be assigned

to Chrosomus but without outlining reasons for this move (McPhail and Lindsey, 1970). The principal differences between Chrosomus and Pfrille are pharyngeal tooth counts (0,5-5,0 versus 2,5-4,2 respectively) and gut shape and length (coiled and elongate versus S-shaped and short respectively). A current trend in taxonomy is to consider trophic characters as insufficient for generic separation. The closeness of these two taxa is also emphasised by the frequent interbreeding of C. eos and Pfrille neogaea which produces fertile hybrids (Legendre, 1970b). McPhail and Lindsey (1970) and Stasiak (1972) however prefer retention of neogaea in the separate genus Pfrille. In marked contrast Mahy (1972b) has suggested that the species C. eos, C. oreas and C. erythrogaster, be lumped as a single species, Phoxinus erythrogaster, with Phoxinus neogaeus a distinct group (sic) close to Phoxinus phoxinus. The present work initially refers to Pfrille neogaea as a species of Chrosomus following Scott and Crossman (1973) and based on information generated in this thesis and retains specific status of other Chrosomus.

The genus Phoxinus has been defined by Berg (1949) and C. neogaeus conforms to it. Banareescu (1964) proposed that Chrosomus s.l. be placed in Phoxinus but without presenting evidence. Bailey et al. (1970) accept this decision uncritically but Scott and Crossman (1973) correctly point out that casual transfer is to be deplored. Reasons for considering Chrosomus congeneric with Phoxinus are outlined below.

Additional sources of data on Chrosomus and Phoxinus to those listed above were Vladykov (1927), Tack (1940), Kulamowicz (1963, 1967), Gasowska and Rembiszewski (1967), Danilkiewicz (1968), Kulamowicz and Jazdzewski (1970) and Kulamowicz and Korkuc (1971). Specimens available for examination are listed in Appendix I and include four species of Chrosomus (eos, erythrogaster, neogaeus and oreas), five species of Phoxinus (czekanowskii, issykkulensis, lagowskii, percnurus and phoxinus) and two Japanese species assigned to the genus Moroco (listed as percnurus and steindachneri jouyi) which are probably referable to Phoxinus (a detailed examination of the genus Moroco and its systematic position was not carried out).

Distribution and zoogeography.

Chrosomus and Phoxinus are of course allopatric but both genera contain species in northern fresh waters. Chrosomus species are found east of the North American Cordillera from the lower reaches of the Mackenzie River in the Arctic Ocean drainage (C. neogaeus) to Atlantic drainages. None have been recorded from Alaska (McPhail and Lindsey, 1970). Phoxinus species range from the British Isles and Spain to the Anadyr River which enters the Bering Sea about 460 miles from Alaska (Berg, 1949) (P. phoxinus). Both Chrosomus and Phoxinus are tolerant therefore of northern climatic conditions and it is worth noting Berg's (1949) observation that P. phoxinus does not avoid brackish waters. Dispersal across a Bering land and water bridge, perhaps even utilising brackish coastal waters,

is not unreasonable for a species of Phoxinus. Dispersal via a transatlantic connection cannot be ruled out however. (see p.283). The present gap in distribution of 1250 miles may be regarded as a consequence of the ice ages (McPhail and Lindsey, 1970) and perhaps recent unfavourable climatic and geographical conditions restricting re-colonisation.

Meristic characters

Close agreement in meristic characters examined is found for Chrosomus and Phoxinus species. Modal counts of dorsal, anal and pelvic rays are 8 in all species except pelvic rays of P. czekanowskii which number 7 (9) or 8 (6). Pectoral ray counts range from 11-19 for Phoxinus species and 13-18 for Chrosomus species. Total vertebrae counts, including four Weberian vertebrae and the hypural plate as one vertebra, range from 36-44 for Phoxinus and 35-40 for Chrosomus.

Gut characters

Pharyngeal tooth counts are modally 2,5-4,2 in all Phoxinus species and in C. neogaeus. Other Chrosomus species are 0,5-5,0 probably a specialisation. Gill raker counts on the entire first left arch are low, 5-12 in Phoxinus and 7-13 in Chrosomus. In all species rakers are small and well separated along the arch. Peritoneum colour in Phoxinus is light to dark brown (very dark brown to black in Moroco steindachneri jouyi) and in Chrosomus very dark brown to black. Gut shape is a simple S (type 1 of Kafuku, 1958) in all Phoxinus, Moroco, and C. neogaeus but more complexly coiled in other Chrosomus species (see Figure 66 and Kafuku, (1958), New (1962) and Legendre (1970b)).

Chromosome number

Chromosome numbers for Chrosomus erythrogaster, C. eos and C. eos x C. neogaeus are $2n = 50$ (Greenfield et al., 1973; Legendre and Steven, 1969) and for Phoxinus phoxinus, P. percnurus, P. percnurus sachalinensis, Moroco percnurus and M. steindachneri $2n = 54$ (Nogusa, 1960; Nikol'skiy and Vasil'yev, 1973). Robertsonian fusions in Chrosomus species may account for these differences in counts between the two genera. However, Berberovic and Sofradzija (1972) give $2n = 50$ for their samples of Phoxinus. A more detailed comparative karyology might yield useful data.

General morphology

All Phoxinus and Chrosomus species are small fish not exceeding 200mm in total length and in general morphology Chrosomus agrees with Phoxinus. The body is rounded or quite deep in cross section, elongate or relatively short. The mouth is moderate in size, without barbels, with protrusible premaxillae, terminal or inferior, lips straight or slightly S-shaped and in lateral view is moderate to very oblique extending to the level of the nostrils or the anterior part of the eye. The dorsal fin is positioned well behind the level of the pelvic fins insertions and the anal fin is at or behind the level of the posterior base of the dorsal fin. There is no pelvic axillary process (rudimentary in Phoxinus percnurus).

Sexual dichromatism and dimorphism

The breeding colour of some male Chrosomus and Phoxinus species has been described as follows. Bright yellow and red abdomens develop although the red element in Chrosomus is transitory and apparently does not develop at all in Phoxinus percnurus and Moroco species. The fins in Chrosomus species develop a yellowish tint while in P. percnurus and P. phoxinus the pectoral and pelvic fins become red and the other fins are yellow. The lips of P. phoxinus and C. erythrogaster are red at the corners of the mouth. P. phoxinus has a distinctive, shining white margin to the operculum and a black colouration may develop on the lower part of the head, the base of the pectoral fins, and the sides and the belly particularly behind the pelvic fins. This colouration has not been recorded for Chrosomus species.

Sexual dimorphism is apparent in length of pectoral and pelvic fins in Phoxinus phoxinus and Chrosomus species (Table 13, see also Vladykov (1927), Philipps (1969)). Males have longer fins than females. Data on C. oreas and other Phoxinus species were not available. Thickened pectoral fin rays are found in both male P. phoxinus and male C. neogaeus although the notched first pectoral ray of C. neogaeus is not seen in P. phoxinus.

Male nuptial tuberculation is very similar in Chrosomus and Phoxinus species. Only P. phoxinus has large, retrorse, pointed head tubercles, all other Phoxinus and Chrosomus species have minute tubercles over the dorsal head surface. (large nuptial males of C. oreas and the new Chrosomus species

TABLE 13.

Sexual dimorphism in pectoral and pelvic fin lengths in Chrosomus and Phoxinus species (P_1-P_2 = pectoral fin base to pelvic fin base length; P_2-A = pectoral fin base to anal fin base length; $P_1 \pm$ length of pectoral fin; P_2 = length of pelvic fin)

	<u>Males</u>				<u>Females</u>			
	Range	Mean	n		Range	Mean	n	t
<u>Chrosomus eos</u>								
$\frac{P_1-P_2}{P_1}$	0.98-1.54	1.22	27		1.14-1.83	1.50	27	6.4862
								<0.001
$\frac{P_2-A}{P_2}$	0.88-1.24	1.09	27		1.04-1.48	1.25	28	5.7904
								<0.001
<u>Chrosomus erythrogaster</u>								
$\frac{P_1-P_2}{P_1}$	1.24-1.39	1.31	5		1.44-1.72	1.62	6	5.7457
								<0.001
$\frac{P_2-A}{P_2}$	1.29-1.39	1.34	5		1.32-1.63	1.48	6	2.6948
								<0.025>
								0.010
<u>Chrosomus neogaeus</u>								
$\frac{P_1-P_2}{P_1}$	1.18-1.78	1.40	16		1.32-1.92	1.64	13	3.5399
								<0.005
$\frac{P_2-A}{P_2}$	1.02-1.50	1.28	13		1.18-1.54	1.36	16	1.5254
								<0.2
								>0.1
<u>Phoxinus phoxinus</u>								
$\frac{P_1-P_2}{P_1}$	0.91-1.21	1.05	10		1.19-1.68	1.35	25	6.8209
								<0.001
$\frac{P_2-A}{P_2}$	1.00-1.23	1.12	10		1.11-1.53	1.26	25	3.8358
								<0.001

not seen). The most characteristic feature of Chrosomus and Phoxinus (but not Moroco) is the presence of comb-like, continuous rows of fine tubercles on the posterior edges of the breast scales. In the most highly tuberculate specimens seen this area of tuberculation reaches back to a level with the posterior pectoral fin bases although continuous rows only extend back from the isthmus for a maximum of 9 rows (P. phoxinus), 10 rows (C. erythrogaster), 6 rows (C. eos), 8 rows (C. oreas) and 5 rows (C. neogaeus). Row extent probably reflects degree of tuberculation development in the available material. Each breast scale has up to 7 tubercle points in Phoxinus and 6 in Chrosomus. Tuberculation in the breast region is not peculiar to Chrosomus and Phoxinus but is also found in e.g. Clinostomus elongatus, Couesius plumbeus, Hesperoleucus symmetricus, Richardsonius balteatus, Margariscus margarita (own observations and Koster, 1939) and also in Canpostoma anomalum, Hemitremia flammea and Nocomis effusus (R. E. Jenkins, pers. comm. 1975). Curiously Clinostomus funduloides differs from its congener by possession of a large, almost centrally placed tubercle on the breast scales in up to about 7 rows rather than small tubercles lining the scale margin. There is variation in the form of the breast tubercles in genera other than Chrosomus and Phoxinus. In Clinostomus elongatus, for example, the tubercles are larger and fewer in number on each scale and the rows are not as well developed. Koster (1939) observed that Semotilus (Margariscus) margarita was closer to Chrosomus than Clinostomus elongatus in these

features. While tubercles lining breast scale edges are relatively common extensive continuous rows of tubercles appear to be restricted to Chrosomus and Phoxinus and in the absence of extensive comparative material the relationship of the various breast tuberculation patterns must remain open to debate.

Elsewhere on the body of P. phoxinus males tubercles are found lining all scale edges from a maximum of 10-12 per scale to only 1 on scales in front of the dorsal fin. Tubercles are best developed on the caudal peduncle. A patch of tubercles is located on the scales immediately behind the head just above the lateral line.

Tubercles are found on all fins but are weak on the caudal fin where there are 1 or 2 per ray segment. Pectoral fin tubercles are found on rays 2-9, apparently one per ray segment and following the ray branches so a patch is formed distally. Pelvic fin tubercles are absent from the first ray and weak on the other rays. Tubercles may develop on the pectoral and pelvic fin ventral surfaces but are weak and sparse compared to those on the dorsal surfaces.

Large, single cusp^{ed} retrorse tubercles are restricted to the head above the level of the mouth and eye. They number 24-48 in specimens of similar size and are scattered from the rear of the head forward on to the snout without any obvious linear pattern. Usually there are 1-2 tubercles anterior to the nares, a square of 4 between the nares and a row of 4-7 over each eye. Minute tubercles are scattered

over the head between these large tubercles. Small tubercles are found on the operculum and slightly larger ones at the anterior operculum base and lower arm of the preoperculum.

In Chrosomus species coalesced tubercles line the body scales but are most evident on the ventral caudal peduncle where there are 3-10 points per scale. The sides of the body have 1-3 tubercles per scale, on the back anterior to the dorsal fin 1-3 tubercles per scale, usually 1, on the back posterior to the dorsal fin 2-9 tubercles and on the ventral body scales 1-3 tubercles. These counts and descriptions are based on an excellent series of tuberculate Chrosomus erythrogastrus but other species seemed to be similar based on more limited material.

Tubercles may be found on all fins but are very weakly expressed on the caudal fin. On the pectoral and pelvic fins they are best developed on the upper surfaces of the fin rays but may also be found on lower surfaces, particularly on the pelvic fin. Rays 2-7 are tuberculate on the pectoral fin upper surface with one tubercle per ray segment and with tubercles following ray branching. The pelvic fin is tuberculate on up to 5 rays, including the first one, in a similar fashion. The dorsal and anal fins are most obviously tuberculate on the first ray with a single file of tubercles, decreasing in number and size posteriorly.

Head tuberculation consists of minute pointed tubercles scattered over the dorsal surface becoming less evident laterally and ventrally.

Scale characters.

These characters have been compared under Chrosomus in the scale section of this thesis. Scales were very similar in the two genera.

Osteology

A comparative osteology of Chrosomus species and Phoxinus phoxinus has been carried out by Mahy (1972a, 1972b, 1975a, 1975b) who did not find any characters to warrant separation of the two genera.

Notemigonus - Abramidini

The Nearctic cyprinid Notemigonus crysoleucas has long been considered as a relative of members of the Eurasian tribe Abramidini which includes such genera as Abramis, Alburnoides, Alburnus, Blicca and Vimba. N. crysoleucas was originally described as a Cyprinus species and it has been placed in Abramis (Jordan and Evermann, 1896). No recent assessment of the proposed relationship has been made though it is commented on frequently in the literature.

This section considers the problem and is based on specimens of Abramis ballerus, A. brama, A. sapa, Alburnoides bipunctatus, Alburnus alburnus, Blicca bjoerkna, Vimba vimba and Notemigonus crysoleucas as listed in Appendix 1. Additional data were obtained from the works listed above and from Oliva and Safranek (1962), Shutov (1967, 1969), Gasowska (1968), Dadikyan (1972), Dorozhkina (1972), Shcherbakha (1973) and Kabisch (1974). Shutov (1967, 1969) and Schcherbukha (1973) place Blicca bjoerkna as

a species of Abramis but Blicca is retained here as a distinct genus for convenience.

Distribution and zoogeography

Notemigonus crysoleucas is restricted to eastern North America from southern Canada to the Gulf of Mexico. Abramidini are distributed in much of Europe and east to Aral Sea drainages. These two distributions are very disjunct probably as a consequence of the ice ages and the failure to recolonise the northern Arctic drainages. Berg (1949) suggests that Abramidini could survive in northern waters and Neogene fossils have been reported from Siberia (Orlov, 1967). N. crysoleucas has some tolerance to salt water which might be a reflection on the vagility of its ancestor. As with other eastern N. American cyprinids entry of Notemigonus or a Notemigonus - like ancestor into the continent could have been via a Bering land and water bridge or via a transatlantic connection (see p. 283).

Meristic characters

The Abramidini have a modal dorsal ray count of 9 except Abramis brama (10). The modal count for N. crysoleucas is 8.

Long anal fins are characteristic of the Abramidini and N. crysoleucas although they are more marked in certain species of Abramidini. Ranges were Abramis ballerus (35-46), A. brama (16-31), A. sapa (33-48), Alburnoides bipunctatus (10-22), Alburnus alburnus (11-23), Blicca bjoerkna (16-26), Vimba vimba (16-25) and N. crysoleucas (8-19).

Thus, there are evident meristic differences, particularly in dorsal ray and total vertebral number, between Abramidini and N. crysoleucas.

Gut characters

Pharyngeal tooth counts are modally 0,5-5,0 for N. crysoleucas, Abramis spp. and Vimba vimba, 2,5-4,2 for Alburnoides bipunctatus and 2,5-5,2 for Alburnus alburnus and Blicca bjoerkna. Shutov (1967) reported young and adult Abramis brama with two rows of teeth and a trend to loss of minor row teeth seems evident in Abramidini.

Gill rakers are short and relatively numerous in N. crysoleucas and usually so in Abramidini. There are differences at the species level in e.g. Alburnoides bipunctatus rakers number 7-9 and are short while in Alburnoides taeniatus they number 17-18 and are long (Berg, 1949). Other counts are Abramis ballerus (30-39), A. brama (15-30), A. sapa (18-23), Alburnus alburnus (13-24), Blicca bjoerkna (13-21), Vimba vimba (12-20), and N. crysoleucas (16-21).

The peritoneum of N. crysoleucas is brown while in Abramidini it is typically silvery although it is sometimes brown in Alburnus alburnus and Alburnoides bipunctatus. The gut shape of large N. crysoleucas is distinctive (Figure 66). Large specimens of the larger species of Abramidini were not available for examination but a distinct anterior loop on the left side was apparent in most Abramidini and corresponded to a pre-adult stage observed in N. crysoleucas.



Chromosome numbers

N. crysoleucas has a chromosome number of $2n=50$ with 8 metacentric pairs, 12 submetacentric or subtelocentric pairs and 5 telocentric pairs (Lieppman and Hubbs, 1969). Chromosome counts for Abramidini range from $2n=48$ (Alburnoides bipunctatus), $2n=50$ (Vimba vimba with 6 metacentric pairs, 10 submetacentric pairs and 8 acrocentric pairs (Rudek, 1974), Alburnus alburnus, Abramis brama) to $2n=52$ (Alburnus alburnus, Blicca bjoerkna, Abramis brama). Conflicting reports are given by Chiarelli and Capanna (1973) and Nikol'skiy and Vasil'yev (1973).

General morphology

The Abramidini contains both large and small species ranging from Alburnoides bipunctatus at 160mm total length to Abramis brama at 800mm total length. Maximum size for Notemigonus crysoleucas appears to be about 300mm total length. Both Notemigonus and the Abramidini are deep-bodied, strongly compressed fishes. The mouth structure differs in that Notemigonus has an oblique mouth with the lower jaw projecting slightly while Abramidini have oblique mouths which are either terminal or sub-terminal with the snout projecting. The dorsal fin in all species is posterior to the level of the pelvic fins insertions and the anal fin begins level with the posterior part of the dorsal fin (except in Vimba vimba where it is posterior to the end of the dorsal fin level). A well-developed fleshy pelvic axillary process is present in all species covered by a modified elongate scale.

Sexual dichromatism and dimorphism

Breeding colouration of male fish has not been recorded in detail in the literature. All species developed red or orange paired and anal fins and in Notemigonus the anal has a black margin.

Tuberculation in male Abramidini is not distinctive according to literature reports. Conical tubercles develop on the head, operculum and cheek region, body scales particularly nuchal ones (singly, in pairs or occasionally 3 per scale in Abramis brama) and in Abramis ballerus above the anal fin, and on the upper surfaces of the paired fin rays, on the anal and on the caudal fins. Tuberculation in Notemigonus males is distinctive. Very small tubercles are found scattered over the dorsal surface of the head, disappearing on the snout and with a few over the lachrymal bone. Also small tubercles are found on the upper and lower operculum, the cheek and the branchiostegal rays. There is a small patch of 4-5 tubercles at the tip of the upper lip and a much larger patch of relatively large tubercles on the chin extending back, but with few tubercles, onto the interopercle and preopercle. Flank scales have up to 15 tubercles mostly near the posterior scale edge but not restricted to it. Mid-flank tubercles are the largest (larger than head tubercles) and become minute on the nape and belly but are found on nearly all scales. Tubercles are on most fins but are very small. The pectoral fin has several rows including the leading edge of the first ray. The caudal fin has a few tubercles on the central rays.

Scale characters.

These have been described in the scale section under Notemigonus (p. 49). Notemigonus is unique in N. America as regards scale characters and is most similar to the Abramidini.

Osteology

In this brief survey of the osteology of some Abramidini complete descriptions are not given but certain points of similarity or difference are noted.

The caudal skeleton of the Abramidini differs from that of Notemigonus by the presence of a third urodermal and sixth hypural. The sixth hypural was only reduced in size in some Vimba vimba and was never absent. The sixth hypural is reduced or lost in Notemigonus and the third urodermal is invariably absent.

The median fins in both Notemigonus and the Abramidini have long proximal pterygiophores, the anterior ones being closely packed together. A tendency to fusion of anterior proximal and intermediate pterygiophores is apparent in Abramidini (3 or 4 dorsal fin pterygiophores fused and 3-6 anal fin pterygiophores) and Notemigonus (3-4 in dorsal fin, 4 in anal fin). The first proximal pterygiophore of the anal fin bears lateral, dorsally-directed branches in some Alburnus, Alburnoides and Notemigonus but these branches are absent from some individual specimens (Figure 42 and 67).).

The interneural bones were slim and elongate in Alburnoides, Alburnus and Notemigonus, elongate and wider in other genera.

The pelvic fin skeleton showed no unusual features in any Abramidini and the variations encompass those shown by the skeleton of Notemigonus.

The chief characteristic of the pectoral girdle of Notemigonus is the much reduced postcleithrum (Figure 43). This bone is also reduced in the Abramidini but not as markedly and the bone may attain sufficient length to be S-shaped. Abramidini carry a small to large foramen on the coracoid below the junction with the mesocoracoid. This foramen is also well developed in Notemigonus but not as strongly as in Alburnus. The coracoid is a very deep bone in Abramis, deep in Alburnoides, Alburnus, Blicca and Vimba but is not as developed in Notemigonus. The coracoid has a large coracoid foramen in Notemigonus, Alburnoides, Alburnus and Vimba but is small in other genera. The postero-ventral corner of the cleithrum is markedly produced in Abramis and to a lesser extent in Alburnus. It is also produced in Notemigonus and other Abramidini but not as noticeably. The dorsal arm or ramus of the cleithrum has mesial and lateral anterior expansions to the dorsal end in Abramis and Notemigonus. The dorsal edge of the anterior ramus is well developed in Abramis, Alburnoides, Blicca and Vimba but low in Alburnus and only a little developed in Notemigonus. The supracleithrum carries a lateral tube with a ventral opening (not the sensory canal) in Abramis, Blicca, and Vimba but not Alburnus. It is weakly developed in Alburnoides and some Notemigonus. Other Notemigonus specimens have a well developed lateral tube (Figures 42 and 68).

The first radial bears two posterior heads in some Notemigonus and the Abramidini. Mesial views of the pectoral girdles of Abramidini are given in Figures 69, 70, 71 and 72.

The suborbital series is similar in all the genera. The maxillary bone bears an antrorse ascending process and the mesial rod is longer than the antero-lateral plate except in Abramis brama and A. sapa where rod and plate are equal. The processes on the plate and the ventral edge are in the form of a spike except in Abramis, Vimba and some Notemigonus where they are ridge-like. An unusual feature of some Abramidini and Notemigonus is a distinct notch on the ventral edge of the dentary near the symphysis. The notch is best developed in Alburnus, weak in Vimba, present or absent in Abramis and Alburnoides and absent in Blicca (Figures 73, 74 and 75). The dorsal edge of the dentary is high and is notched before the ascending process particularly in Alburnus and Notemigonus. The angular rises to a high point behind the retrorse ascending process of the dentary in Notemigonus, Alburnus, and some Alburnoides but the process may be vertical e.g. in Blicca and the angular low and rounded.

The metapterygoid carries two posterior struts and from the dorsal strut a strong ridge running anteriorly and occasionally forking. The lateral wing is strong to moderate in Notemigonus but weakly developed in Abramidini except Abramis.

The posterior flange of the hyomandibular bone is not expanded much posteriorly in Abramidini and Notemigonus at its ventral end but dorsally it forms a strong ridge. The lateral ridge is weakly to moderately developed. The anterior wing curves in abruptly well above the base of the hyomandibular in Notemigonus, Abramis, some Alburnoides and Vimba but not in Alburnus and some Blicca.

The lateral line canal extends to the tip of the preopercle and perforates the antero-dorsal corner of the opercle in all these fishes. The dorsal arm of the preopercle is longest and the interopercle has a dorsal arm in the Abramidini and Notemigonus. The interopercle is longer than subopercle except in Abramis ballerus where they are equal.

In the branchial region the basihyal projects anteriorly and is not expanded. The third and fourth epibranchials bear mesial spikes and the fourth has the posteriormost lateral articulating head directed posteriorly. The epibranchials are strongly curved in Abramis species. Branchiostegals are broadest at their mid-point, pointed distally and the third branchiostegal is proximally forked or not within species. The position of the foramen formed by the junction of the hypohyals varies in all these genera. The urohyal is an elongate slim bone with short anterior branches and the vertical plate extends posterior to the horizontal plate (reverse in Alburnoides).

There is a large interorbital septum in both Notemigonus and the Abramidini but the pterosphenoids of the latter meet in the mid-line and not in Notemigonus. The orbitosphenoid sends a process meso-anteriorly under the lateral ethmoid in Alburnus but this is generally weak to absent in other genera. The lateral walls of the ethmoid do not meet in the mid-line in Notemigonus and Abramidini. The lateral preethmoid ossification is weak to absent and not fused to its mesial partner in these fishes. Abramidini lack a process from the masticatory plate of the basioccipital over the aortic canal, a structure usually found in Notemigonus. The pharyngeal process is quite deep in Notemigonus while in Abramidini it has a tendency to be slim. The supratemporal-intertemporal meets the frontal in Notemigonus but this junction is variably expressed in Alburnus and Alburnoides and meets in all Abramis, Blicca and Vimba seen. The supraorbital canal turns laterally on the posterior part of the parietal in Notemigonus, Alburnoides, Alburnus, Blicca, Abramis brama and some Abramis sapa but meets the supratemporal canal in Abramis ballerus, Vimba and some Abramis sapa. A ventral spike is found over the foramen on the ventro-lateral surface of the exoccipital in Notemigonus, Alburnus and variably in Alburnoides but not in Abramis, Blicca and Vimba. The parasphenoid has a ventral ridge near the arms in Notemigonus and the Abramidini. In Abramis brama two dorsal vertical, parallel wings develop on the posterior part of the parasphenoid matched by similar ventral wings from the basioccipital. Abramis sapa is similar but less developed. The structure is absent from Notemigonus.

The Weberian apparatus is similar in Notemigonus and Abramidini. The second rib is invariably and obviously longer than the first rib although in Notemigonus it may rarely have an anterior rather than a lateral slant. The fourth neural spine slopes anteriorly in Notemigonus, Alburnoides and some Alburnus but in other Abramidini the slope is usually posterior. The intercalaria shape varies from a "Y" to almost a triangle in Notemigonus and this variation is matched by Abramidinid species.

Differences in pharyngeal tooth counts have been noted previously. The anterior limb of the pharyngeal arch is shorter in Notemigonus than in Abramidini, particularly Abramis. The anterior and posterior angles are better developed in Notemigonus than in Abramidini in general.

Gila - Tribolodon

The genus Tribolodon of Asia has been suggested to be a possible relative of the western N. American genus Gila (Miller, 1959). Tribolodon has been assigned to the Eurasian genus Leuciscus and even the N. American Richardsonius (see Okada 1959-1960) but is now recognised as a distinct northeast Asian genus. The nomenclatorial history of Tribolodon has been confused but the latest work by Gritsenko (1974) recognises three species, T. hakonensis, T. ezoe and T. brandti. Other sources of general information were Sauvage (1883), Gritsenko (1972), Miyadi, Kawanabe and Mizuno (1965), Lindberg and Legeza (1967) and Svetovidova (1973).

Specimens of Tribolodon hakonensis, Gila alvordensis, G. atraria, G. bicolor, G. orcutti and G. robusta were available for this study (see Appendix 1).

Distribution and zoogeography

The species of Gila are distributed principally in western Pacific drainages of N. America although some occur east of the Cordillera in the Rio Grande (Miller, 1959). Tribolodon species are found in Japan, Korea, Sakhalin and the Sea of Japan. Both genera are absent from northern drainages in Siberia, Alaska, British Columbia and Washington probably as a consequence of the ice ages and also perhaps recent unfavourable climatic conditions. Tribolodon is very tolerant of sea water and is commonly found as the adult in estuarine and shallow shelf waters, ascending rivers to spawn (Svetovidova, 1973). Under more favourable climatic conditions in the past a coastal dispersal of Tribolodon-like species to North America may be envisaged.

Meristic characters

The genus Gila exhibits a variety of modal values for meristic characters. Modal dorsal ray number varies from 7 (1 species), 8(9), 9(4) to 10(1); modal anal ray number varies from 7(2), 8(10), 9(1), to 10(2); and pelvic rays may be 8(6), 9(7), or 10(1). Modal figures for Tribolodon species are 8 dorsal, 9 anal and 9 pelvic rays. Pectoral rays in Gila have a range of 12-20, in Tribolodon 17-18. A wide range in vertebral number is shown by Gila (35-50) but this, like pectoral ray counts, encompasses the range shown by Tribolodon (45-50).

Gut characters

Pharyngeal tooth counts are modally 2, 5-4, 2 for the majority of *Gila* species and all *Tribolodon* species, though some *Gila* are one-rowed. Range in gill raker number is 10-21 for *Tribolodon* and 5-40 in *Gila*. Rakers are short in *Tribolodon* and short or long in *Gila*, the latter owing to trophic specialisation. Peritoneum colour was dark brown to black in specimens of *T. hakonensis* but literature reports cite black, light brown, pale grey and silvery peritonea for members of this genus. The peritoneum of *Gila* may be black, dusky or silvery with brown speckles, depending on the species. The gut is a simple 'S' in *Tribolodon* with or without a slight anterior loop (types 1 and 2 of Kafuku, 1958 q.v.). *Gila* also conforms to the simple type 1 or type 2 gut shape in the species seen. However, the anterior loop was very well developed in young *G. atraria* and the adult condition was not seen.

Chromosome number

Chromosome numbers are $2n=50$ for both genera according to the available information (Greenfield and Greenfield (1972), Makino (1939), Itoh and Niijama (1972), Uyeno and Miller, (1973)). Chromosome morphology differs however; in *G. orcutti* there are 6 telocentric pairs, 12 subtelocentric including submetacentric pairs and 7 metacentric pairs of chromosomes while in *T. hakonensis* and *T. ezoe* there are 5 metacentric pairs, 10 submetacentric pairs, 6 subtelocentric pairs and 4 telocentric pairs. However Makino (1939) cites

6 metacentric and 44 submetacentric chromosomes for T. hakonensis.

General morphology

Both Gila and Tribolodon contain relatively large species about 500mm in total length. The largest Tribolodon are found in sea-run populations and land-locked ones are smaller. Some Gila species and sub-species may be smaller than 100mm. T.L. in the Great Basin. In Tribolodon the body is elongate and somewhat compressed and this is matched by certain Gila species while other Gila have developed bizarre body forms (see Minckley, 1973). In Tribolodon the mouth is oblique and subterminal. In Gila the mouth is horizontal or oblique, terminal or inferior. The dorsal fin in both genera is over or slightly behind the level of the pelvic fin insertion and the anal lies behind the level of the dorsal fin. Tribolodon has a well-developed fleshy pelvic axillary process but this is absent in Gila.

Sexual dichromatism and dimorphism

Nuptial colouration in male T. hakonensis has been described by Okada (1959-1960). A reddish-orange colour develops on the edges of the upper and lower jaws, on the cheek, operculum, ventro-lateral parts of the body and on the proximal portion of the anal fin. Then two narrow reddish bands appear, one running along the lateral line and one above it. The head and dorso-lateral parts of the body, except the areas coloured red, become black. In Gila

species red or orange colours develop at the bases of the paired fins, the anal fin and ventro-laterally on the body, including the caudal peduncle (at least in G. intermedia). Red or orange lower cheeks and posterior lips have been recorded for G. intermedia. In G. atraria a narrow golden streak is found along the upper sides. Apparently red fin bases and lip corners are typical of western American genera including Gila and also Tribolodon (R.E. Jenkins, pers. comm. 1975).

Male nuptial tuberculation in T. hakonensis after Okada (1959-1960) and based on a single available sea-run adult is as follows. Small and minute tubercles are found on the dorsal head surface forward on to the snout, on the cheeks, opercular bones and branchiostegal rays. Minute tubercles are found on all fins (not seen on caudal in specimen examined) with development decreasing posteriorly on each fin. Tubercles are absent from the first pectoral and pelvic fin rays. On each fin ray tubercles are uniserial and branch with the ray and there seems to be more than one tubercle per ray segment though this was not positively determined. The scales are all tuberculate with a fine fringe lining each scale. Scales on the back and upper flanks also have usually one tubercle but may have up to three larger tubercles close to the posterior scale edge and centrally placed. There is some difference in tuberculation in the marine and freshwater forms of this species.

The freshwater form has fin tuberculation limited to the anterior rays of the pectoral and dorsal fins. The dorsal surface tubercles are arranged longitudinally in the freshwater form and transversely in the marine form.

There are very few detailed descriptions of tubercles for Gila species and the following is taken from Hubbs and Miller (1972) on G. alvordensis and Hubbs, Miller and Hubbs (1974) on G. bicolor. Tuberculation in males is almost entirely confined to the upper surfaces of the pectoral fin rays although weak tubercles were noted on the pelvic fins and minute excrescences (? tubercles) were scattered over the top and sides of the head in G. alvordensis. Tubercles are best developed on pectoral rays 2 and 3, moderately developed on the first ray and progressively weaker on the more posterior rays. They are uniserial on the first ray, branching once on other rays. Each tubercle is on a single ray segment, is pointed and has a slight mesad hook.

Hence there are evident differences in tuberculation according to the scant data and no similarities which can be used to indicate a relationship between Gila and Tribolodon.

Scale characters

Scale characters of Tribolodon have been described in the scale section under Gila (p. 36-38), and are encompassed by the observed variation in Gila.

Osteology

In addition to the available material listed above the osteological studies of Uyeno (1961) were used for this comparison.

The caudal skeleton of Tribolodon has six hypural bones and the third urodermal is present. Certain Gila species have these bones while others lack them.

The suborbital series is characterised by an enlarged fourth suborbital bone, a slim, elongate fifth suborbital and no sixth suborbital unless it is indistinguishably fused with the supratemporal-intertemporal in Tribolodon (Figure 76). An enlarged fourth suborbital is seen in some Gila e.g. G. crassicauda (see Miller, 1963b) but is followed by a horizontally expanded fifth suborbital. A sixth suborbital is absent or present in Gila. Expanded posterior suborbital bones are also characteristic of such western N. American genera as Algansea and Xystrosus.

The hyomandibular bone has a weakly developed posterior flange which dorsally curves anteriorly or antero-dorsally in Tribolodon and some Gila bicolor but not all Gila species (Figure 77). This structure may be related to the strong lateral ridge typical of the western genus Ptychocheilus.

The cephalic lateral line canal on the preopercle goes to the dorsal tip but the opercle is not perforated in either Tribolodon or Gila. Miyadi, Kawanabe and Mizuno (1965) illustrate T. taczanowskii with the preoperculomandibular and infraorbital canals connected but whether this involves perforation of the operculum is not clear.

Some Tribolodon individuals have a posterior meso-ventral process on the autopalatine in addition to the dorsal one. This is also seen in Gila atraria. (Figure 77).

The coronomeckelian bone of Tribolodon is large and dorsally pointed in some fish and projects dorsally higher than the angular behind the ascending process of the dentary. (Figure 77). This is not seen in Gila where the low rounded angular is highest.

The parasphenoid bears a dorsal ridge which between the wings forms a dorsal spike in Tribolodon and Gila.

A lateral preethmoid ossification is absent in Tribolodon but may be present in some Gila, eg. G. bicolor.

The lateral ethmoid of Tribolodon has a strong posterior and lateral process ventral to the frontal and orbitosphenoid (Figure 75). Large Gila bicolor and small G. alvordensis have a similar structure but it is not as well developed as that of Tribolodon.

The supraethmoid is dorsally convex in Tribolodon but concave in Gila.

The lateral edges of the ethmoid do not meet in Tribolodon and most Gila (Uyeno, 1961) although the distance may vary somewhat in the latter genus.

The pterospheneids meet in the ventral mid-line in Tribolodon and some Gila e.g. G. atraria, G. bicolor, G. caerulea, G. robusta and variably in certain other species (Uyeno, 1961).

A large opisthotic and a large posterior process on the exoccipital is present in Tribolodon and is matched by large G. bicolor but not smaller species.

The supratemporal - intertemporal does not reach the frontal anteriorly in Tribolodon but does in Gila (Uyeno, 1961)

In Tribolodon the supraorbital head canal terminates at the antero-lateral corner of the parietal and curves laterally. Miyadi, Kawanabe and Mizuno (1965) figure Tribolodon where the supraorbital canal extends to the supratemporal canal. The extent of the canal in Gila species is variable. It may terminate on the frontal, eg. G. alvordensis or on the posterior part of the parietal, eg. G. robusta.

The masticatory plate of the basioccipital lacks an anteriorly directed process over the aortic canal in Tribolodon but G. bicolor and rarely G. mohavensis have one.

The pharyngeal arch of Tribolodon is characterised by a short anterior arm, a well developed sharp anterior angle, a weak posterior angle and hooked teeth. These characters are also found in certain Gila species while others have longer anterior arms and weak and rounded anterior angles in different combinations.

The intercalaria of Tribolodon are generally triangular while in Gila shape ranges from a "Y" to triangular. The fourth neural spine slopes posteriorly in Tribolodon and either anteriorly or posteriorly in Gila species. The second rib is about twice as long as the first in both Tribolodon and Gila.

Character analyses for Nearctic-Palae~~arctic~~ cyprinids.

The relationship of the Palae~~arctic~~ cyprinids examined to the Nearctic genera was assessed using Hennig's coefficients. Seven additional characters were used and these are briefly analyzed below. Character states for Palae~~arctic~~ genera are given in Table 12. Characters 29 to 35 were all state 0 (primitive) for Nearctic genera except where indicated in Table 12.

Character 29 - Naked ventral keel

A naked ventral keel extending from the pelvic fin origin to the anus is regarded as a derived condition (state 100) for Nearctic and Palae~~arctic~~ cyprinids (criteria 1, 4, 8).

Character 30 - Perforated operculum

The antero-dorsal corner of the operculum may be perforated for the preoperculamandibular canal. This condition is derived (criteria 1, 4, 8)

Character 31 - Anal ray counts

Anal ray counts have been assessed previously (character 13) but wide ranging counts were omitted from this assessment which was based on strong modes. Wide ranging counts may be analysed thus:-

State 0 - Strong modal count (7,8,9,10,12)

State 33 - Range 10-19~

TABLE 12

Character states of Palaearctic genera

Character																		
Genus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Phoxinus	999	0	0	0	0	100	0	999	100	50	50	0	0	0	40	999	999	999
Abramis	999	0	0	0	0	100	100	25	100	0	0	50	999	33	100	999	999	999
Alburnoides	999	0	0	0	0	100	0	75	0	0	0	50	999	33	60	999	999	999
Alburnus	999	0	0	0	0	100	0	25	100	0	0	50	999	33	60	999	999	999
Blicca	999	0	0	0	0	100	0	50	100	0	0	50	999	33	40	999	999	999
Vimba	999	0	0	0	0	100	100	0	100	0	0	50	999	33	80	999	999	999
Tribolodon	999	0	0	0	0	100	0	0	0	0	0	0	50	0	100	999	999	999

Character																		
Genus	19	20	21	22	23	24	25	26	27	28	29*	30*	31*	32*	33	34*	35*	
Phoxinus	999	0	100	60	0	0	0	0	0	0	0	0	0	0	0	0	100	
Abramis	999	67	25	60	100	0	0	0	0	0	100	100	100	100	100	0	0	
Alburnoides	999	67	0	100	0	0	0	0	0	0	100	100	33	0	0	0	0	
Alburnus	999	67	0	100	100	0	0	0	0	0	100	100	33	100	0	0	0	
Blicca	999	67	0	60	100	0	0	0	0	0	100	100	67	100	100	0	0	
Vimba	999	100	0	60	100	0	0	0	0	0	100	100	67	100	100	0	0	
Tribolodon	999	67	50	40	0	0	0	0	0	0	0	0	0	0	0	100	0	

* Character state 100 for Notemigonus+ " " 33 for Notemigonus and Richardsonius- " " 100 for Lavinia- " " 100 for Chrosomus

State 67 - Range intermediate between 10-19 and 20-29

State 100 - Range > 30 .

Increasing numbers of anal rays are derived (criteria 1,4,7,8).

Character 32 - Scale type

Scales may bear numerous fine concentric circuli around a central focus and are large to moderate. This condition is derived (criteria 1,7,8).

Character 33 - Supracleithrum tube

The supracleithrum may carry a large, ventrally open lateral tube (not the sensory canal). This is derived and an intermediate condition where its presence is variable was scored as 50 (criteria 1,4,7,8).

Character 34 - Connection of head canals

The preoperculomandibular and infraorbital head canals may be connected over the antero-dorsal corner of the operculum rather than through the operculum. This is a derived condition (criteria 1,4,8) (see Gosline, 1974).

Character 35 - Breast tuberculation

Tuberculation immediately behind the operculum on the breast in continuous rows is scored as a derived condition. It is discussed above in this section of the thesis (criteria 1,4,8).

The highest Hennig's coefficients for Palaearctic with Nearctic genera are given below:-

<u>Phoxinus</u>	with	<u>Chrosomus</u>	0.556
<u>Abramis</u>	with	<u>Notemigonus</u>	0.389
<u>Alburnoides</u>	with	<u>Notemigonus</u>	0.467
<u>Alburnus</u>	with	<u>Notemigonus</u>	0.471
<u>Blicca</u>	with	<u>Notemigonus</u>	0.353
<u>Vimba</u>	with	<u>Notemigonus</u>	0.375
<u>Tribolodon</u>	with	<u>Mylopharodon</u>	0.500
<u>Tribolodon</u>	with	<u>Acrocheilus</u>	0.455
<u>Tribolodon</u>	with	<u>Mylocheilus</u>	0.444
<u>Tribolodon</u>	with	<u>Ptychocheilus</u>	0.400
<u>Tribolodon</u>	with	<u>Gila</u>	0.273

DISCUSSION

The congeneric status of Chrosomus and Phoxinus is indisputable. Differences are limited to trophic characters in some species while the majority of other characters are the same in both genera. Breast tuberculation can be regarded as a shared derived character. Banareescu (1964) has synonymised these genera and as first reviser selected Phoxinus since these names have identical dates.

Notemigonus shows evident affinities with the Abramidini, particularly Alburnus and Alburnoides. There are however differences in meristic characters, tuberculation and some osteological features which warrant retention of Notemigonus as a separate genus. The Eurasian genera have doubtless evolved since Notemigonus or a Notemigonus-like ancestor split

off and this can account for the observed differences. A more detailed and widespread examination of Leuciscinae genera would provide useful information on primitive and derived states of characters in this subfamily and facilitate determination of generic relationships in Eurasian and North American members of this taxon.

The purported relationship of Gila and Tribolodon is not confirmed. On the basis of the characters examined Tribolodon is closer to other large western American genera such as Mylopharodon, Acrocheilus, Mylocheilus and Ptychocheilus. Further studies should be undertaken in an attempt to establish unequivocal apomorphic characters that would show whether or not these genera are related.

Figure 66. Diagrams of gut patterns in some cyprinid fishes (ventral view, anterior at top of page):-

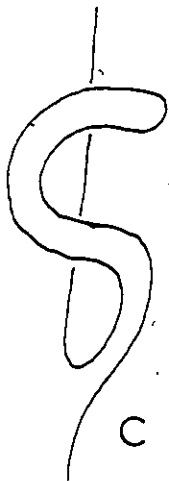
A- Chrosomus neogaeus, Phoxinus spp., Moroco, steindachneri, some Tribolodon hakonensis (Type 1 gut pattern of Kafuku, 1958); B- some Tribolodon hakonensis (Type 2 of Kafuku, 1958); C and D- common patterns in Chrosomus eos; E, F and G- developmental series of patterns for Notemigonus crysoleucas (partly after unpublished studies by F. F. Snelson).



A



B



C



D



E



F



G

Figure 67. Anterior views of first anal proximal pterygiophores of:-

- A- Abramis ballerus
- B- A. brama
- C- A. sapa
- D- Alburnoides bipunctatus
- E- Alburnus alburnus
- F- Blicca bjoerkna
- G- Vimba vimba

Scales: 1 mm.

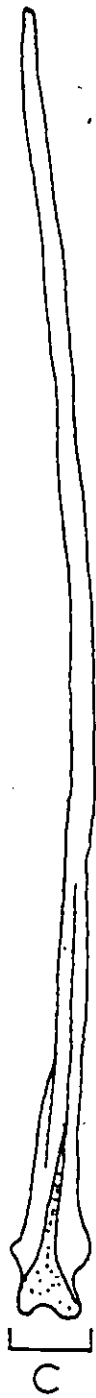
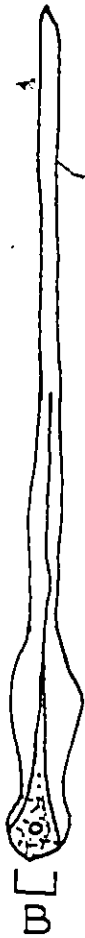


Figure 68. Lateral views of supracleithra of:-

- A- Abramis ballerus (right supracleithrum).
- B- A. brama (right).
- C- A. sapa (left).
- D- Alburnoides bipunctatus (left).
- E- Alburnus alburnus (left).
- F- Vimba vimba (right).
- G- Blicca bjoerkna (left).

Scales: 1 mm.

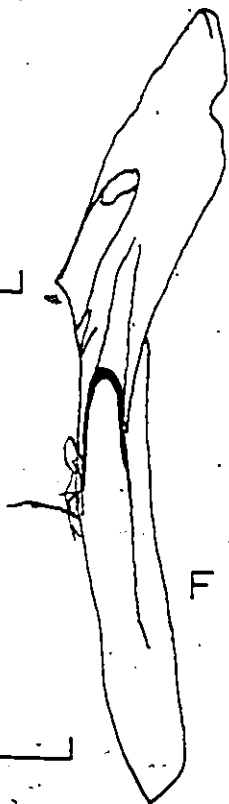
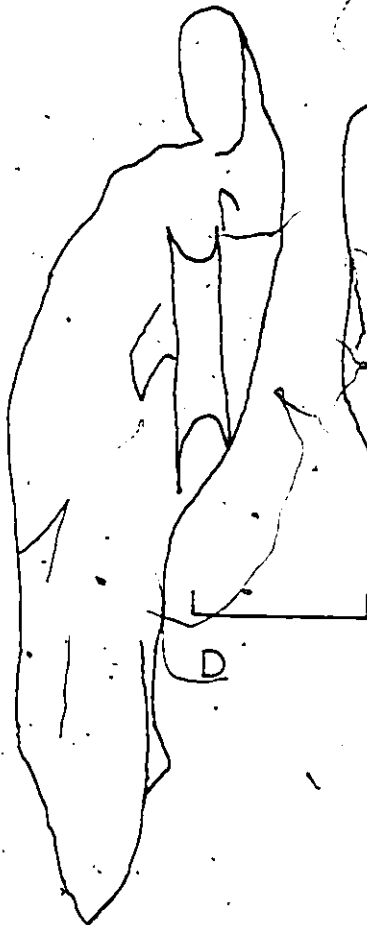
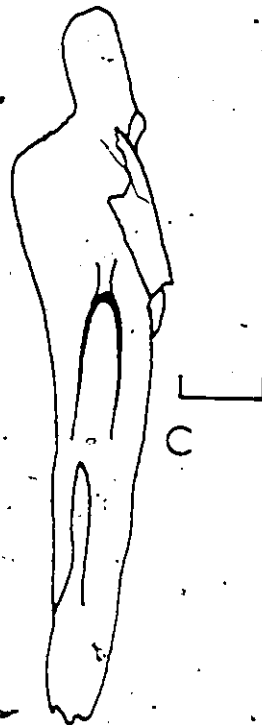
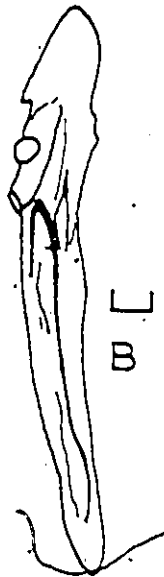
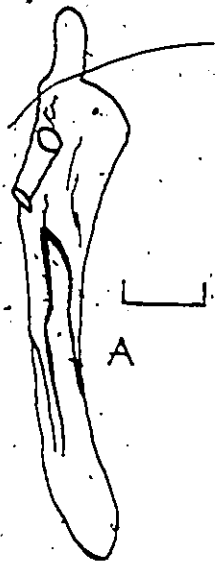


Figure 69. Mesial view of left pectoral girdle of Abramis
ballerus; fin rays removed and pectoral radials
slightly detached.

Scale: 0.5 cm.

cc: coracoid, cl: cleithrum, gf: glenoid fossa,
mc: mesocoracoid, pcl: postcleithrum, pr₄: fourth
pectoral radial.

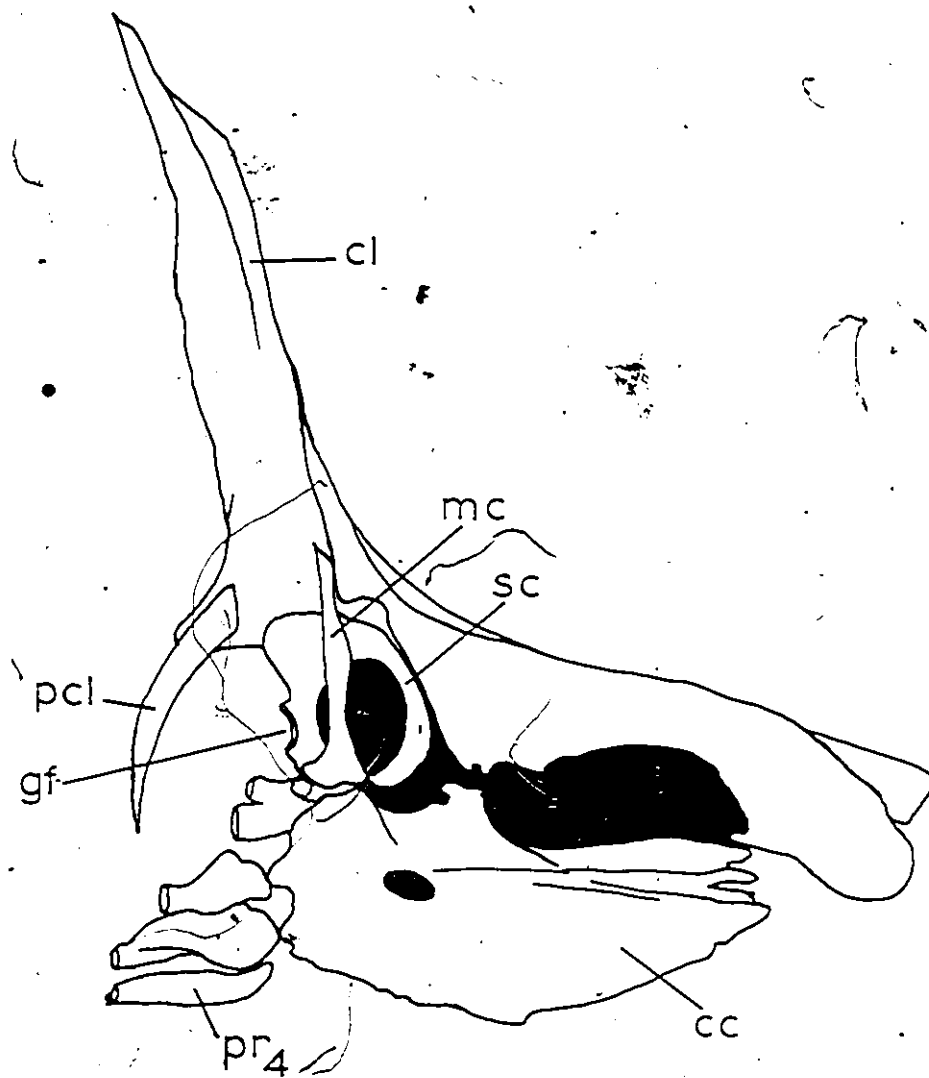


Figure 70. Mesial views of left pectoral girdles of Abramis
brama (above) and A. sapa (below); fin rays &
removed and pectoral radials slightly detached.
Scale: 1 cm.

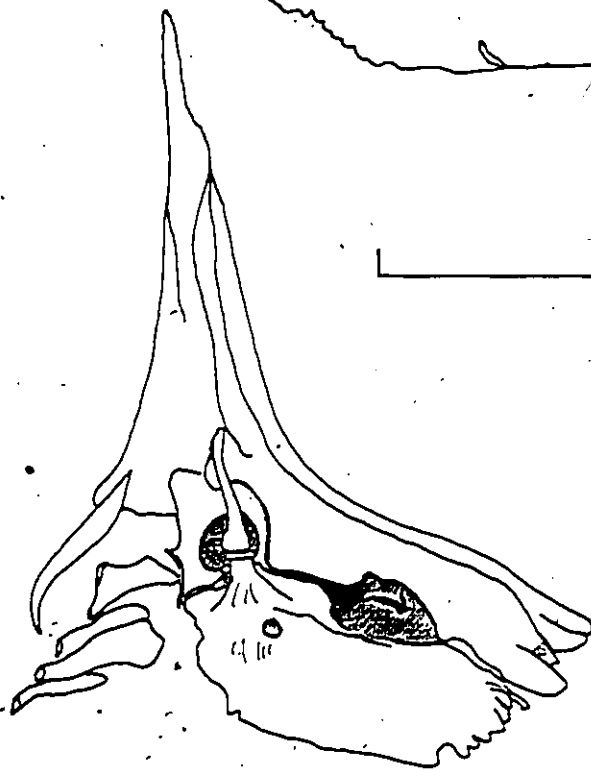
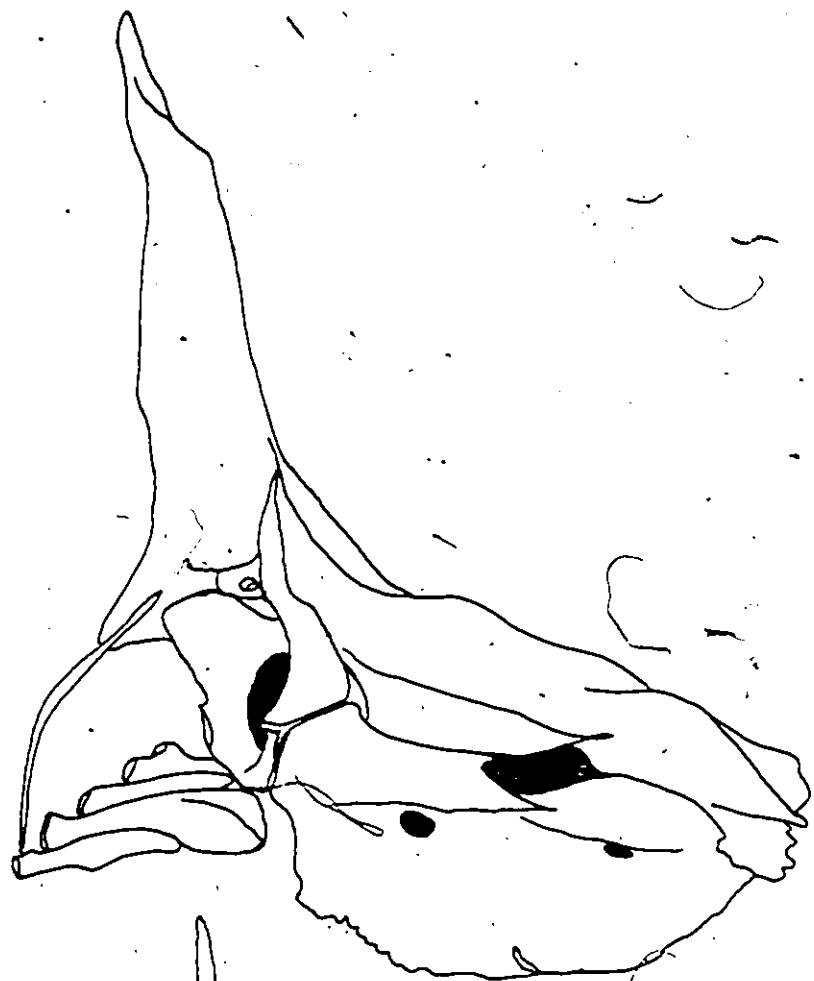


Figure 71. Mesial views of left pectoral girdles of Blicca
bjoerkna (above) and Alburnus alburnus (below);
fin rays removed and pectoral radials slightly
detached.
Scales: 1 mm. and 0.5 cm. respectively.

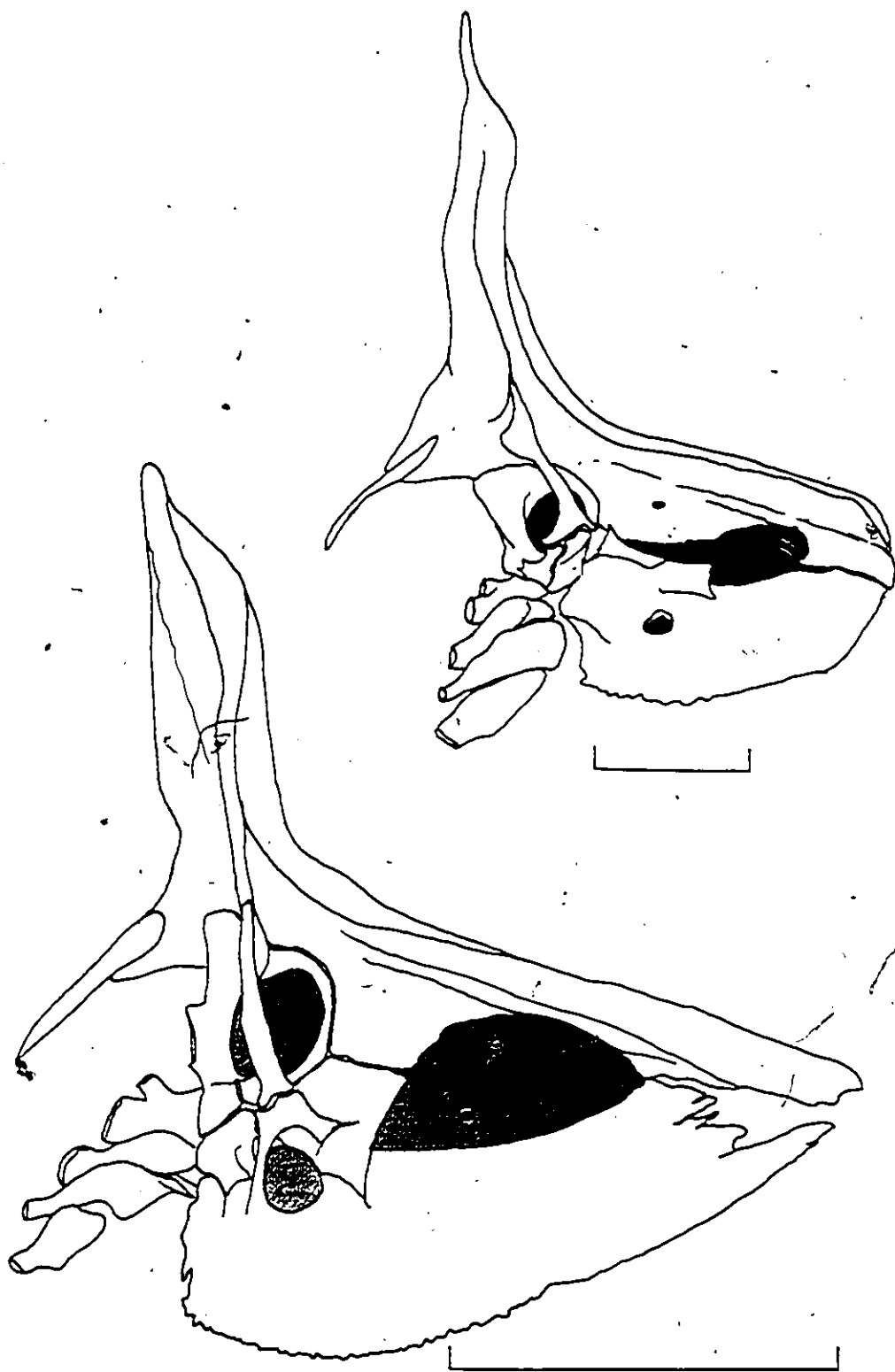
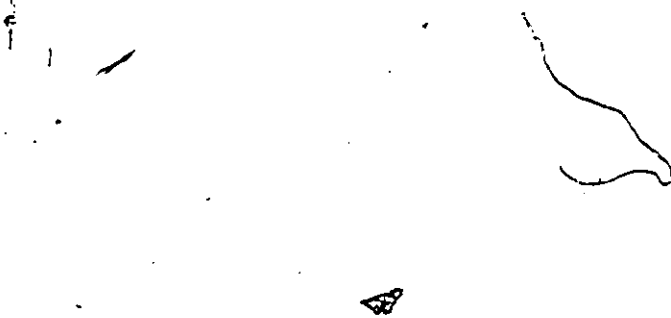




Figure 72. Mesial views of left pectoral girdles of Vimba vimba (above) and Alburnoides bipunctatus (below); fin rays removed and pectoral radials slightly detached.

Scales: 0.5 cm.



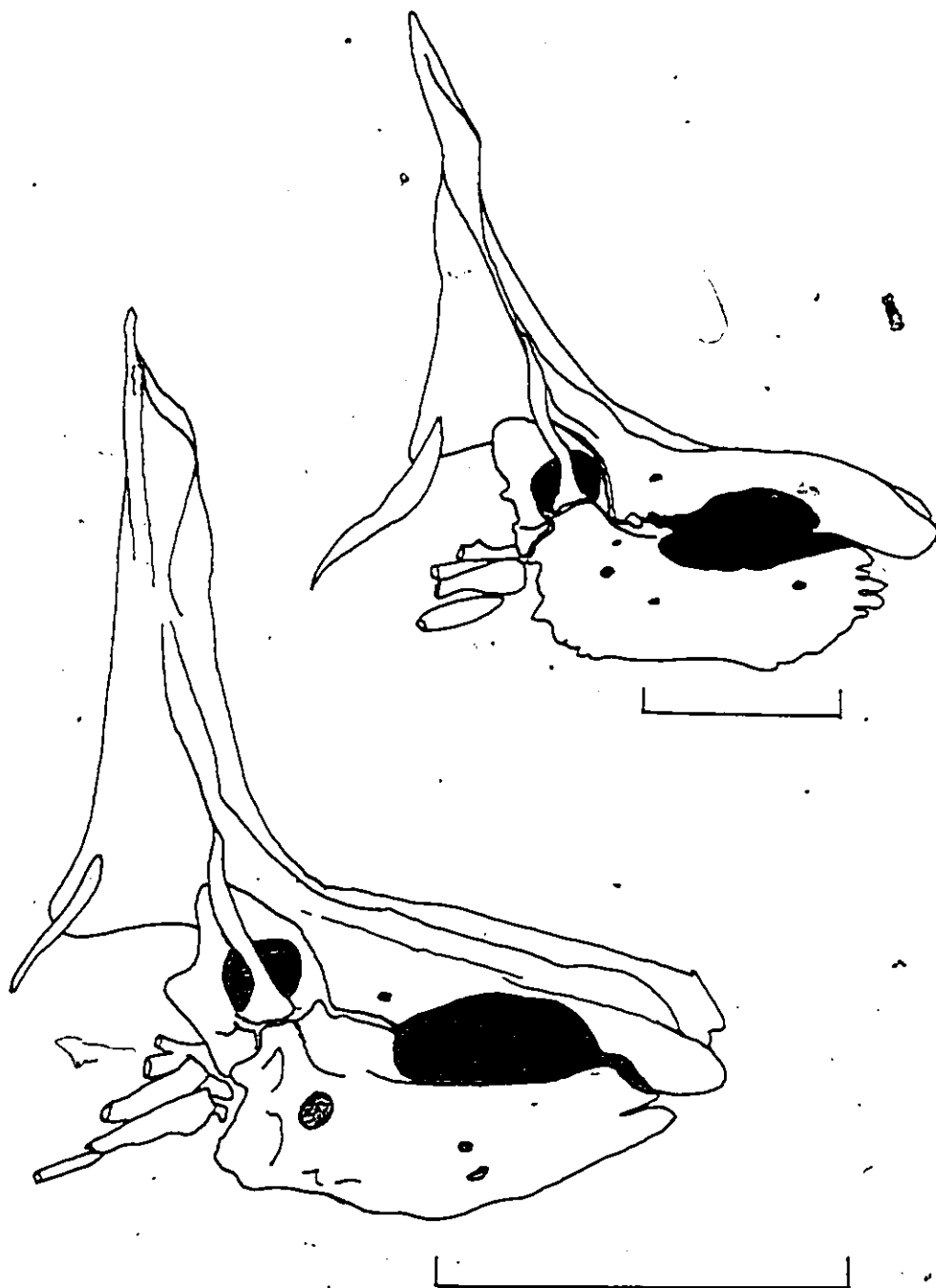


Figure 73. Lateral views of left lower jaws of A- Alburnoides bipunctatus, B- Alburnus alburnus and C- Blicca bjoerkna.

Scale: 0.5 cm.

a: angular, d: dentary, ra: retroarticular.

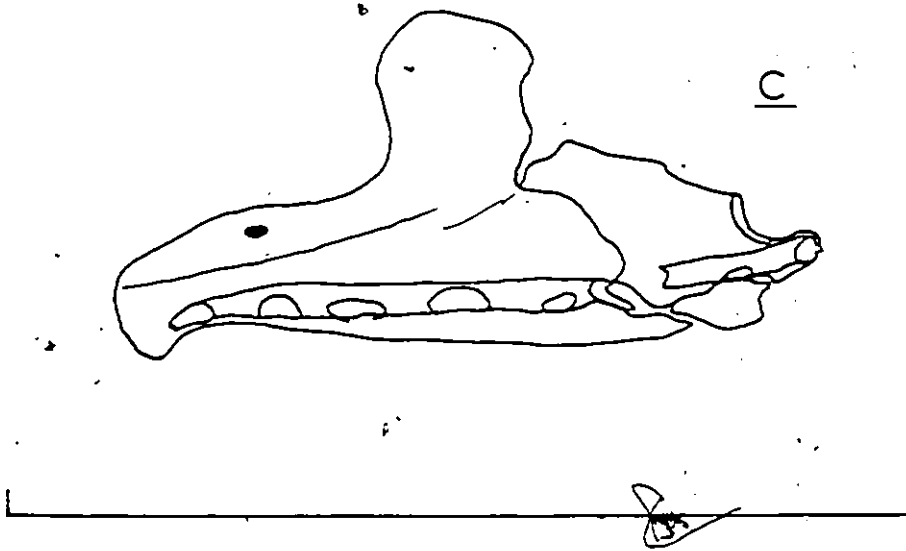
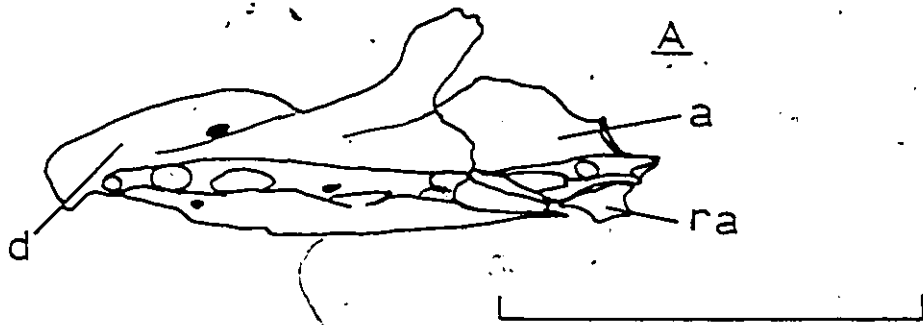
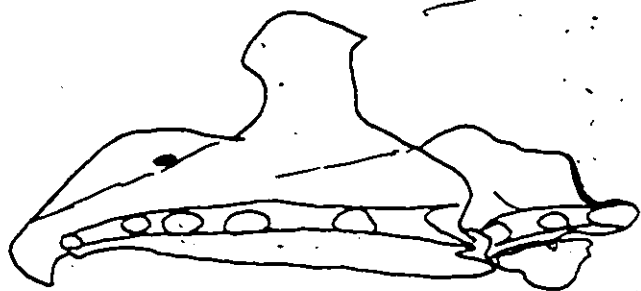
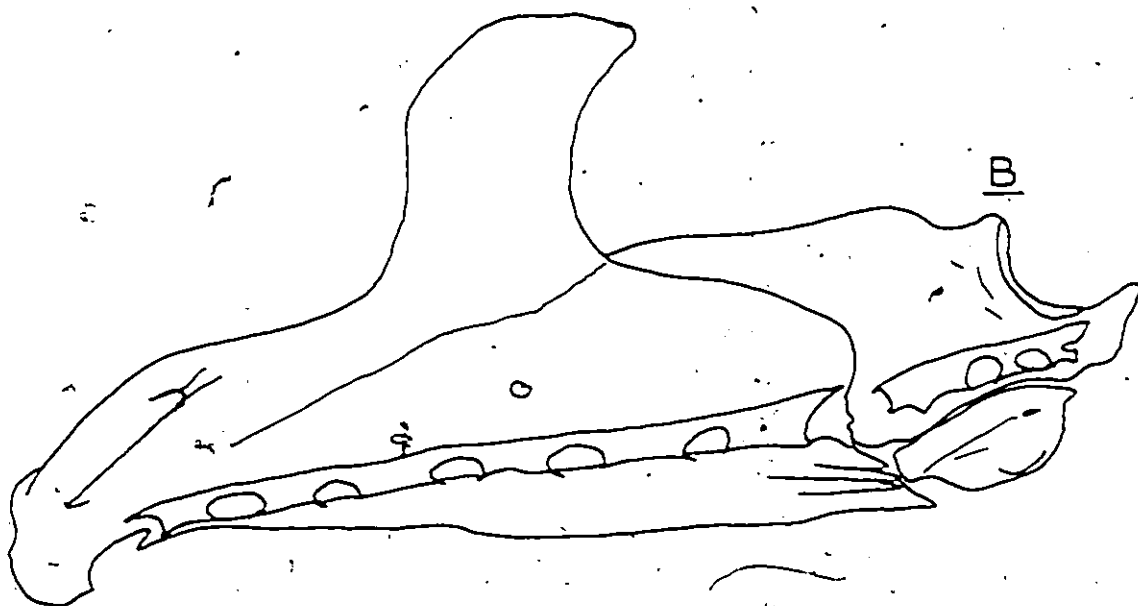


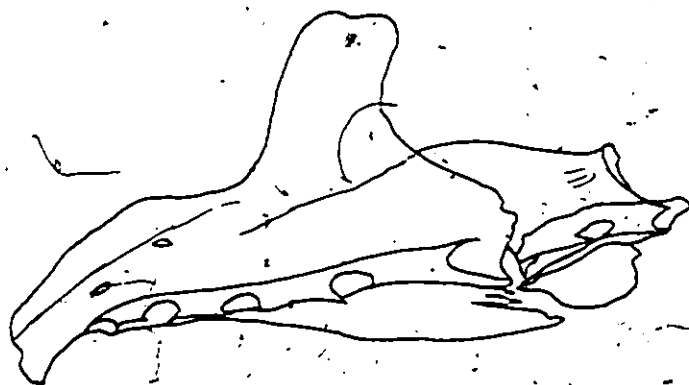
Figure 74. Lateral views of left lower jaws of A. Abramis
ballerus, B- A. brama and C- A. sapa
Scale: 0,5 cm.



A



B



C



Figure 75. A- Lateral view of left lower jaw of Vimba vimba,

B- Ventral view of lateral ethmoid and associated bones of Tribolodon hakonensis.

Scales: 1 mm.

f: frontal, le: lateral ethmoid, os: orbitosphenoid,
sp: supraorbital.

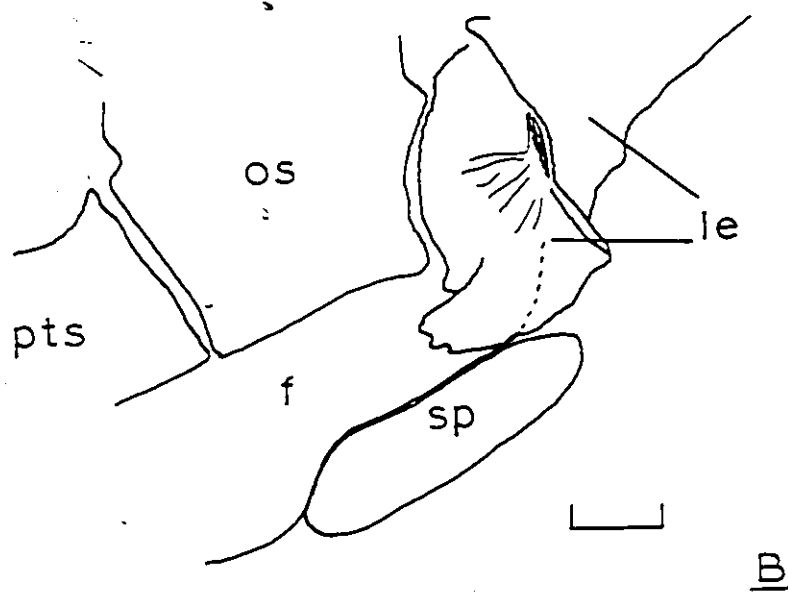
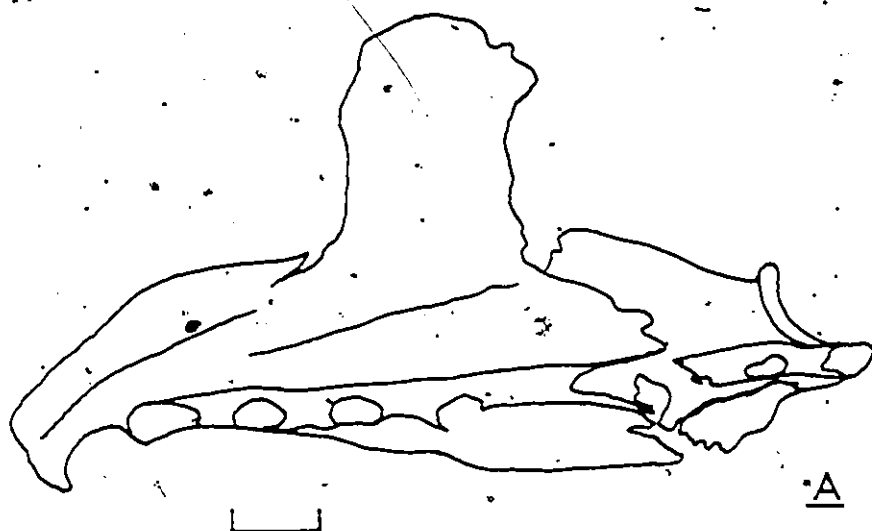


Figure 76. Suborbital bones of Tribolodon hakonensis.

Scale: 1 cm.

SO₁₋₅: first to fifth suborbitals.

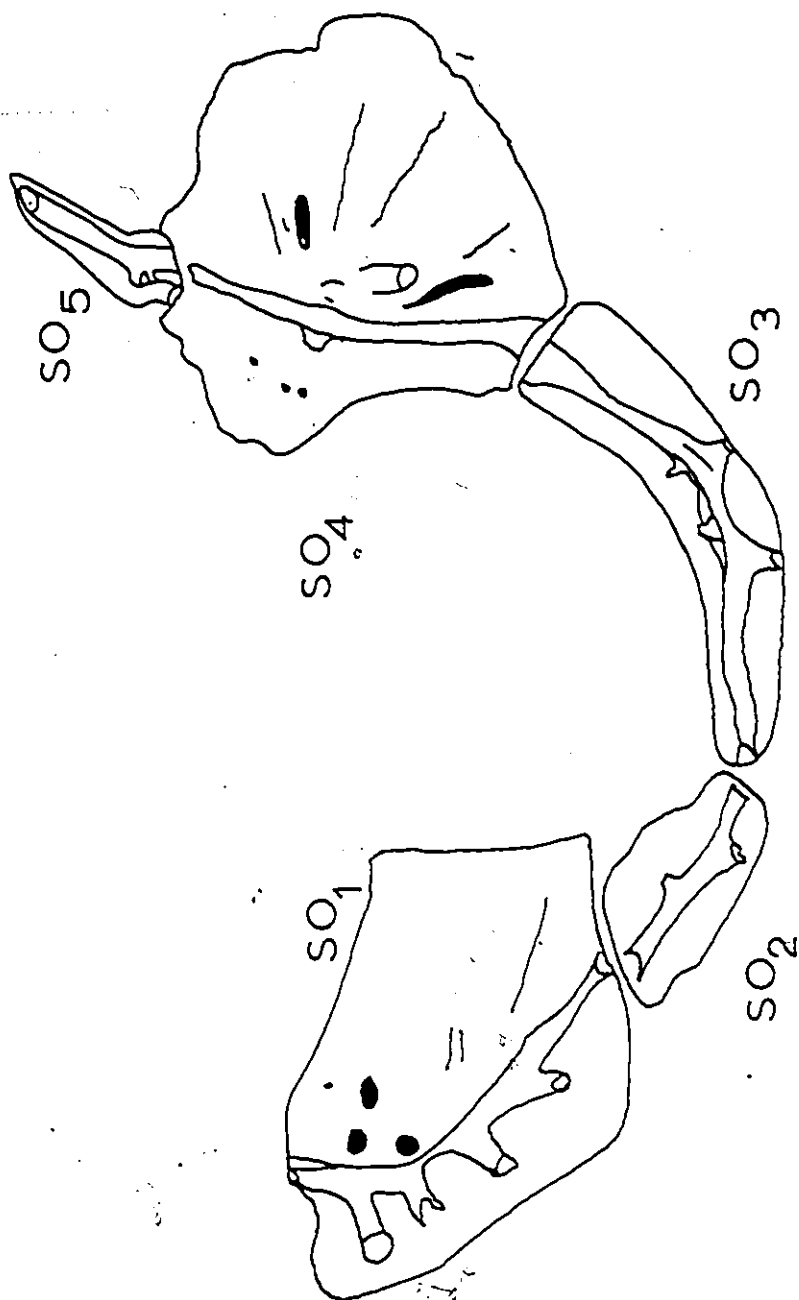
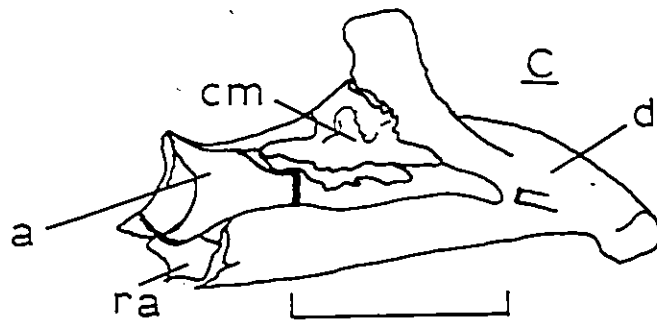
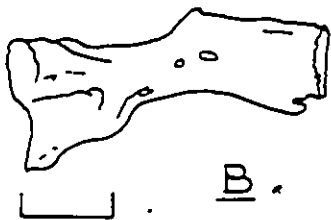


Figure 77. A- Lateral view of left hyomandibular, B- Mesial view of right autopalatine, and C- Mesial view of left lower jaw of Tribolodon hakonensis. Scale: 0.5 cm., 1 mm., and 0.5 cm. respectively. a: angular, cm: coronomeckelian, d: dentary, ra: retroarticular.



Suggestions for future studies

Papers by Evans (1952) and Davis and Miller (1967) have shown that brain patterns differ between species but that these differences are intimately related to functional specialisations such that convergence and divergence are extremely difficult to ascertain. Nevertheless, Reno (1969b) has pointed out that in conjunction with other characters brain pattern may be of use in elucidating relationships, if not in general, at least in certain specific cases. Other detailed studies on various organs and systems might yield useful data, e.g. on the muscular, nervous and blood systems, on soft body parts like the intestines and gas bladder, and histological studies on the barbels to establish similarities and differences in the various genera. Osteological characters might prove useful even though many show variation at the species level if sufficiently large series of adult specimens are examined so that trends could be adequately summarised. The work of Menzel (1970) and Rainboth and Whitt (1974) indicate that pertinent information can be obtained from biochemical investigations. Such studies might usefully be concentrated on certain problem areas such as the relationships of and in Hybopsis s.l. Gusev and Luk'yantseva (1971) present some limited comparisons of monogenean parasites from Eurasian and North American cyprinids and comment on the

relationships of the fishes as revealed by their parasites.

Chen (1971) has studied the monogenean parasites of Nocomis and considers that phylogeny and speciation of this cyprinid genus can be traced on this basis. Much work remains to be done on parasite systematics before it can be of general use in relating hosts. It may prove possible to obtain apomorphic characters to relate taxa from a study of the eggs, embryos and larvae of cyprinids (see Ivankov and Kurdayeva, 1973; Balon, 1975).

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APPENDIX 1

List of Specimens

The material examined is listed on the following pages in alphabetical order. A catalogue number, number of specimens, range in standard length (mm) and capture data are given with an indication of which study they were used in (OA = Osteology alizarin preparation; OX = Osteology X-ray plate; S = Scale study; T = Tubercle study). All specimens were utilised in the character analysis.

Uncatalogued material marked Pers. Coll. (personal collection) has been deposited at the National Museum of Natural Sciences, Ottawa and certain registered material received as gifts or in exchange is included.

Abbreviations for catalogued material

AMNH	American Museum of Natural History
BC	University of British Columbia Institute of Fisheries
BM(NH)	British Museum (Natural History)
CAS	California Academy of Sciences
KU	University of Kansas Museum of Natural History
NLU	Collection of Vertebrates, Northeast Louisiana University
NMC	National Museum of Natural Sciences, Ottawa
ROM	Royal Ontario Museum, Toronto
SCB	Collection of S. Contreras - Balderas, Universidad de Nuevo Leon, Monterrey, México
SU	Stanford University (now in California Academy of Sciences)
UAMZ	University of Alberta Museum of Zoology

UM University of Minnesota
 UMMZ University of Michigan Museum of Zoology
 USNM National Museum of Natural History, Washington
 WKU Western Kentucky University
 WSU Wisconsin State University Museum of Natural History
 ZIAS Zoological Institute Academy of Sciences, Leningrad

North American Cyprinidae

Acrocheilus alutaceus BC 54-22 (4 specimens, 118-133 mm. S.L., OX) British Columbia, Okanagan River side channel between Vaseaus Lake and Osoyoos Lake ($49^{\circ}07'N$, $119^{\circ}32'W$), June 1951. BC 72-83 (1 specimen, 84 mm S.L., OX) British Columbia, N.W. Skaha Lake ($49^{\circ}27'N$, $119^{\circ}35'W$), 22 November 1971. Pers. Coll. (8 specimens, 82-108 mm S.L., OA(5), S), Oregon, Sherman Co. Deshutes River at Bakeoven Creek, 17 September 1952.

Agosia chrysogaster AMNH 27250 (10 specimens, 44-61 mm S.L., OA(5), OX, S), Arizona, Cochise Co., San Pedro River on State Highway 92 south of Bisbee, 20 April 1950. UMMZ 162668 (5 specimens, 64-67 mm S.L., OA(5), OX, S), Arizona, Santa Cruz Co., Peck Canyon area $\frac{1}{2}$ mile above Kane Ranch, 18 April 1950. SU 16140 (10 specimens, 25-60 mm S.L., OX), México, Sonora, Sonoyta River, Sonoyta, pools and rapids above and below ford, 25 March 1948.

Algansea monticola UMMZ 192266 (20 specimens, 24-54 mm S.L., OA(4), OX, S). México, Zacatecas, Rio Juchipila $\pm$ 1 mile N.E. Jalpa at hwy. 70 crossing, 30 April 1969.

Algansea tincella UMMZ 179754 (20 specimens, 25-69 mm S.L., OA(4), OX, S), México, Jalisco, Rio Ancho, ca. 5 miles W. of Yahualica, on road to Teicaltiche (hwy 80 alternate), 15 March 1961.

Campostoma anomalum Pers. Coll. (4 specimens, 32-37 mm S.L., OA(2), S), Texas, Blanco River at Interstate Highway 35 2 miles N. of San Marcos, 19 June 1973. Pers. Coll. (3 specimens, 37-64 mm S.L., OA(2), S), Texas, Comal Co., Guadalupe River immediately below Canyon Lake dam, 17 June 1973. NMC 70-395 (3 specimens, 43-55 mm S.L., OX), Texas, Val Verde Co., Devil's River at entrance to Amistad Reservoir, 25 April 1969.

Chrosomus eos Pers. Coll. (UM 64-006) (3 specimens, 43-50 mm S.L., OA(3), S), Minnesota, Hubbard and Clearwater Co., Mississippi River at source just below outlet from Lake Itasca, 22 June 1964. Pers. Coll. (9 specimens, 42-52 mm S.L., OA(2), S, T), Québec, Joliette Co., Parc Joliette, Lac Simard, 14 July 1972. NMC 68-2062 (4 specimens, 48-50 mm S.L., OA(2)), Alberta, Peace River area, Simonette River 5 miles south of Goodwin, 2 July 1968. Pers. Coll. (UAMZ 2146) (2 specimens, 42-47 mm S.L., OA(2), S), Alberta, Wood Buffalo National Park, Rainbow Lake, 26 June 1970. NMC 62-201 (2 specimens, 40-45 mm S.L., OA(4), S), Nova Scotia, Kings Co., Coldbrook, ponds along Cornwallis River, 16 September 1961. Pers. Coll. (1 specimen, 41₉ mm S.L., OA, S), Québec, Gatineau Park, Ramsay Lake, 18 August 1972. NMC 61-209 (5 specimens, 40-53 mm

S.L., OX), Ontario, Frontenac Co., Mosque Lake Lodge, S. end of Mosque Lake, 20 August 1961. NMC 68-2066 (10 specimens, 39-50 mm S.L., OX), Alberta, Economy Creek, 12 miles S. and $\frac{1}{2}$ mile W. of Goodwin, 3 July 1968. NMC 67-622 (2 specimens, 48-52 mm S.L., OA(2)), Montana, Milk River, below Fresno Reservoir spillway, 10 June 1967. Pers. Coll. (4 specimens, 42-44 mm S.L., OA(4)), Ontario, White Lake pond near Perth.

Chrosomus erythrogaster Pers. Coll. (UM68-005) (336 specimens, 50-60 mm S.L., OA(8), S.T.), Minnesota, Dodge Co., North Branch Zumbro River middle fork, 25 May 1968.

Chrosomus neogaeus Pers. Coll. (2 specimens, 73-77 mm S.L., OA(2), S), Minnesota, Hubbard and Clearwater Co., tributary to Mississippi River in Itasca State Park, August 1972. NMC 64-602 (2 specimens, 55-56 mm S.L., OA(2), S), Manitoba, Whiteshell Provincial Park, Rennie River, Rennie, 4 August 1964. Pers. Coll. (UAMZ 2150) (2 specimens, both 54 mm S.L., OA(2), S), Northwest Territories, Wood Buffalo National Park, Sass River, 28 June 1970. Pers. Coll. (4 specimens, 77-81 mm S.L., OA(2), S), Minnesota, Hubbard and Clearwater Co., LaSalle Creek, 20 August 1972. NMC 60-420 (2 specimens, 60-72 mm S.L., OA(2), S), Ontario, Carleton Co., $6\frac{1}{2}$ miles N.W. Burritt's Rapids, 26 miles S.E. Ottawa, 23 May, 1960. Pers. Coll. (4 specimens, 48-50 mm S.L., OA(4), S), Québec, Gatineau Park, Holly Lake, 18 August, 1972. NMC 64-45 (8 specimens, 55-71 mm S.L., OX), Ontario, Thunder Bay Co., Jeff Lake, Lybster Turp., approx.

32 miles S.W. of Arthur, 12 May 1951. NMC 64-601 (6 specimens 61-69 mm S.L., OX), Manitoba, The Lily Pond, 1 mile W. of Caddy Lake, Whiteshell Provincial Park, 22 July 1964.

Chrosomus oreas Pers. Coll. (5 specimens, 48-55 mm S.L., OA(4), S), Virginia Montgomery Co., Roanoke River $\frac{1}{2}$ mile S. of Shawville and U.S. Route 11, 1.4 miles S.W. of Salem, 9 miles N.E. of Christianburg, 18 July 1955.

Clinostomus elongatus ROM 22517 (5 specimens, 58-65 mm S.L., T), Ontario, York Co., Highland Creek, 1954. ROM 24663 (1 specimen, 70 mm S.L., T), Ontario, Lincoln Co., Twelve Mile Creek, Summer 1958.

Clinostomus funduloides Pers. Coll. (8 specimens, 55-72 mm S.L., OA(2), S, T.), Maryland, Allegany Co., North Branch Jennings Run, June 1970. ROM 23105 (4 specimens, 67-77 mm S.L., T), North Carolina, Burke Co., Upper Steele Creek, Daniel Boone Wildlife Management Area, 6 September, 1962.

Couesius plumbeus NMC 66-79 (12 specimens, 60-83 mm S.L., OA(2), S), British Columbia, Moyie Lake, 10 August, 1965. NMC 59-292 (10 specimens, 60-88 mm S.L., OA(2), S), Nova Scotia Pictou Co., Cariboo River at Hwy 6 bridge about 8 miles W. of Pictou, 19 July, 1959. NMC 68-2070 (4 specimens, 56-69 mm S.L., OA(4)), Alberta, Peace River area, 4 July, 1968. NMC 66-390 (10 specimens, 60-69 mm S.L., S), Alberta, Milk River, Sage Creek 10.5 miles N. and $1\frac{1}{2}$ miles W. of Wild Horse, 28 July, 1966.

NMC 70-198 (10 specimens, 60-69 mm S.L., S), Saskatchewan, Wood River 8 miles N. and 2 miles E. of Gravelburg, 10 July, 1970. NMC 73-202 (2 specimens, 111-144 mm S.L., S), N.W.T., Creek pool 2 miles S of Norman Wells (east side of Mackenzie River), 24 August, 1972. Pers. Coll. (2 specimens, 80-122 mm S.L., OA(2)), Ontario, Lake Superior, Pukaskwa National Park, Bonamie Cove and Simon Harbour, 24-25 September, 1972. Pers. Coll. (11 specimens, 60-81 mm S.L., OA(2), T), Québec, Parc Joliette, Ruisseau Girondin, 11 July, 1972.

Dionda episcopa

NMC 70-382 (14 specimens, 37-63 mm S.L., OA(3), S), Texas, Reaves Co., irrigation ditches from San Solomon Springs near Toyahvale, 24 January, 1970. Pers. Coll. (3 specimens, 64-81 mm S.L., OA(2), S, T), Texas, San Marcos River above Loop 82 in San Marcos, 19 June, 1973). Pers. Coll. (5 specimens, 57-75 mm S.L., OA(3), S), Texas, San Marcos River below Chaetum St. Bridge, 19 June, 1973.

Eremichthys acros

AMNH 27236 (10 specimens, 34-49 mm S.L., OX, S), Nevada, Humboldt Co., spring fed reservoirs above Soldier Meadows Ranch, 21 August, 1965. UMMZ 186515 (5 specimens, 46-54 mm S.L., OA(5), OX, S), Nevada, Humboldt Co., spring fed reservoirs above Soldier Meadows Ranch circa $\frac{1}{2}$ mile above ranch house, 21 August, 1965. Pers. Coll. (8 specimens, 46-53 mm S.L., OA(5), S), No data, 24 September, 1973.

Ericymba buccata

Pers. Coll. (20 specimens, 38-49 mm S.L., OA(6), S), Kentucky, Spencer Co., Plum Creek below Highway 44 bridge, 10 November, 1967.

Pers. Coll. (10 specimens, 47-60 mm S.L., OA(2), S), Illinois, Vermilion Co., East Branch 5 miles E.S.E. Rossville, 26 August, 1970.

Exoglossum maxillingua

NMC 64-455 (1 specimen, 57 mm S.L., OA, S), Pennsylvania, southern tributary to Bermudian Creek, 18 miles S. of Harrisburg, 27 August, 1964. NMC 71-249 (1 specimen, 31 mm S.L., OA, S), Québec, Beauce Co., Rivière Chaudière, Vallée Juction, région de Beauce, 13 August, 1949. Pers. Coll. (2 specimens, 55-103 mm S.L., OA(2), S), Pennsylvania, Condoquimet Creek, Susquehanna drainage. Pers. Coll. (8 specimens, 47-90 mm S.L., S), Québec, St. Maurice Co., Grande Rivière Yamachiche at Yamachiche, 13 July, 1972. Pers. Coll. (8 specimens, 45-80 mm S.L., S), Québec, St. Maurice Co., Grande Rivière Yamachiche at Saint Etienne des Grès, 27 July, 1972.

Gila alvordensis

Pers. Coll. (6 specimens, 37-53 mm S.L., OA(2), S), Oregon, Pueblo Slough 7½ miles N. Denio, 24 August, 1965. Pers. Coll. (15 specimens, 31-75 mm S.L., OX, S), Oregon, Harney Co., Borax Lake, 24 September, 1972. Pers. Coll. (5 specimens, 49-57 mm S.L., OX, S), Oregon, spring on Waldkirsh Ranch near Fields, 24 July, 1972.

Gila atraria

Pers. Coll. (UMMZ 14137) (6 specimens, 41-79 mm S.L., OA(2), S), Utah, Millard Co., spring on Salt Flat, S. of old Salt Works, Snake Valley, 13 June, 1942.

Gila bicolor

Pers. Coll. (UMMZ 124883) (6 specimens, 52-109 mm S.L., OA (2), S), Nevada, Reese River 10 miles S.W. of Austin, 4 August, 1938. Pers. Coll. (8 specimens, 104-232 mm S.L., OA(2), S), Nevada, Pyramid Lake off Sutcliffe and Nine-Mile Canyon, 28 April, 1972.

Gila orcutti

Pers. Coll. (6 specimens, 39-55 mm S.L., OA(2), S), California, Los Angeles Co., Santa Clara River at Soledad Sulphur Spring (abandoned), Soledad Canyon 7 miles by road above U.S. 6 crossing, 9 November, 1948.

Gila robusta

Pers. Coll. (UMMZ 162773) (6 specimens, 53-103 mm S.L., OA(2)), Arizona, Gila Co., Carrizo Creek 66 miles N.E. of Globe, 18 May, 1950.

Hemitremia flammea

WKU 714 (1 specimen, 40 mm S.L., OX), Tennessee, Pine Creek at Highway 56 Bridge 3 miles S. of Smithville and Center Hill Reservoir, 16 August, 1971. WKU 981 (1 specimen, 22 mm S.L., OX), Tennessee, Pine Creek 6 miles down from Highway 56, 11/5/1971. WKU 993 (1 specimen, 42 mm S.L., OX), Tennessee, Pine Creek at Highway 56 Bridge, 11/6/1971. WKU 1026 (4 specimens, 34-44 mm S.L., OX), Tennessee, Coney Creek drainage, Sink Creek 1 mile down from Highway 56 Bridge, 11/6/1971. Pers. Coll. (5 specimens, 35-41 mm S.L.,

OA(2), S), Tennessee, Coffee Co., creek 4 miles N. Manchester,
29 April, 1967.

Hesperoleucus symmetricus

Pers. Coll. (5 specimens, 50-65 mm S.L., OA(2), S), California, Mendocino Co., Russian River, August, 1973. Pers. Coll. (10 specimens, 57-62 mm S.L., OA(3), S), California, Navarro River, August, 1973. UMMZ 186623 (5 specimens, 57-76 mm S.L., OA(5), OX, S), California, Colusa Co., Bear Creek at Highway 20, 3½ miles E. of Colusa-Lake Co. Line junction California 16, 15 miles S.W. Williams, 29 June, 1967. CAS 28770 (9 specimens, 37-97 mm S.L., OA(4), OX, S), California, Santa Cruz Co., San Lorenzo River.

Hybognathus hankinsoni

NMC 73-125 (6 specimens, 54-63 mm S.L., OX), Québec, Gatineau Co., Black Lake in Gatineau Park, 17 July, 1971. Pers. Coll. (5 specimens, 50-62 mm S.L., OA(5), S), Québec, Gatineau Park, Holly Lake, 18 August, 1972.

Hybognathus hayi

Pers. Coll. (2 specimens, 44-46 mm S.L., OA(1), S), Kentucky, Ballard Co., Prairie Lake 3 miles W. Gum Corners, 30 August, 1970.

Hybognathus nuchalis

Pers. Coll. (3 specimens, 56-64 mm S.L., OA(3), S), Ontario, Ottawa River at Ottawa, July-August, 1972.

Pers. Coll. (2 specimens, 52-79 mm S.L., OA(2), S), Ontario, Kettle Island, Ottawa River at Ottawa, 7 June, 1972. Pers. Coll. (2 specimens, 69-78 mm S.L., OA(2), S), Quebec, Rouville Co., Rivière Yamaska at Saint-Césaire, 23 July, 1969.

Hybognathus placitus

Pers. Coll. (5 specimens, 69-82 mm S.L., OA(4), S), Missouri, Mercer Co., Weldon Fork, Grand River 3½ miles N. Princeton, 22-23 October, 1950.

Hybopsis (Extrarius) aestivalis

Pers. Coll. (KU 8542) (12 specimens, 45-60 mm S.L., OA(5), S), Kansas, Sedgewick Co., north fork Ninnescah River on U.S.

Route 54 Sec. 33, T27S, R4W, 22 July, 1964. Pers. Coll. (6 specimens, 31-34 mm S.L., OA(2), S), Missouri, Pemiscot Co., drainage ditch at Highway crossing "EE" 2 miles each of Peach Orchard, T20N, R11E, S17, 2 September, 1970. Pers. Coll.

(NLU 19757) (20 specimens, 41-50 mm S.L., S), Mississippi, Simpson Co., Strong River, Mississippi Highway 28, 2 miles W. of Pinola, 11 June, 1971. Pers. Coll. (10 specimens, 32-45 mm S.L., OA(2), S), Indiana, Gibson Co., Wabash River opposite Rochester (Illinois), 5 November, 1964.

Hybopsis (Yuriria) alta

UMMZ 178328 (20 specimens, 17-56 mm S.L., OA(4), OX, S), México, Jalisco, Rio Verde near mouth in Rio Grande de Santiago (1 mile below Juntos Hydro-electric plant in Barranca, 18 miles E. of Guadalajara, 2 March, 1957. SCB-89 (5 specimens, 80-103 mm S.L.), México, Jalisco, Lago de Chapala, E. Chapala.

Hybopsis (Hybopsis) amblops

AMMH 8878 (5 specimens, 37-44 mm S.L., OA(5), OX, S),
 Illinois, Charleston, Kickapoo Creek, 20 May, 1905. WKU 107
 (2 specimens, 46-49 mm S.L., OX), Kentucky, Allen Co.
 Trammel Creek at Old State Road Bridge, 14 February, 1970.
 Pers. Coll. (8 specimens, 40-43 mm S.L., OA(2), S), Missouri,
 Madison Co., St. Francis River at crossing Highway "C", T31N,
 RSE, S11, 2 September, 1970. Pers. Coll. (6 specimens, 33-
 61 mm S.L., OA(2), S), Virginia, Scott Co., Tennessee drainage,
 Copper Creek circa 1 mile above mouth, 12 November, 1972.
 Pers. Coll. (NLU 20075) (20 specimens, 48-61 mm S.L., OA(2),
 S), Arkansas, Independence Co., White River below lock and
 dam no. 3 approx. 15 miles N.W. of Batesville, 20 August, 1971.

Hybopsis (Oregonichthys) crameri

Pers. Coll. (8 specimens, 41-44 mm S.L., OA(4), OX, S),
 Oregon, Douglas Co., Cow Creek 1 mile below Polan Creek, 7
 August, 1970.

Hybopsis (Erimystax) dissimilis

WKU 486 (1 specimen, 70 mm S.L., OX), Kentucky, Simpson Co.,
 Drakes Creek at 1711 Bridge, 6 July, 1970. WKU 502 (1 specimen,
 66 mm S.L., OX), Kentucky, Simpson Co., Drakes Creek 1½ miles N.
 of Highway 100 at ford, 6 July, 1970. Pers. Coll. (USNM 206478)
 5 specimens, 68-86 mm S.L., OA(3), S), Kentucky, Monroe Co.,
 Salt Lick Creek, ¾ mile S. and 1 mile E. Akersville, 29
 October, 1955. Pers. Coll. (6 specimens, 82-84 mm S.L., OA(3),
 S), Virginia, Washington Co., Tennessee drainage, North Fork

Holston River off Route 802, 0.3 air miles S.W. Roebuck at Hines Island, 29 August, 1973. Pers. Coll. (3 specimens, 65-89 mm S.L., OA(2), S), Missouri, Barry Co., White River between Shell Knob and Viola, 2-10 September, 1948.

Hybopsis (Macrhybopsis) gelida

Pers. Coll. (KU 2171) (4 specimens, 24-36 mm S.L., OA(3), S), Kansas, Douglas Co., Kansas River below Dam at Lawrence , 5 April, 1952. Pers. Coll. (KU 4488) (4 specimens, 20-42 mm S.L., S), Kansas, Douglas Co., Kansas River at Eudora, 14 March, 1959. Pers. Coll. (KU 4654) (1 specimen, 59 mm S.L., S), Kansas, Douglas Co., Kansas River below Dam at Lawrence, 18 April, 1959.

Hybopsis (Erimystax) harperi

WKU 597 (10 specimens, 46-54 mm S.L., OX), Louisiana, Bogue Tulaya-Covington, 8 April, 1970.

Hybopsis (Macrhybopsis) meeki

Pers. Coll. (KU 9675) (5 specimens, 43-55 mm S.L., OA(4), S), Missouri, St. Louis Co., Missouri River 9 miles above its mouth T47N, R7E, 23 September, 1963.

Hybopsis (Erimystax) x-punctata

WKU 730 (1 specimen, 54 mm S.L., OX), Kentucky, Middle Fork Drakes Creek, 1 mile S.E. Massey's Mill and Highway 240 Bridge, 9/3/1971. Pers. Coll. (3 specimens, 55-77 mm S.L., OA (2), S), Missouri, Maries Co., Gasconade River 4 1/2 miles E.S.E. Vienna, 11 October, 1969.

Iotichthys phlegthontis

UMMZ 141429 (5 specimens, 26-35 mm S.L., OA(5), OX, S),
Utah, Millard Co., "The Chimneys", Snake Valley, 12 June, 1943.

Lavinia exilicauda

Pers. Coll. (3 specimens, 81-233 mm S.L., OA(2), S), California,
Lake Co. Clear Lake, August, 1973. UMMZ 133178 (5
specimens, 53-60 mm S.L., OA(5), OX, S), California, Contra
Costa Co., Marsh Creek tributary to San Joaquin River, 19
February, 1939. CAS 28760 (2 specimens, 167-177 mm S.L.,
OA(2), OX, S), California, Contra Costa Co., Lake Anza
(Tilden Regional Park), 22 August, 1961. CAS 28771 (9
specimens, 60-83 mm S.L., OX), California, Lake Anza, Tilden
Regional Parks, Berkeley Hills, 25 November, 1952.

Lepidomeda mollispinis

UMMZ 141674 (5 specimens, 52-59 mm S.L., OA(5), OX, S), Utah,
Washington Co., Santa Clara River 4½ miles by road N.W. of
Santa Clara, 29 July, 1942.

Lepidomeda vittata

Pers. Coll. (40 specimens, 54-91 mm S.L., OA(3), OX(20), S),
Nevada, Windsor Dam behind spillway, 19 June, 1970. Pers.
Coll. (1 specimen, 68 mm S.L., OA, OX, S), Arizona, Springer-
ville, Little Colorado River, 8 September, 1966.

Meda fulgida

AMNH 21241 (10 specimens, 44-47 mm S.L., OX, S), New Mexico,

Grant Co., Gila River at U.S. 260 Bridge, south of Gila,
4 May, 1950. UMMZ 125030 (5 specimens, 46-51 mm S.L.,
OA(5), OX, S), Arizona, Yavapai Co., Verde River, 2
September, 1938.

Moapa coriacea

UMMZ 177086 (5 specimens, 45-70 mm S.L., OA(5), OX, S),
Nevada, Clark Co., warm spring ditches and pools on
Pederson's, Iverson's and Warm Spring's Ranch Resorts,
2 July, 1959. CAS 22980 (4 specimens, 39-60 mm S.L., OX,
S), Nevada, Clark Co., Rupport Spring, Moapa Valley, 23
December, 1947. Pers. Coll (11 specimens, 40-55 mm S.L.,
OA(5), OX, S), Nevada, Clark Co., Big Pool, Warm Springs,
8 August, 1948.

Mylocheilus caurinus

Pers. Coll (UAMZ 2661) (2 specimens, 91-146 mm S.L., OA(2),
S), British Columbia, Mara Lake, July, 1971. NMC 66-70
(4 specimens, 189-219 mm S.L., OA(2), S), British Columbia,
Deer Creek, 13 September, 1965.

Mylopharodon conocephalus

Pers. Coll. (6 specimens, 38-111 mm S.L., OA(4), S),
California, Mendocino Co., Russian River, August, 1973.
Pers. Coll. (1 specimen, 121 mm S.L., OA (S), California,
Modoc Co., Ash Creek, July, 1973.

Nocomis asper

Pers. Coll. (USNM 204854) (3 specimens, 93-121 mm S.L., OA(2),

S), Oklahoma, Delaware Co., Flint Creek of Arkansas River Drainage, 3.3 miles E. of Highway 33 crossing of Flint Creek then 3.1 miles N. on dirt road, 12 June, 1967.

Nocomis biguttatus

WKU 485 (1 specimen, 65 mm S.L., OX), Kentucky, Simpson Co., Drakes Creek at 1711 Bridge, 6 July, 1970. Pers. Coll. (1 specimen, 101 mm S.L., OA, S), Ontario, Laurel Creek at University of Waterloo, 24 July, 1972.

Nocomis effusus

Pers. Coll. (USNM 221444-F1) (6 specimens, 41-123 mm S.L., OA(3), S), Kentucky, Green dr., October, 1955.

Nocomis leptcephalus

Pers. Coll. (USNM 194669) (4 specimens, 95-152 mm S.L., OA(3), S), Virginia, Craig Co., James River drainage, Craig Creek, Route 616 ford 1.2 air miles N.E. Newcastle, 15 May, 1963.

Nocomis micropogon

WKU 940 (10 specimens, 43-80 mm S.L., OX), Kentucky, Clay Co., Red Bird River, Highway 66 3 miles S. Highway 80, 10/9/1971. Pers. Coll. (USNM 177393) (4 specimens, 87-147 mm S.L., OA(3), S), Virginia, Rockingham Co., north fork Shenandoah River at Fulkes Run on Route 259, 18 July, 1956. Pers. Coll. (USNM 194689) (1 specimen, 162 mm S.L., S), Virginia, Smyth Co., North Fork Holston River at Nebo, Tennessee drainage, 2 July, -1963.

Nocomis platyrhynchus

Pers. Coll. (USNM 203916) (.3 specimens, 130-148 mm S.L., OA(2), S), West Virginia, Raleigh Co., New River 8.2 miles downstream from Hinton, 1 September, 1966.

Notemigonus crysoleucas

NMC 73-27 (2 specimens, 60-94 mm S.L., OA(2), S), Nova Scotia, Queens Co., High Lake, Kejimikujik National Park, 11 July, 1972. NMC 70-380 (1 specimen, 65 mm S.L., OA, S), Texas, Mays and — ? Co., San Marcos River downstream from Hwy 35 to Old Town, 17 April, 1970. Pers. Coll. (ROM Acc.1843) (20 specimens, 67-88 mm S.L., OA(2), S), Ontario, Nipissing District, Airy Township, Poverty Lake (45° 29' N., 78° 3' W), 23 May, ? . Pers. Coll. (23 specimens, 48-109 mm S.L., OA(4), S), Ontario, Rideau River at Long Island, Manotick, 25 May, 1972. Pers. Coll. (1 specimen, 45 mm, S.L., OA), Ontario, Ottawa River at Ottawa, head of Kettle Island, 7 June, 1972. Pers. Coll. (10 specimens, 18-60 mm S.L., OA (2)), Ontario, Ottawa River at Ottawa, Britannia Beach, 8 August, 1972. Pers. Coll. (11 specimens, 32-64 mm S.L., OA (1), S), Québec, Gatineau Park, Holly Lake, 18 August, 1972. Pers. Coll. (7 specimens, 83-130 mm S.L., S), Québec, Yamaska Co., north branch Rivière St. Louis, 3 September, 1970. ROM 25433 (10 specimens, 33-42 mm S.L., OA(10)), Québec, Iberville Co., Ruisseau Russell, Henryville, December, 1967. NMC 62-165 (11 specimens, 75-99 mm S.L., OX), Ontario, Rideau River 10½ miles S. of Ottawa, 4-5 August, 1962.

Notropis atherinoides

Pers. Coll. (6 specimens, 70-82 mm S.L., OA(6), S), Québec, Yamaska Co., Rivière St. Louis, branche nord, 3 September, 1970. Pers. Coll. (6 specimens, 57-69 mm S.L., S), Ontario, Ottawa River at Ottawa, head of Kettle Island, 15 August, 1972.

Notropis atrocaudalis

NMC 70-387 (6 specimens, 39-50 mm S.L., OA(2), S), Texas, Houston Co., Bracken Creek Highway 21, 24 April, 1970.

Notropis bifrenatus

NMC 66-491 (6 specimens, 30-33 mm S.L., OA(2), S), Québec, Châteauguay, Lac St. Louis, Ile de la Paix, Léry, 24 June, 1965.

Notropis blennius

NMC 58-187 (6 specimens, 56-62 mm S.L., OA(2), S), Alberta, Morrin 65 miles NE of Calgary, 18 September, 1916.

Notropis cornutus

Pers. Coll. (6 specimens, 109-114 mm S.L., OA(2), S), Québec, Berthier Co., Rivière Thérien, under bridge 1 mile NW Lac Maskinongé. Pers. Coll. (2 specimens, 116-135 mm S.L., S), Québec, Joliette Co., Lac Brandon, Parc Joliette, June, 1971.

Notropis hudsonius

Pers. Coll. (6 specimens, 68-71 mm S.L., OA(2), S), Québec, Yamaska Co., Rivière St. David, 3 September, 1970.

Notropis labrosus

Pers. Coll. (4 specimens, 34-42 mm S.L., OA(3), S), North Carolina, Wilkes Co., Peedee drainage, Roaring Fk., 1½ miles below junction 3 prongs, 25 July, 1949.

Notropis lutrensis

NMC 70-389 (8 specimens, 38-49 mm S.L., OA(2), S), Texas, Brazos Co., ca 3 miles W. of Navasota River on Highway 190, 24 April, 1970.

Notropis procne

NMC 64-455 (5 specimens, 29-43 mm S.L., OA(2), S), Pennsylvania, York, southern tributary to Bermuda Creek about 18 miles S. of Harrisburg, 28 August, 1964.

Notropis proserpinus

NMC 70-349 (6 specimens, 36-44 mm S.L., OA(2), S), Texas, Val Verde Co., Dolon Creek at confluence with Devil's River, 26 April, 1969.

Notropis texanus

NMC 70-414 (5 specimens, 45-51 mm S.L., OA(2), S), Texas, Comal Co., Hueco Springs, W. of New Braunfels on Guadalupe River, 1969.

Notropis umbratilis

NMC 72-201 (6 specimens, 36-43 mm S.L., OA(2), S), Ontario, Lambton Co., Bear Creek, 4 miles N.E. of Petrolia, 13 August, 1972. NMC 72-202 (6 specimens, 37-45 mm S.L., OA(1), S), Ontario, Lambton Co., Bear Creek, 3½ miles S.W. of Petrolia,

13 August, 1972.

Notropis venustus

NMC 70-379 (6 specimens, 49-61 mm S.L., OA(2), S), Texas, Guadalupe River, Gonzales, golf course bridge off Highway 183, 5 March, 1970.

Notropis volucellus

NMC 73-488 (6 specimens, 52-63 mm S.L., OA(2), S), Ontario, St. Lawrence River, Thwartway Island west central beach, 19 July, 1973. Pers. Coll. (6 specimens, 51-58 mm S.L., OA(2), S), Québec, Missisquoi Co., Etang de Cowansville, 2 July, 1969.

Osopeodius emiliae

Pers. Coll. (6 specimens, 34-37 mm S.L., OA(2), S), Kentucky, McCracken Co., Metropolis Lake 3 miles N. Grahamville, 10 September, 1968.

Orthodon microlepidotus

AMNH 21048 (6 specimens, 99-128 mm S.L., OX, S), California, Sacramento Co., Elk Grove, Central Valleys Hatchery, August, 1949. AMNH 17698 (1 specimen, 69 mm S.L., OA, S), No data. Pers. Coll. (10 specimens, 72-90 mm S.L., OA(5), S), California, Lake Co., Clear Lake, August, 1973. UMMZ 131620 (1 specimen, 128 mm S.L., OA, S), California, Mariposa Co., Miles Creek near Mariposa, 17 August, 1940. CAS 26285 (1 specimen, 228 mm S.L., OA, OX, S), California, Alameda Co., Alameda Creek, 21 July, 1957. CAS 25695 (9 specimens,

42-62 mm S.L., OX, S), California, Putah Creek, 27 August, 1950: Pers. Coll. (3 specimens, 59-106 mm S.L., S), Oregon, Sherman Co., Deshutes River at Bakeoven Creek, 17 September, 1952.

Parexoglossum laurae

UMMZ 180867 (20 specimens, 24-73 mm S.L., OA(4), OX, S), New York, Chautauqua Co., Goose Creek, tributary of Chautauqua Lake, 7/8 mile N.E. Ashville, 24 August, 1937.

Phenacobius crassilabrum

Pers. Coll. (4 specimens, 50-81 mm S.L., S), Tennessee, Unicoi Co., S. Indian Creek (Nolichucky River System).

Phenacobius mirabilis

Pers. Coll. (USNM 176248) (1 specimen, 79 mm S.L., OA, S), Texas, Travis Co., Austin Colo. River below Lamar Street Bridge, rapids at water plant, 20 December, 1954. Pers. Coll. (4 specimens, 42-50 mm S.L., OA(3), S), Kansas, Lyon Co., Neosho River of Arkansas River drainage, below U.S. Highway 50.

Phenacobius uranops

Pers. Coll. (6 specimens, 54-91 mm S.L., OA(4), S), Virginia, Washington Co., Tennessee drainage, North Fork Holston River off Route 802, 0.3 air miles S.W. Roebuck at Hines I., 29 August, 1973.

Pimephales notatus

NMC 68-215 (2 specimens, 62-64 mm S.L., S), Québec, Lac

Desormeux adjacent to Lac Heney, 59 miles N. of Hull, 9 July, 1968. Pers. Coll. (10 specimens, 53-71 mm S.L., OA(2), S), Québec, Missisquoi Co., Rivière Yamaska near Farnham, 1.8 miles above railway bridge, 14 July, 1969.

Pimephales promelas

Pers. Coll. (31 specimens, 22-61 mm S.L., OA(2), S), Québec, Richelieu Co., Rivière Pot-au-Beurre, 1.1 miles N. of Saint-Robert, 1 September, 1970.

Pimephales vigilax

Pers. Coll. (WSU 2325) (10 specimens, 40-52 mm S.L., OA(4), S), Wisconsin, Iowa Co., Wisconsin River, 8 August, 1962.

Plagopterus argentissimus

UMMZ 124770 (5 specimens, 58-70 mm S.L., OA(5), OX, S), Utah, Washington Co., Virgin River near LaVarkin, 3 July, 1938.

Pers. Coll. (25 specimens, 35-63 mm S.L., OA(4), OX, S), Nevada, Clark Co., Virgin River near Misquite, 27 January, 1973.

Platygobio gracilis

Pers. Coll. (UAMZ 1658) (7 specimens, 62-93 mm S.L., OA(2), S), Alberta, Smoky River at Highway 34, 25 miles west of High Prairie, 24 July, 1968. NMC 66-387 (2 specimens, 200-370 mm S.L., OA(2), S), Alberta, Milk River 16½-19½ miles W. of Wild Horse, 28 July, 1966. NMC 66-300 (1 specimen, 180 mm S.L., S), Alberta, Milk River, 26 May, 1966. NMC 66-338 (1 specimen, 338 mm S.L., S), Alberta, Milk River, 17 miles E. and 3 miles S. of Milk River Town, 14 June, 1966.

Pogonichthys macrolepidotus

UMMZ 94438 (1 specimen (tank), 105 mm S.L. OA, OX, S),
California, Stony Creek tributary to Sacramento River near
Orland, 29 August, 1926.

Ptychocheilus oregonensis

Pers. Coll. (UAMZ 2659) (2 specimens, 117-182 mm S.L.),
British Columbia, Mara Lake, July, 1971. NMG 66-69 (2 specimens,
320-375 mm S.L., S), British Columbia, Columbia Lake, Canal
Flats, 16 August, 1965. NMC 66-80 (3 specimens, 285-310 mm
S.L., S), British Columbia, Donleal Farm Ferry, Kootenay
Channel near Sirdar, 5-6 August, 1965. NMC 66-443 (2
specimens, 102-104 mm S.L., OA(2), S), British Columbia,
Carp Lake near creek mouths $54^{\circ} 46.3'N$, $123^{\circ} 25'W$., 2-4
August, 1966.

Relictus solitarius

Pers. Coll. (15 specimens, 43-52 mm S.L., OA(2), S), Nevada,
Steptoe Valley, Twin Springs, 4 August, 1972. Pers. Coll.
(2 specimens, 63-66 mm S.L., OA(2), OX, S), Nevada, Ely,
Steptoe Creek, 13 July, 1972.

Rhinichthys atratulus

Pers. Coll. (26 specimens, 49-67 mm S.L., OA(4), S), Maryland,
Garrett Co., North Branch Jennings Run and Savage River, 1972.
Pers. Coll. (9 specimens, 47-57 mm S.L., OA(4), S), Québec,
Bagot Co., Rivière Saint-Nazaire juste en aval du barrage de
Saint-Nazaire ($72^{\circ}37'07''W$, $45^{\circ}44'06''N$.), 24 September, 1970.

Pers. Coll. (5 specimens, 45-53 mm S.L., S), Illinois, Carroll Co., Millers Creek, Savanna, { 2 September, 1967. NMC 60-519A (10 specimens, 42-54 mm S.L., OX), Ontario, Huron Co., culvert $\frac{1}{2}$ mile N. of Drysdale on Highway , 18 miles S. of Goderich ($43^{\circ}27'N$, $81^{\circ}42'N$), 12 August, 1960. NMC 69-10 (8 specimens, 34-59 mm S.L., OX), New Brunswick, Kings Co., Flaglor Brook, Oak Point, 11 September, 1968. NMC 64-454 (2 specimens, 49-54 mm S.L., OX), Pennsylvania, Montour Co., Fishing Creek 13 miles from Redrock near Stillwater, 27 August, 1964. Pers. Coll. (2 specimens, 47-53 mm S.L., OA(2), S), Ontario, Laurel Creek at University of Waterloo campus, 24 July, 1972.

Rhinichthys cataractae

Pers. Coll. (34 specimens, 41-71 mm S.L., OA(4), S), Québec, Joliette Co., Rivière Bayonne, Saint-Cléophas-de-Brandon, près du pont, 1.75 milles au nord-ouest de l'église de Saint-Cléophas ($46^{\circ}14'41"N$, $73^{\circ}27'07"W$), 28 July, 1971. Pers. Coll. 4 specimens, 50-68 mm S.L., S), Illinois, Lake Co., Lake Michigan, Highland Park, 2 June, 1964. Pers. Coll. (18 specimens, 62-105 mm S.L., OA(4), S), Maryland, Garrett Co., North Branch Jennings Run and Savage River, 1972. NMC 64-197 (7 specimens, 69-92 mm S.L., OA(1), OX, S), Ontario, Lanark Co., creek into Mississippi River 7 miles S. of Pakenham, 16 August, 1962. NMC 66-68 (12 specimens, 61-85 mm S.L., OX), British Columbia, Canal Flats Co.,

Kootenay River, 16 August, 1965. Pers. Coll. (2 specimens, 71 mm S.L., OA(2), S), Ontario, Pukaskwa National Park, Lake Superior, 23 September, 1972.

Rhinichthys evermanni

Pers. Coll. (7 specimens, 57-84 mm S.L., OA(4), OX, S), Oregon, Douglas Co., Cow Creek at Quines Creek Road, 30 July, 1970.

Rhinichthys falcatus

Pers. Coll. (3 specimens, 63-71 mm S.L., OA(2), S), Oregon, Malheur Co., Malheur River 5 miles below Juntura, 16 November, 1969. SU 37784 (6 specimens, 68-75 mm S.L., OA(3), OX, S), Oregon, Grande Ronde River, Elgin, 8/3/1894.

Rhinichthys lariversi

Pers. Coll. (16 specimens, 37-55 mm S.L., OA(9), OX, S), Nevada, Nye Co., 3rd spring north of Charnock Ranch, 15 April, 1972.

Rhinichthys osculus

ANMH 27240 (10 specimens, 38-67 mm S.L., OA(5), OX, S), Nevada, Lincoln Co., outlet of Big Spring 1 mile north of Panaca, 4 July, 1959. CAS 21058 (8 specimens, 45-64 mm S.L., OA(2), OX, S), California, San Lorenzo River, 22 July, 1955. Pers. Coll. (16 specimens, 37-62 mm S.L., OA(4), OX, S), Nevada, Washoe Co., Steamboat Creek $\frac{1}{2}$ mile above Steamboat, hot springs, 4 July, 1973.

Richardsonius balteatus

UAMZ 1656 (10 specimens, 46-65 mm S.L., S), Alberta, Smoky River at Highway 34, 25 miles west of High Prairie, 24 July, 1968. Pers. Coll (UAMZ 2660) (2 specimens, 45-62 mm S.L., OA(2), S), British Columbia, Mara Lake, July 1971.

Semotilus atromaculatus

Pers. Coll. (8 specimens, 88-127 mm S.L., OA(1), S), Ontario, Algonquin Park, Lake Opeonogo, 3 September, 1971. Pers. Coll. (22 specimens, 76-147 mm S.L., OA(3), S), Québec, Joliette Co., Ruisseau Saint-Martin, 9 August, 1971. Pers. Coll. (2 specimens, 81-141 mm S.L., S), Ontario, Laurel Creek at University of Waterloo, 24 July, 1972. Pers. Coll. (13 specimens, 81-116 mm S.L., S), Québec, Joliette Co., Lac Marguerite in Parc Joliette, 5 July, 1972.

Semotilus corporalis

Pers. Coll. (4 specimens, 65-143 mm S.L., OA(3), S), Ontario, Ottawa River at Ottawa, head of Kettle Island, 17 July, 1972. NMC 71-876 (1 specimen, 236 mm S.L., S), Québec, mouth of Lapêche stream where it enters St-Maurice River, 28 May, 1971. Pers. Coll. (3 specimens, 114-164 mm S.L., OA(2), S), Québec, Shefford Co., Rivière Yamaska-nord, under Shefford Vale bridge, 28 July, 1969.

Semotilus (Margariscus) margarita

Pers. Coll. (10 specimens, 80-105 mm S.L., OA(1), S), Québec, Berthier Co., Parc Joliette, Lac Crépeau, 3 August, 1972.

Pers. Coll. (ROM Acc 1563) (8 specimens, 74-101 mm S.L., OA(2), S.) Ontario, Kenora Dist., Collenso Twp., Chanley Lake, 30 July, 1969. Pers. Coll. (2 specimens, 68-75 mm S.L., OA(2), S), Aquarium fish; May, 1972.

Tiaroga cobitis

UMMZ 162754 (5 specimens, 37-51 mm S.L., OA(5), OX, S), Arizona Graham Pinal Cos., Aravaipa Creek, N.W. of Klondyke, 10-11 May, 1950. CAS 25574 (1 specimen, 39 mm S.L. OA, OX, S), Arizona, Aravaipa Creek, 26 May, 1949. SU 5341 (3 specimens, 37-40 mm S.L., OA(2), OX, S), Arizona, Chino. CAS 25579 (3 specimens, 24-43 mm S.L., OA(2), OX, S), Arizona, Aravaipa Creek, 26 May, 1949. CAS 13042 (3 specimens, 60-67 mm S.L. OA(3), OX, S), Arizona, mouth of Garden Creek, Grand Canyon National Park, 30 July, 1932.

Xystrosus popoche

UMMZ 167717 (20 specimens, 89-140 mm S.L., OA(5), OX, S), México, Jalisco, N.W. side of Lago de Chapala, 5,000 feet elevation, 10 July, 1949.

Eurasian Cyprinidae

Abramis ballerus

BM(NH) 1967-12-18:21-30 (5 specimens, 205-225 mm S.L., OX), Czechoslovakia, Danube near Medredove. Pers. Coll. (8 specimens, 133-203 mm S.L., OA(3), S), Romania, Damlake at Portile-de-Fier (Iron-Gates) near Orsova, Banat, 13-17 June, 1972.

Pers. Coll. (ZLAS 142-936) (3 specimens, 88-108 mm S.L., OA(2), S), U.S.S.R., Ural River, Blind branch, 1 August, 1927.

Abramis brama

BM(NH) 1972-4-18-4 (1 specimen, 210 mm S.L., OX), England, Fulham, River Thames. Pers. Coll. (9 specimens, 92-150 mm S.L., OA(2), S), Romania, Lake Jijila, floodplain of the Danube near Macin, S.E. Romania. NMC 72-215 (2 specimens, 215-220 mm S.L., S), England, Tooting Common Pond, London, 9 May, 1972. NMC 73-214 (1 specimen, 200 mm S.L., S), England, Clapham Common Pond, London, 9 May, 1972. NMC 73-76, (2 specimens, 90 mm S.L., OA(2)), Denmark, Furesø Lake, Sjaelland, May 1969. Pers. Coll. (1 specimen, 207 mm S.L., S), England, Cheshire, Lymm Dam, 19 July, 1969. Pers. Coll. ZLAS 26262, (5 specimens, 39-56 mm S.L., OA(2), S), U.S.S.R., channel from Istemes Lake to Kun-Darya River (Basin Amu-Darya River), 24 September, 1903. Pers. Coll. (ZLAS 24420), (2 specimens, 93-97 mm S.L., OA(1), S), U.S.S.R., Yaskhan Lake, Usboy, 21 September, 1928.

Abramis sapa

BM(NH) 1967-7-17:3-4 (3 specimens, 109-118 mm S.L., OX), Romania, Lake Crapina. BM(NH) 1891-3-18:33 (1 specimen, 245 mm S.L., OX), Askraan, River Volga. Pers. Coll. (10 specimens, 110-119 mm S.L., OA(3), S), Romania, Lake Crapina, floodplain of the Danube near Macin, S.E. Romania, 22-24 June, 1966. Pers. Coll. (ZLAS 25573), (10 specimens, 37-44 mm S.L., OA(2), S), U.S.S.R., Sorochinka River, Redut. Basin of Baltic

Sea, 20 April, 1927.

Alburnoides bipunctatus

BM(NH) 1963-7-25:42-8 (7 specimens, 47-83 mm S.L., OX),
Rumania, River Timis. BM(NH) 1958-2-13:10-17, (8 specimens,
44-66 mm S.L., OX), Transylvania, River Aries. Pers. Coll.
(3 specimens, 69-75 mm S.L., OA(2), S), France, Cher à
Saint-Agnan, September, 1972. Pers. Coll. (3 specimens, 69-
77 mm S.L., OA(2), S), France, La Besbre, affluent de la
Loire, August, 1960. Pers. Coll. (18 specimens, 39-73 mm S.L.,
OA(1), S), Romania, River Minis tributary to Nera River at
Bozovici, S. Banat, 23 July, 1968. Pers. Coll. (10 specimens,
60-82 mm S.L., OA(1), S), Romania, River Radimna 10 Km. N.
of Moldova-Noua, S. Banat, 7 May, 1968. NMC 73-195 (11 spe-
cimens, 77-93 mm S.L., OA(4), S), Poland, San River (upper),
5 June, 1968.

Alburnus alburnus

BM(NH) 1935-2-27:1 "A. lucidens" (1 specimen, 122 mm S.L.)
Bray on Thames. Pers. Coll. (4 specimens, 95-114 mm S.L.,
OA(5), S), France, Cher à Saint-Aignan, August, 1972. Pers.
Coll. (2 specimens, 99-111 mm S.L., OA(2), S), France, La
Bidouse affluent de l'Adour, 13 March, 1968. Pers. Coll.
(3 specimens, 82-106 mm S.L., OA(1), S), France, La Besbre,
affluent de la Loire, August, 1960. Pers. Coll. (9 speci-
mens, 78-102 mm S.L., OA(3), S), Romania, River Mures at
Iernut near Ludus, Transylvania, 5 June, 1974. Pers. Coll.

(10 specimens, 91-107 mm S.L., OA(3), S), Romania, River Mures at Cuci near Ludus, Transylvania, 5 June, 1974. NMC 73-214

(2 specimens, 137-145 mm S.L., S), England, Clapham Common Pond, London, 9 May, 1972. BM(NH) 1961-4-19:74-8 (6 specimens, 99-110 mm S.L.), River Thames, Reading.

Blicca bjoerkna

Pers. Coll. (20 specimens, 47-67 mm S.L., OA(3), S), Romania, River Timis, at Sag, near Timisoara, Banat, 17 September, 1965. NMC 59-253 (1 specimen, 150 mm S.L., OX, S), Ukraine, Uzhorod on Uz River, sub-Carpathian region Tisa-Danube drainage; 10 September, 1926. NMC 59-204A (2 specimens, 122-129 mm S.L., OX), Ukraine, Uz River at Vajaniij, sub-Carpathian district, 1927.

Aspius aspius

Pers. Coll. (4 specimens, 90-120 mm S.L., S), Romania, River Mures, at Cuci between Iernut and Ludus, Transylvania, 5 June, and 3 July 1974.

Barbus meridionalis

Pers. Coll. (8 specimens, 49-82 mm S.L., S), Romania, River Nera at Naidasm, S. Banat, 20 June, 1968. Pers. Coll. (23 specimens, 35-152 mm S.L., S), Romania, Danube drainage.

Barbus tetrazona

Pers. Coll. (2 specimens, 36-39 mm S.L., S), Aquarium specimens, June 1974.

Brachydanio rerio

Pers. Coll. (1 specimen, 26 mm S.L., S), Aquarium specimen, June, 1973.

Carassius auratus

Pers. Coll. (5 specimens, 49-52 mm S.L., S), Aquarium specimens. NMC 60-462A (4 specimens, 158-220 mm S.L., S), Ontario, Haldiman Co.; Grand River at Dunnville, 1 July, 1960.

Carassius carassius

NMC 73-214 (4 specimens, 124-170 mm S.L., S), England, Clapham Common Pond, London, 9 May, 1972.

Chondrostoma nasus

Pers. Coll. (2 specimens, 243-256 mm S.L., S), France, Cher à Saint-Aignan, June 1968. Pers. Coll. (23 specimens, 67-82 mm S.L., S), Romania, River Mures at Iernut, Transylvania, 3 July, 1974.

Gobio albipinnatus

Pers. Coll. (10 specimens, 69-88 mm S.L., S), Romania, River Mures at Cuci, near Ludus, Transylvania, 5 June, 1974. Pers. Coll. (18 specimens, 30-60 mm S.L., S), Romania, River Timis at Urseni near Timisoara, Banat, 7 August 1959.

Gobio gobio

Pers. Coll. (17 specimens, 58-120 mm S.L., S), Romania, River Mures at Iernut, near Ludus, Transylvania, 4 July, 1974. Pers. Coll. (1 specimen, 88 mm S.L., S), England, Cheshire, Lymm Dam, 19 July, 1969.

Gobio kessleri

Pers. Coll. (25 specimens, 33-60 mm S.L., S), Romania, River Timis at Albina near Timisoara, Banat., 20 September, 1967.

Gobio uranoscopus

Pers. Coll. (4 specimens, 59-93 mm S.L., S), Romania, River Vilsan at Vilsanesti, distr. Arges, 26 June, 1964. Pers.

Coll. (8 specimens, 46-78 mm S.L., S), Romania, River Nera, Banat.

Leucaspius delineatus

Pers. Coll. (12 specimens, 30-44 mm S.L., S), Romania, ponds on Olt River near Dragasani, October, 1973. Pers. Coll. (2 specimens, 40-45 mm S.L., S), Romania, fishpond at Sarata, N. Moldavia, February, 1955. NMC 73-74 (2 specimens, 41-42 mm S.L., S), Denmark, Lake near Hareskov, Sjaelland, 21 April, 1968.

Leuciscus borysthenticus

Pers. Coll. (13 specimens, 66-94 mm S.L., S), Romania, Lake Caraorman, Danube delta, St. Dragasanu.

Leuciscus cephalus

Pers. Coll. (5 specimens, 70-88 mm S.L., S), Romania, River Timis at Peciul-Nou, Banat, 16 September, 1965. Pers. Coll. (11 specimens, 28-103 mm S.L., S), Romania, River Tur at Porumbesti, near Halmei, N.W. Romania, 24 September, 1967. Pers. Coll. (5 specimens, 96-103 mm S.L., S), Romania, River Crasna at Acis, W. Romania, 21 September, 1962.

Leuciscus idus

Pers. Coll. (7 specimens, 60-103 mm S.L., S), Romania, River Timis near Timisoara, Banat. Pers. Coll. (4 specimens, 71-80 mm S.L., S), Romania, River Tisovita at confluence with Danube, S. Banat, 24 May, 1966.

Leuciscus leuciscus

NMC 59-211 (3 specimens, 140-154 mm S.L., S), Czechoslovakia, Usti near Orlice, River Trebovka, Ticha-Orlice River System, 25 August, 1924.

Leuciscus soufia

Pers. Coll. (5 specimens, 69-115 mm S.L., S), France, La Filière, (Savoie), April, 1960. Pers. Coll. (2 specimens, 92-110 mm S.L., S), France, Le Gapeau (Var), 16 May, 1968.

Moroco jouvi

BM(NH) 1907-12-23: 11-4 (5 specimens, 76-95 mm S.L., OX), (Leuciscus jouvi) Japan, Lake Biwa. Pers. Coll. (6 specimens, 85-110 mm S.L., S), (~~Moroco~~ steindachneri jouvi) Japan, Shimane Prefecture, Shiso River (Takatsu River System), Sasayama, Hikimi-cho, Mino-gun, 26 May, 1972.

Pelecus cultratus

Pers. Coll. (11 specimens, 97-124 mm S.L., S), Romania, confluence of the Danube with the Black Sea at Sulina, 15 September, 1968. Pers. Coll. (3 specimens, 170-174 mm S.L., S), Romania, Lake Bugeac, floodplain of the Danube, September, 1962.

Phoxinus czekanowskii

Pers. Coll. (ZIAS 15694) (10 specimens, 32-50 mm S.L., S), U.S.S.R., King-Uryab - small river, Wilyuy district, Eastern Siberia, 20 February, 1912. Pers. Coll. (ZIAS 15696) (5 specimens, 41-61 mm S.L., S), U.S.S.R., Marka River, 9 Km from Yakutsk Town, 3 March, 1912.

Phoxinus issykkulensis

Pers. Coll. (ZIAS 26374) (4 specimens, 19-42 mm S.L., S), U.S.S.R., brook mouth Issyk-kul Lake punct (sic?) Jamy-Oguz 1909. Pers. Coll. (ZIAS 25061) (10 specimens, 33-52 mm S.L., S), U.S.S.R., Issyk-kul Lake punct (sic?) Karakol, 28 July, 1933.

Phoxinus lagowskii

BM(NH) 1871-7-19:19 (1 specimen, 120 mm S.L., OX), Onon River, Godeffroy Museum. BM(NH) 1879-11-14:111-112 (2 specimens, 74-80 mm S.L., OX), Ichilka River. BM(NH) 1925-8-6:23 (1 specimen, 97 mm S.L., OX), Near Eugenieuka, Amur District. BM(NH) 1875-10-14:51 (2 specimens, ~~83-106~~ mm S.L., OX), Daima. BM(NH) 1899-7-25:30 (1 specimen, 88 mm S.L., OX), River Ussuri, East Siberia. Pers. Coll. (ZIAS 13798) (20 specimens, 88-137 mm S.L., S), U.S.S.R., mountain stream influent of Ussury Bay, 17 June, 1900. Pers. Coll. (ZIAS 38 300) (2 specimens, 67-88 mm S.L., S), U.S.S.R., Tumangan River (Talni River), Basin of Hassan Lake, July, 1964.

Phoxinus percnurus

BM(NH) 1875-10-14:70-3 (4 specimens, 72-81 mm S.L., OX), Lake Baical (sic). BM(NH) 1899-7-25:35 (1 specimen, 100 mm S.L., OX), River Jana, East Siberia. BM(NH) 1893-1-27:14-17 (4 specimens, 71-74 mm S.L., OX), Vladivostok. BM(NH) 1871-7-19:19 (2 specimens, 75-98 mm S.L., OX), Lake Baical (sic). NMC 73-196 (10 specimens, 60-72 mm S.L., S), Poland, pond in Rynarzewo near Bydgoszcz. Pers. Coll. (ZLAS 25153) (10 specimens, 61-128 mm S.L., S), U.S.S.R., Lake in the infra current (?sic) of the Tugur River (Basin of Okhotsk Sea) 25-27 March, 1936. Pers. Coll. (ZLAS 25544) (2 specimens, 53-54 mm S.L., S), U.S.S.R., Lake in the basin of Wychehda River near Syktyvkar town, 1927. Pers. Coll. (ZLAS 24861) (5 specimens, 84-98 mm S.L., S), U.S.S.R., Kolyma River, small lake near punct (sic?) Verhne-Kolymskoe, 21 October, 1928.

Phoxinus phoxinus

BM(NH) 1968-11.5:47-63 (17 specimens, 49-66 mm S.L., OX(12), T), River Roding, Shank's Mill, Navestock side, Essex. BM(NH) 1971-7.12:1-12 (20 specimens, 45-56 mm S.L., T), River Roding, Shank's Mill, Navestock, Essex. Pers. Coll. (2 specimens, 65-67 mm S.L., T), France, Vaucluse, Argoud. NMC 64-381 (10 specimens, 53-63 mm S.L., S), England, Dartmoor, December, 1963. NMC 59-250 (9 specimens, 43-65 mm S.L., S), Czechoslovakia, Usti near Orlici in brook, Ticha-Orlice River drainage, 20 June,

1925. NMC 59-199 (2 specimens, 56-66 mm S.L., S), U.S.S.R., Ukraine, Jasin in Cerna-Tisa River, sub-Carpathian district, 14 July, 1924. Pers. Coll. (27 specimens, 39-58 mm S.L., S), Romania, River Minis, tributary to Nera River at Bozovici S. Banat, 23 July, 1968. NMC 73-77 (2 specimens, 63-73 mm S.L., S), Denmark, Sjaelland, Koge a Brook, 22 November, 1969. NMC 73-194 (15 specimens, 58-69 mm S.L., S., T), Poland, upper San River, 15 June, 1966. Pers. Coll. (ZIAS 25037) (11 specimens, 48-72 mm S.L., S), U.S.S.R., Kolyma River 587 Km above Middle-Kolymsk town, 28 July, 1929. Pers. Coll. (ZIAS 12002) (4 specimens, 47-56 mm S.L., S), U.S.S.R., Western Siberia, Teletsk Lake, vicinity of Kamma River, 31 May, 1901. Pers. Coll. ZIAS 15641) (6 specimens, 35-51 mm S.L., S), U.S.S.R., Baikal Lake, Little Kunul, 16 June, 1908. Pers. Coll. (ZIAS 15587) (14 specimens, 24-56 mm S.L., S), U.S.S.R., Tuloma River (influent of Kola Bay Barentz Sea), 15-18 July, 1904. Pers. Coll. (ZIAS 13756) (6 specimens, 63-76 mm S.L., S), U.S.S.R., small river influent of Kosogol Lake, S.W. from Baikal Lake, June, 1880. Pers. Coll. (ZIAS 40922) (1 specimen, 35 mm S.L., S), U.S.S.R., Venta River (influent of Ural River), 25 June, 1956. Pers. Coll. (ZIAS 25935) (8 specimens, 29-49 mm S.L., S), U.S.S.R., Upper Warzuga River (Basin of White Sea), 11 September, 1931. Pers. Coll. (17 specimens, 30-70 mm S.L., S), England, ? Windermere Lake.

Pseudorasbora parva

Pers. Coll. (14 specimens, 40-83 mm S.L., S), Romania, various localities, introduced from Yangtze River at Wuchang, Hupeh, China.

Rasbora trilineata

Pers. Coll. (1 specimen, 49 mm S.L., S), Aquarium specimen, November, 1973.

Rhodeus sericeus amarus

Pers. Coll. (8 specimens, 47-60 mm S.L., S), Romania, fish-pond at Nucet, near Tirgoviste, November, 1960. Pers. Coll. (56 specimens, 24-43 mm S.L., S), Romania, River Timis at Albina near Timisoara, Banat., October, 1958.

Rutilus rutilus

BM(NH) 1961-4.19:40-65 (10 specimens, 103-146 mm S.L., S), England, Reading, River Thames. Pers. Coll. (4 specimens, 86-127 mm S.L., S), Romania, Lake Rosulet, Danube delta, 20 October, 1972. Pers. Coll. (8 specimens, 63-80 mm S.L., S), Romania, River Barcau (=Beretau) at Rosiori-Bihor, N. of Oradea, W. Romania, 23 September, 1967. Pers. Coll. (1 specimen, 97 mm S.L., S), England, Cheshire, Lymm Dam, 14 September, 1969. NMC 73-215 (4 specimens, 156-210 mm S.L., S), England, Tooting Common Pond, London, 9 May, 1972.

Scardinius erythrophthalmus ♀

Pers. Coll. (1 specimen, 140 mm S.L., S), Romania, Busorca near Sulina, Danube delta, Spring 1970. Pers. Coll. (1 specimen, 120 mm S.L., S), Romania, Lake Crapiņa, floodplain of the Danube, 14-15 November, 1968. Pers. Coll. (8 specimens, 54-84 mm S.L., S), Romania, thermal pond "1 Mai" on Petea rivulet near Oradea, W. Romania..

Tribolodon hakonensis

BM(NH) 1905-2-4:70-2 (3 specimens, 35-108 mm S.L., OX(2)), River Kitakami, Japan. BM(NH) 1905-2-4:68-9 (2 specimens, 115-136 mm. S.L., OX), Marioka, Japan. BM(NH) 1890-2-26:184 (1 specimen, 160 mm S.L., OX), Lake Hakou. BM(NH) 1905-2-4:73-82 (28 specimens, 27-89 mm S.L., OX(9)), River Iwai, Japan. Pers. Coll. (2 specimens, 231-325 mm S.L., S., T), Japan, Kyushu, Matura River in Okawano, Imari-shi, Saga Prefecture, 11 March, 1972. Pers. Coll. (1 specimen, 220 mm S.L., OA, S), As above, April, 1972. Pers. Coll. (1 specimen, 170 mm S.L., OA, S), Japan, Kyushu, Shiso River of the Takatsu River System in Sasayama, Hikioni-cho Mino-gun, Shimane Prefecture, 25 May, 1972. Pers. Coll. (8 specimens, 113-126 mm S.L., OA(2), S), Japn, Lake Aoki, Nagano-ken, 8 July, 1974.

Vimba vimba

Pers. Coll. (9 specimens, 81-127 mm S.L., OA(5), S), Romania, River Mures, at Iernut, Transylvania, 3 July, 1974. BM(NH) 1864-4-6:19-20 (2 specimens, 208-209 mm S.L., OX), Gestrückland.

APPENDIX 2

List of species of North American Cyprinidae

The genera and species of native North American cyprinids are listed on the following pages. Common and scientific names are taken from Bailey et al. (1970) which lists cyprinids from Canada and the U.S.A. Mexican species are taken mostly from Alvarez del Villar (1970) and Miller (1956). Species described since these publications appeared are also included with suggested common names in inverted commas. Doubtless more species remain to be discovered, particularly in Mexico, and the generic allocation of many species is still in a state of flux. A "Notes" section at the end of the species list provides some comment on generic placement of species and gives the sources for recently described species. Further comments may be found in Bailey et al. (1970). Miller (1956) lists several manuscript names for purely Mexican species of cyprinids but only one of these has since been described (Dionda erimyzonops Hubbs and Miller, 1974). Hopkirk (1967, 1973) described two species of cyprinids endemic to Clear Lake, California - Pogonichthys ciscoides and Endemichthys grandipinnis - but the status of these species is in dispute (Hubbs, 1974) and some nomenclatural confusion has arisen over the latter genus name (see Appendix 4).

Several cyprinid species have been introduced from Europe and Asia and may or have become established in various localities (Moore, 1968; Whitworth et al., 1968; Bailey et al.,

1970; Buchanan, 1973; Minckley, 1973). These are:

<u>Carassius auratus</u> (Linnaeus)	Goldfish
<u>Ctenopharyngodon idellus</u> Cuvier and Valenciennes	Grass carp
<u>Cyprinus carpio</u> (Linnaeus)	Carp
<u>Leuciscus idus</u> (Linnaeus)	Ide
<u>Rhodeus sericeus</u> (Pallas)	Bitterling
<u>Scardinius erythrophthalmus</u> (Linnaeus)	Rudd
<u>Tinca tinca</u> (Linnaeus)	Tench

The number of native species within genera of this list is as follows:

Total number of species	244
Total number of genera	44
Monotypic genera	26
Genera with 1 - 9 species	15
Genera with 10 - 19 species	3
Genera with more than 100 species	1
Mean number of species per genus	5.5

<u>Scientific Name</u>	<u>Common Name</u>	<u>Notes</u>
<u>Acrocheilus alutaceus</u> Agassiz and Pickering	Chiselmouth	
<u>Agosia chrysoqaster</u> Girard	Longfin dace	1
<u>Algansea affinis</u> Regan	-	2,3
" <u>alvarezi</u> Romero	-	
" <u>barbata</u> Alvarez and Cortes	-	
" <u>dugesi</u> : Bean	-	
" <u>lacustris</u> Steindachner	-	
" <u>monticola</u> Barbour and Contreras	-	
" <u>paratincella</u> Alvarez	-	
" <u>rubescens</u> Meek	-	
" <u>stigmatura</u> Regan	-	
" <u>tincella</u> Cuvier and Valenciennes	-	
<u>Campostoma anomalum</u> (Rafinesque)	Stoneroller	4
" <u>ornatum</u> Girard	Mexican stoneroller	
<u>Clinostomus elongatus</u> (Kirtland)	Redside dace	5
" <u>funduloides</u> Girard	Rosyside dace	
<u>Couesius plumbeus</u> (Agassiz)	Lake chub	2,6,7
<u>Dionda diaboli</u> Hubbs and Brown	Devils River minnow	
" <u>episcopa</u> Girard	Roundnose minnow	
" <u>erimyzonops</u> Hubbs and Miller	-	8
" <u>nubila</u> (Forbes)	Ozark minnow	9
" <u>rasconis</u> (Jordan and Snyder)	-	2
<u>Eremichthys acros</u> Hubbs and Miller	Desert dace	
<u>Ericymba buccata</u> Cope	Silverjaw minnow	

<u>Scientific Name</u>	<u>Common Name</u>	<u>Notes</u>
<u>Evarra bustamantei</u> Navarro	-	2
" <u>eigenmanni</u> Woolman	-	
" <u>tlahuacensis</u> Meek	-	36
<u>Exoglossum maxilllingua</u> (Lesueur)	Cutlips minnow	10
<u>Falcularius chapalae</u> (Jordan and Snyder)		2, 43
<u>Gila</u> (<u>Siphateles</u>) <u>alvordensis</u> Hubbs & Miller	-	11, 12
" (<u>Gila</u>) <u>atraria</u> (Girard)	Utah chub	
" (<u>Siphateles</u>) <u>bicolor</u> (Girard)	Tui chub	
" (<u>Gila</u>) <u>coerulea</u> (Girard)	Blue chub	
" (<u>Snyderichthys</u>) <u>copei</u> (Jordan & Gilbert)	Leatherside chub	
" (<u>Gila</u>) <u>crassicauda</u> (Baird and Girard)	Thicktail chub	
" " <u>cypha</u> Miller	Humpback chub	
" " <u>ditaenia</u> Miller	Sonora chub	
" " <u>elegans</u> Baird and Girard	Bonytail	
" (<u>Siphateles</u>) <u>mohavensis</u> (Snyder)	Mohave chub	
" (<u>Gila</u>) <u>nigrescens</u> (Girard)	Rio Grande chub	
" " <u>orcutti</u> (Eigenmann and Eigenmann)	Arroyo chub	
" " <u>purpurea</u> (Girard)	Yaqui chub	
" " <u>robusta</u> Baird and Girard	Roundtail chub	44
<u>Hemitremia flammea</u> (Jordan and Gilbert)	Flame chub	
<u>Hesperoleucus symmetricus</u> (Baird & Girard)	California roach	13

<u>Scientific Name</u>	<u>Common Name</u>	<u>Notes</u>
<u>Hybognathus hankinsoni</u> Hubbs	Brassy minnow	
" <u>hayi</u> Jordan	Cypress minnow	
" <u>nuchalis</u> Agassiz	Silvery minnow	41
" <u>placitus</u> Girard	Plains minnow	
<u>Hybopsis</u> (<u>Erimystax</u>) <u>cahni</u> Hubbs & Crowe	Slender chub	7,14
" " <u>dissimilis</u> Kirtland	Streamline chub	
" " <u>harperi</u> (Fowler)	Redeye chub	15
" " <u>insignis</u> Hubbs & Crowe	Blotched chub	
" " <u>monacha</u> (Cope)	Spotfin chub	
" " <u>x-punctata</u> Hubbs & Crowe	Gravel chub	
" (<u>Extrarius</u>) <u>aestivalis</u> (Girard)	Speckled chub	
" (<u>Hybopsis</u>) <u>amblops</u> (Rafinesque)	Bigeye chub	
" " <u>linneapunctata</u> Clemmer and Suttkus		16
" " <u>hypsinotus</u> (Cope)	Highback chub	
" " <u>labrosa</u> (Cope)	Thicklip chub	17
" " spp., cf. <u>labrosa</u>		17,18
" " <u>rubrifrons</u> (Jordan)	Rosyface chub	

<u>Scientific Name</u>	<u>Common Name</u>	<u>Notes</u>
<u>Hybopsis</u> (<u>Hybopsis</u>) <u>storeriana</u> Kirtland	Silver chub	
" (<u>Macrhybopsis</u>) <u>gelida</u> (Girard)	Sturgeon chub	
" " <u>meeki</u> Jordan & Evermann	Sicklefin chub	
" (<u>Oregonichthys</u>) <u>crameri</u> Snyder	Oregon chub	
" (<u>Yuriria</u>) <u>alta</u>		
<u>Iotichthys</u> <u>phlegethontis</u> (Cope)	Least chub	43
<u>Lavinia</u> <u>exilicauda</u> (Baird & Girard)	Hitch	
<u>Lepidomeda</u> <u>albivallis</u> Miller and Hubbs	White River spinedace	
" <u>altivelis</u> Miller and Hubbs	Pahranaagat spinedace	
" <u>mollispinis</u> Miller and Hubbs	Virgin spinedace	
" <u>vittata</u> Cope	Little Colorado spinedace	
<u>Meda</u> <u>fulgida</u> Girard	Spikedace	
<u>Moapa</u> <u>coriacea</u> Hubbs and Miller	Moapa dace	
<u>Mylocheilus</u> <u>caurinus</u> (Richardson)	Peamouth	
<u>Mylopharodon</u> <u>conocephalus</u> (Baird & Girard)	Hardhead	
<u>Nocomis</u> <u>asper</u> Lachner and Jenkins	Redspot chub	7
" <u>biguttatus</u> (Kirtland)	Hornyhead chub	
" <u>effusus</u> Lachner and Jenkins	Redtail chub	
" <u>leptocephalus</u> (Girard)	Bluehead chub	

<u>Scientific Name</u>	<u>Common Name</u>	<u>Notes</u>
<u>Nocomis micropogon</u> (Cope)	River chub	
" <u>platyrhynchus</u> Lachner and Jenkins	Bigmouth chub	
" <u>raneyi</u> Lachner and Jenkins	Bull chub	
<u>Notemigonus crysoleucas</u> (Mitchill)	Golden shiner	
<u>Notropis albeolus</u> Jordan	White shiner	20,30,40
" <u>alborus</u> Hubbs and Raney	Whitemouth shiner	
" <u>altipinnis</u> (Cope)	Highfin shiner	
" <u>amabilis</u> (Girard)	Texas shiner	
" <u>amnis</u> Hubbs and Greene	Pallid shiner	21
" <u>amoenus</u> (Abbott)	Comely shiner	
" <u>analostanus</u> (Girard)	Satinfin shiner	
" <u>anogenus</u> Forbes	Pugnose shiner	
" <u>ardens</u> (Cope)	Rosefin shiner	22
" <u>ariomus</u> (Cope)	Popeye shiner	29
" <u>asperifrons</u> Suttkus and Raney	Burrhead shiner	
" <u>atherinoides</u> Rafinesque	Emerald shiner	23
" <u>atrapiplus</u> Snelson	Blacktip shiner	24
" <u>atrocaudalis</u> Evermann	Blackspot shiner	
" <u>aztecus</u> Woolman		2
" <u>baileyi</u> Suttkus and Raney	Rough shiner	
" <u>bairdi</u> Hubbs and ortenburger	Red River shiner	
" <u>bellus</u> (Hay)	Pretty shiner	
" <u>bifrenatus</u> (Cope)	Bridle shiner	

<u>Scientific Name</u>	<u>Common Name</u>	<u>Notes</u>
<u>Notropis blennius</u> (Girard)	River shiner	
" <u>boops</u> Gilbert	Bigeye shiner	
" <u>boucardi</u> (Gunther)	-	2
" <u>braytoni</u> Jordan and Evermann	Tamaulipas shiner	
" <u>buccula</u> Cross	Smalleye shiner	
" <u>buchanani</u> Meek	Ghost shiner	
" <u>caeruleus</u> (Jordan)	Blue shiner	
" <u>calientis</u> Jordan and Snyder	-	2
" <u>callisema</u> (Jordan)	Ocmulgee shiner	
" <u>callistius</u> (Jordan)	Alabama shiner	
" <u>callitaenia</u> Bailey and Gibbs	Bluestripe shiner	
" <u>camurus</u> (Jordan and Meek)	Bluntface shiner	
" <u>celayensis</u> Alvarez	-	2
" <u>cerasinus</u> (Cope)	Crescent shiner	
" <u>chalybaeus</u> (Cope)	Ironcolor shiner	
" <u>chihuahua</u> Woolman	Chihuahua shiner	
" <u>chiliticus</u> (Cope)	Redlip shiner	
" <u>chloristius</u> (Jordan and Brayton)	Greenfin shiner	
" <u>chlorocephalus</u> (Cope)	Greenhead shiner	25
" <u>chrosomus</u> (Jordan)	Rainbow shiner	
" <u>chrysocephalus</u> (Rafinesque)	Striped shiner	42

<u>Scientific Name</u>	<u>Common Name</u>	<u>Notes</u>
<u>Notropis</u> <u>coccogenis</u> (Cope)	Warpaint shiner	
" <u>cornutus</u> (Mitchill)	Common shiner	
" <u>cummingsae</u> Myers	Dusky shiner	
" <u>dorsalis</u> (Agassiz)	Bigmouth shiner	
" <u>edwardranevi</u> Suttkus and Clemmer	Fluvial shiner	
" <u>euryzonus</u> Suttkus	Broadstripe shiner	
" <u>formosus</u> (Girard)	Beautiful shiner	
" <u>fumeus</u> Evermann	Ribbon shiner	
" <u>galacturus</u> (Cope)	Whitetail shiner	
" <u>garmani</u> Jordan	-	2
" <u>gibbsi</u> Howell and Williams	-	26
" <u>girardi</u> Hubbs and Ortenburger	Arkansas River shiner	
" <u>greenei</u> Hubbs and Ortenburger	Wedgespot shiner	
" <u>heterodon</u> (Cope)	Blackchin shiner	
" <u>heterolepis</u> Eigenmann and Eigenmann	Blacknose shiner	
" <u>hudsonius</u> (Clinton)	Spottail shiner	
" <u>hypselopterus</u> (Gunther)	Sailfin shiner	
" <u>hypsilēpis</u> Suttkus and Raney	Highscale shiner	
" <u>imeldae</u> Cortes	-	2
" <u>ipni</u> Alvarez	-	2, 39
" <u>jemezianus</u> (Cope)	Rio Grande shiner	
" <u>leedsi</u> Fowler	Ohoopee shiner	

<u>Scientific Name</u>	<u>Common Name</u>	<u>Notes</u>
<u>Notropis lepidus</u> (Girard)	Plateau shiner	
" <u>lermae</u> Evermann and Goldsborough	-	2
" <u>lauciodus</u> (Cope)	Tennessee shiner	
" <u>lirus</u> (Jordan)	Mountain shiner	
" <u>longirostris</u> (Hay)	Longnose shiner	
" <u>lutipinnis</u> (Jordan and Brayton)	Yellowfin shiner	25
" <u>lutrensis</u> (Baird and Girard)	Red shiner	
" <u>maculatus</u> (Hay)	Taillight shiner	
" <u>mekistocholas</u> Snelson	-	27
" <u>moralesi</u> De Buen	-	2
" <u>nazas</u> Meek	-	2
" <u>niveus</u> Cope	Whitefin shiner	
" <u>ornatus</u> (Girard)	-	2
" <u>ortenburgeri</u> Hubbs	Kiamichi shiner	
" <u>oxyrhynchus</u> Hubbs and Bonham	Sharpnose shiner	
" <u>ozarcanus</u> Meek	Ozark shiner	
" <u>perpallidus</u> Hubbs and Black	Colorless shiner	
" <u>petersoni</u> Fowler	Coastal shiner	
" <u>photogenis</u> (Cope)	Silver shiner	
" <u>pilsbryi</u> Fowler	Duskystripe shiner	
" <u>potteri</u> Hubbs and Bonham	Chub shiner	
" <u>procne</u> (Cope)	Swallowtail shiner	
" <u>proserpinus</u> (Girard)	Proserpine shiner	

<u>Scientific Name</u>	<u>Common Name</u>	<u>Notes</u>
<u>Notropis pyrrhomelas</u> (Cope)	Fieryblack shiner	
" <u>roseipinnis</u> Hay	Cherryfin shiner	
" <u>rubellus</u> (Agassiz)	Rosyface shiner	
" <u>rubricroceus</u> (Cope)	Saffron shiner	
" <u>rutilus</u> (Girard)	-	2
" <u>sabinae</u> Jordan and Gilbert	Sabine shiner	
" <u>saladonis</u> Hubbs and Hubbs	Salado shiner	2
" <u>sallaei</u> (Gunther)	-	2
" <u>santamariae</u> Evermann and Goldsborough	-	2
" <u>scabriceps</u> (Cope)	New River shiner	
" <u>scepticus</u> (Jordan and Gilbert)	Sandbar shiner	
" <u>semperasper</u> Gilbert	Roughhead shiner	
" <u>shumardi</u> (Girard)	Silverband shiner	28
" <u>signipinnis</u> Bailey and Suttkus	Flagfin shiner	
" <u>simus</u> (Cope)	Bluntnose shiner	
" <u>spectrunculus</u> (Cope)	Mirror shiner	
" <u>spilopterus</u> (Cope)	Spotfin shiner	
" <u>stilbius</u> (Jordan)	Silverstripe shiner	
" <u>stramineus</u> (Cope)	Sand shiner	
" <u>telescopus</u> (Cope)	Telescope shiner	29
" <u>texanus</u> (Girard)	Weed shiner	
" <u>topeka</u> Gilbert	Topeka shiner	

<u>Scientific Name</u>	<u>Common Name</u>	<u>Notes</u>
<u>Notropis trichroistius</u> (Jordan and Gilbert)	Tricolor shiner	
" <u>umbratilis</u> (Girard)	Redfin shiner	
" <u>uranoscopus</u> Suttkus	Skygazer shiner	
" <u>venustus</u> (Girard)	Blacktail shiner	
" <u>volucellus</u> (Cope)	Mimic shiner	
" <u>welaka</u> Evermann and Kendall	Bluenose shiner	
" <u>whipplei</u> (Girard)	Steelcolor shiner	
" <u>winchelli</u> Girard	Clear chub	
" <u>xaenocephalus</u> (Jordan)	Coosa shiner	21
" <u>xaenurus</u> (Jordan)	Altamaha shiner	
" <u>zonatus</u> (Putnam)	Bleeding shiner	
" <u>zonistius</u> (Jordan)	Bandfin shiner	
<u>Opsopoeodus emiliae</u> Hay	Pugnose shiner	19
<u>Orthodon microlepidotus</u> (Ayres)	Sacramento blackfish	
<u>Parexoglossum laurae</u> Hubbs	Tonguetied minnow	10
<u>Phenacobius catostomus</u> Jordan	Riffle minnow	
" <u>crassilabrum</u> Minckley & Craddock	Fatlips minnow	
" <u>mirabilis</u> (Girard)	Suckermouth minnow	
" <u>teretulus</u> Cope	Kanawha minnow	
" <u>uranops</u> Cope	Stargazing minnow	
<u>Phoxinus (Chrosomus) eos</u> (Cope)	Northern redbelly dace	31, 46

<u>Scientific Name</u>	<u>Common Name</u>	<u>Notes</u>
<u>Phoxinus</u> (<u>Chrosomus</u>) <u>erythrogaster</u> (Rafinesque)	Southern redbelly dace	
" (<u>Pfrille</u>) <u>neogaeus</u> Cope	Finescale dace	
" (<u>Chrosomus</u>) <u>oreas</u> (Cope)	Mountain redbelly dace	
<u>Pimephales</u> (<u>Hyborhynchus</u>) <u>notatus</u> (Rafinesque)	Bluntnose minnow	
" (<u>Pimephales</u>) <u>promelas</u> Rafinesque	Fathead minnow	
" (<u>Ceraticthys</u>) <u>tenellus</u> (Girard)	Slim minnow	
" (<u>Ceraticthys</u>) <u>vigilax</u> (Baird and Girard)	Bullhead minnow	
<u>Plagopterus</u> <u>argentissimus</u> Cope	Woundfin	
<u>Platygobio</u> <u>gracilis</u> (Richardson)	Flathead chub	7
<u>Pogonichthys</u> <u>macrolepidotus</u> (Ayres)	Splittail	
<u>Ptychocheilus</u> <u>grandis</u> (Ayres)	Sacramento squawfish	32
" <u>lucius</u> Girard	Colorado squawfish	
" <u>oregonensis</u> (Richardson)	Northern squawfish	
" <u>umpquae</u> Snyder	Umpqua squawfish	
<u>Relictus</u> <u>solitarius</u> Hubbs and Miller	-	12
<u>Rhinichthys</u> (<u>Rhinichthys</u>) <u>atratus</u> (Hermann)	Blacknose dace	33
" (<u>Rhinichthys</u>) <u>cataractae</u> (Valenciennes)	Longnose dace	

<u>Scientific Name</u>	<u>Common Name</u>	<u>Notes</u>
<u>Rhinichthys</u> (<u>Rinichthys</u>) <u>evermanni</u> Snyder	Umpqua dace	
" (<u>Apocope</u>) <u>falcatus</u> (Eigenmann & Eigenmann)	Leopard dace	
" <u>lariversi</u> Lugaski		34
" (<u>Apocope</u>) <u>osculus</u> (Girard)	Speckled dace	
<u>Richardsonius</u> <u>balteatus</u> (Richardson)	Redside shiner	5
" <u>egregius</u> (Girard)	Lahontan redside	
<u>Semotilus</u> (<u>Semotilus</u>) <u>atromaculatus</u> (Mitchill)	Creek chub	45
" (<u>Leucosomus</u>) <u>corporalis</u> (Mitchill)	Fallfish	
" (<u>Margariscus</u>) <u>margarita</u> (Cope)	Pearl dace	35
<u>Stypodon</u> <u>signifer</u> Garman	"Stumptooth"	2, 36
<u>Tiaroga</u> <u>cobitis</u> Girard	Loach minnow	
<u>Xystrosus</u> <u>popoche</u> Jordan & Snyder	"Popoche"	2, 30

Notes

1. See Miller (1956) where it is suggested another Mexican species may exist.
2. After Alvarez del Villar (1970).
3. The genus Algansea is currently under revision by R.R. Miller and C.D. Barbour (R.R. Miller, pers. comm. 1974 and 1975). This study will probably synonymise Xystrosus with Algansea, describe two new Algansea species and synonymise other listed here such that the species are A. barbata, lacustris, monticola, popoché (formerly Xystrosus popoché), tincella plus the two new species.
4. C. oligolepis Hubbs and Greene, the largescale stone-roller is regarded as a distinct species by Pflieger (1971) and is listed as such by Buchanan (1973).
5. Clinostomus has been synonymised with Richardsonius by Uyeno (1961) and this was accepted by Moore (1968) but not Bailey et al. (1970). A third undescribed Clinostomus is mentioned by Buhan (1970).
6. Couesius adustus Woolman listed by Alvarez del Villar (1970) is a synonym of Couesius plumbeus (Reno, 1969a).
7. These genera and sub-genera have all been submerged in Hybopsis by Bailey (1951) but Nocomis was removed by

Lachner and Jenkins (1967) and the status of Couesius, Oregonichthys and Platygobio in particular is uncertain.

8. Described by Hubbs and Miller (1974) from the Gulf coastal plain of Mexico. Another unnamed species is referred to in this work and they note that Dionda might better be referred to Notropis.
9. Placed in the subgenus Hydrophlox of Notropis by Swift. (1970).
10. Parexoglossum laurae (including P. hubbsi) has been placed in Exoglossum by Jenkins and Lachner (1971) and Gilbert and Bailey (1972).
11. The genera Siphateles and Snyderichthys were reduced to sub-generic rank by Uyeno (1961) and this is generally accepted (Moore, 1968; Bailey et al., 1970). The specific status of many Gila species is in dispute and this listing is open to considerable modification. (see note 44 also).
12. Gila alvordensis and Relictus solitarius were described by Hubbs and Miller (1972).
13. Four species of Hesperoleucus are recognised in Moore (1968) but Bailey et al. (1970) regard this genus as monotypic.
14. Hybopsis is a valid genus but may eventually be placed in

Notropis when the status of the included species is resolved (Cortes, 1968; Clemmer, 1971; Gilbert, pers. comm. 1974). Hybopsis is retained here to avoid tortuous nomenclatorial problems.

15. Assigned to Notropis by Gilbert and Bailey (1972).
16. Hybopsis lineapunctata was described by Clemmer and Suttkus (1971) from the upper Alabama River system.
17. Belong to the sub-genus Cyprinella of Notropis (Gilbert, pers. comm. 1974).
18. Probably two species here "zanema" MS and "leptocheilis" MS under study by R. Jenkins and E. Lachner (Gilbert, pers. comm., 1974; see also Menhinick, Burton and Bailey, 1974).
19. Opsopoeodus has been reduced to a sub-genus of Notropis by Gilbert and Bailey (1972), and separated again by Campos and Hubbs (1973) on the basis of karyological data (see note 35).
20. The genus Notropis has been divided into numerous subgenera. C.R. Gilbert (pers. comm., 1974) is preparing a generic synonymy and type catalogue of the genus and suggests that the following sub-genera may be valid nomenclatorially:

Notropis Rafinesque

Luxilus Rafinesque

Hybopsis Agassiz
Alburnops Girard
Cyprinella Girard
Hudsonius Girard
Graodus Gunther
Lythrurus Jordan
Episema Cope and Jordan
Chriope Jordan
Hydrophlox Jordan
Opsopoeodus Hay
Miniellus Jordan
Orcella Jordan and Evermann
Pteronotropis Fowler

At the present time it is not possible to allocate all the described Notropis species to sub-genera and so they are listed here alphabetically. Certain sub-genera have been studied in detail (Cyprinella by Gibbs (1957a); Hybopsis in part by Clemmer (1971); Hydrophlox by Swift (1970); Luxilus by Gilbert (1964); Lythrurus by Snelson (1972); Notropis in part by Snelson (1968); Pteronotropis by Suttikus (1951)).

21. Placed in Hybopsis s.s. by Clemmer (1971).
22. Notropis matutinus, the pinewoods shiner, is a synonym of N. ardens (Bailey et al., 1970).

23. Notropis percobromus, the plains shiner, is said to be a synonym of N. atherinoides (Bailey and Allum, 1962) but syntypes of N. percobromus are actually N. rubellus (Gilbert pers. comm., 1974).
24. Described by Snelson (1972) from Alabama, Georgia and Florida.
25. Notropis chlorocephalus and N. lutipinnis may be subspecies of one another; the former name has priority (Gilbert, pers. comm., 1974).
26. Described by Howell and Williams (1971) from the Tallapoosa River system in Alabama and Georgia.
27. Described by Snelson (1971) from the Cape Fear River basin, North Carolina.
28. Notropis shumardi was previously known as N. illecebrosus and is also synonymous with N. brazosensis (Bailey et al., 1970).
29. Notropis telescopus, the telescope shiner, was removed from the synonymy of N. ariommus by Gilbert (1969).
30. N. micropteryx Cope referred to by Howell (1957) is not listed by Bailey et al. (1970).
31. The synonymy of the American genus Pfrittle (Chrosomus s.l.)

with the Eurasian genus Phoxinus was proposed by Berg (1949) and Banareescu (1964) but without extensive evidence. Recent studies (present work and osteological work by Mahy, 1972a, 1975a, 1975b) confirm this action. Stasiak (1972) prefers retention of Phoxinus neogaeus in Pfrille as a genus separate from Chrosomus s.s. and presumably Phoxinus while Mahy (1972b) advocated lumping C. eos and C. oreas in C. erythrogaster.

32. It has been suggested that Ptychocheilus umpqua is only sub-specifically distinct, and should be included in P. oregonensis (Bond, 1961).
33. Rhinichthys nubilus (Girard) listed from Mexico by Alvarez del Villar (1970) is included in Rhinichthys osculus by Hubbs, Miller and Hubbs (1974).
34. Rhinichthys lariversi Lugaski, 1972 may be a subspecies of Rhinichthys osculus (Hubbs, Miller and Hubbs, 1974).
35. Semotilus margarita has been placed in Phoxinus by Legendre (1970b) on the basis of hybridization with Phoxinus eos, a diploid number of 50 chromosomes shared by S. margarita, P. eos and P. eos x P. neogaeus hybrids and the observation that S. corporalis and S. atromaculatus have 52 chromosomes. While the chromosome count emphasises the distinction of

S. margarita from other Semotilus it should be noted that Semotilus s.s. also hybridizes with Phoxinus, hybrids between diverse North American genera are common (Hubbs, 1955) and chromosomal counts are of limited value when the range is small. Difference in chromosome number is not always a reason for generic distinction (for an obvious exception see the "muntjac scandal" in Chiarelli and Capanna, 1973, and this may be apposite here.)

36. Apparently extinct.
37. Not listed by Alvarez del Villar (1970) but by Miller (1956) from the Rio Nazas basin, Coahuila, Mexico.
38. Not listed by Alvarez del Villar (1970) but by Miller (1956) from the Rio Salinas basin, Coahuila, Mexico.
39. Notropis ipni is regarded as a species of Dionda by Hubbs and Miller (1974).
40. Howell (1957) refers to a Notropis species and N. sp. (chevron shiner) undescribed species from Alabama and other undescribed species are referred to in Jenkins, Lachner and Schwartz (1972).
41. Pflieger (1971) tentatively considers that there are two species here, Hybognathus nuchalis Agassiz, the central silvery minnow of the central Mississippi valley, and Hybognathus argyritus Girard, the western silvery minnow of the Missouri system and the Mississippi River

from the Missouri mouth to about Scott Co., Missouri.

42. Menzel (1970) found a distinct genetic divergence between Notropis chrysocephalus isolepis Hubbs and Brown and N. c. chrysocephalus (Rafinesque) and so N. isolepis Hubbs and Brown was accorded full specific status on biochemical evidence. (Rainboth and Whitt, 1974).
43. Falcularius chapalae (Jordan and Snyder) is apparently a synonym of Hybopsis alta (R.R. Miller, 1975 pers. comm.).
44. A subspecies "intermedia" of Gila robusta has been elevated to species rank by Rinne (1969).
45. A new species of Semotilus is recorded by Jenkins, Lachner and Schwartz (1972) and in passing by Menhinick, Burton and Bailey (1974).
46. A new species, a montaine ally of Phoxinus oreas is noted in passing by Menhinick, Burton and Bailey (1974).

APPENDIX 3

The cyprinid sub-families

Fishes belonging to the Family Cyprinidae are distributed in the fresh waters of Africa, Eurasia and North America and comprise the most speciose freshwater fish family with about 2000 species in 200 genera. Definition of sub-families and relationships between cyprinids from broad zoogeographical areas are accordingly of some interest and utility.

The number of sub-families varies with the author. In addition there is some nomenclatorial confusion over sub-family names. A literature review is given here to facilitate comparisons between New and Old World cyprinids and to define the sub-family names referred to in other sections of this thesis.

Table 14 compares the sub-families according to several authors. Under each sub-family a list of genera is given where these were mentioned by the author. These lists are not complete but help to define the sub-family. Annotations comment on placement of genera and the confusion over sub-family names.

The following section describes characteristic features of the cyprinid sub-families. It is based principally on Banarescu (1973b) who has made the most recent "splitters" assessment of the family and also on Wu (1963) and Nikol'skii (1961). The sub-families are arranged in alphabetical not

phylogenetic order.

Sub-family Acheilognathinae (Europe, S.E. Asia).

Body small and high-set with a pointed snout and a narrow caudal peduncle. Dorsal and anal fins medium in length, the anal positioned just behind the level of the dorsal. A spine may be present in the dorsal fin. Mouth small and terminal with upper lip barbels in some species. Scales intermediate in size, lateral line complete or incomplete. There is one row of pharyngeal teeth and the gut is long. Females develop an egg-laying tube (also in gobionine Sarcocheilichthys) for introducing eggs into mussels.

Sub-family Barbinae (Africa, Asia and Europe)

Body elongate and slightly compressed or high-set and laterally compressed but not as much as in the breams (Abramidini-Leuciscinae). The mouth is ventral or almost terminal with one or two pairs of barbels. The lips may be thin or fleshy and folded, warty or covered by a horny layer, while others have sucking discs. There is a terminal mouth and belly keel in Rohtee only. The last unbranched dorsal ray is ossified and may bear teeth or not. The dorsal fin is at the middle or anterior part of the body. The anal fin is usually short. The lateral line when complete is straight and ends below the middle of the caudal peduncle. Some species lack scales. There are typically three rows of pharyngeal teeth but two and one rows are also found. The gut length is variable. In some genera the swim-bladder is degenerate. Eggs are laid on the substrate.

Sub-family Cultrinae (S.E. Asia, India, Pelecus in eastern Europe).

Body high-set or elongate and greatly compressed. A scaleless belly keel extends from the anus to the pectoral fin level or to the throat. The mouth is without barbels, terminal or on the upper half of the body and wide in some species. Many genera have a toothlike process on the lower jaw. Gill rakers number from 9-106. The dorsal fin has 7 rays, the last unbranched ray a spine. This fin is located behind the middle of the body (far back in many genera) and behind the base of the medium to long anal fin. The caudal fin is deeply forked and usually the lower lobe is slightly longer than the upper. The lateral line is usually complete, often arching down sharply. The pharyngeal teeth are in three rows, rarely two, usually with hooked points. The gut is short and the swimbladder has two or three chambers. Eggs of East Asian members develop while drifting downstream.

Sub-family Cyprininae (Asia, Europe)

Body high to very high-set, terminal or half-inferior mouth, with or without barbels. Scales are large and there are one to three rows of pharyngeal teeth. The dorsal fin is long and the anal fin is short. The last unbranched ray of both fins is bony and toothed. Spawning takes place on plants.

Sub-family Danioninae (Asia, Africa, ? North America)

Body elongate in some genera, others high-set. Ventrally rounded, belly keel in only a few species. Mouth at end of

body or on upper side, sometimes wide, lips thin and never fringed, one or two pairs of barbels in several genera.

Teeth usually in three rows, occasionally two or one, almost always pointed. Dorsal and anal fins are short and the dorsal tends to be located posteriorly on the body. The lateral line is straight or decurved, complete or absent, and usually runs on the lower half of the caudal peduncle. One genus, Swamba, lacks scales. Eggs are pelagic or laid on the bottom.

Sub-family Gobioninae (Europe, Asia)

Body elongate, low or medium high-set, ventral surface flattened or rounded. A pair of upper lip barbels in many genera, lips thin or fleshy and fringed with warts or with horny plates. Dorsal and anal fins short, a smooth spine in the dorsal fin of some genera. Pharyngeal teeth in one or two rows, gut length variable. The swimbladder is degenerate in e.g. Microphysobio, Gobiobotia which have a bony or fibrous capsule. Eggs are pelagic or laid in nests, rarely laid in mussels.

Sub-family Hypophthalmichthyinae (East Asia)

Large and high-set body with laterally flattened sides. Head large and broad with an upward-pointed mouth. The eyes are small and below the central head axis. The lateral line is complete and the scales are very small. The dorsal fin is short and the anal fin long. There is one row of greatly flattened teeth and the gut is very long. A ventral keel

runs from the throat to the anus. The branchiostegal membranes are not joined to the isthmus. A suprabranchial organ is present (see Berg, 1949) and the gill rakers coalesce. The eggs are pelagic.

Sub-family Leuciscinae (Eurasia excluding India, ? North America)

Elongate or high set body, generally compressed laterally. Mouth terminal, horse-shoe shaped, inferior or superior, sometimes with barbels. Lips complete or interrupted, fleshy or thin, or with a horny plate but never fringed or warty as in many Gobioninae and Danioninae. Usually without spiny rays in the dorsal fin, anal fin long or medium in size. Scales medium to very small. Generally lacking a ventral keel but if present incomplete. Pharyngeal teeth in one or two rows. Eggs usually laid on bottom but also said to be pelagic.

Sub-family Schizothoracinae (High Asia and S. India)

Mouth inferior, body and caudal peduncle compact. Barbels present or absent. Ventrally flattened or rounded and paired fins horizontal. Large scales around anus and anal fin. Other scales are small or absent. There are two or three rows of pharyngeal teeth, the peritoneum is black and the gut long. There is a serrated spine in the dorsal fin of young fish. The swimbladder is two-chambered, the posterior chamber long and slender. Eggs are laid on stones.

Sub-family Xenocyprininae (China)

Mouth almost terminal or sub-terminal, small and with stunted lower lip, lower jaw with thin, sharp cutting edge. There are one, two or three rows of hookless teeth with very long chewing surfaces. The dorsal fin has a smooth spine and is slightly shorter than the anal fin. There is a keel between the pectoral and anal fins in some species. The gut is long. Eggs develop while drifting downstream.

In considering Table 14 and the above descriptions it is obvious that sub-familial designation is open to several interpretations. Many characters are shared between sub-families making separation difficult. Banarescu (1972b) acknowledged that the Danioninae is possibly as un-natural sub-family and earlier (1967a) stated that "there are no trenchant and diagnostic morphological differences between the Leuciscinae and the Danioinae (sic), but phyletically they seem distinct". Wu (1964) also commented on the difficulties of sub-family separation. Osteological studies by Ramaswami (1955a, 1955b) and Sorescu (1968, 1970a, 1970b, 1970c, 1971, 1972) have not provided clear cut evidence for sub-family distinction.

For the purposes of this thesis 10 sub-families are recognized following Banarescu (1972b, 1973b) except that Schizothoracinae are not included in the Barbinae. "Splitting" facilitates comparison with N. American cyprinids and the list should not be taken as a carefully judged assessment of cyprinid sub-families.

North American cyprinids

Nearctic cyprinids are usually classified with the Leuciscinae (Miller and Hubbs, 1960; Banarescu, 1969; Eastman and Underhill, 1973). Attempts at erecting sub-families, e.g. Plagopterinae, Pimephalinae, Notropinae, within N. America have not met with much success (Miller and Hubbs, 1960; Hubbs and Black, 1947). Banarescu (1972b) has placed all the Nearctic cyprinids, except the leuciscine Notemigonus, in the Danioninae on the basis of unpublished osteological work by Ted Cavender. Until this work is available for consideration no assessment can be made of this placement.

Most of the Old World cyprinid sub-families possess peculiar characters which eliminate them from consideration, always assuming that these are not of relatively recent origin acquired since the Nearctic cyprinids left Asia. Such characters include the egg-laying tube of Acheilognathinae (also in the gobionine Sarcocheilichthys presumably an example of convergence), spiny fin elements of some Acheilognathinae, Barbinae, Cultrinae, Cyprininae, some Gobioninae, juvenile Schizothoracinae and Xenocyprininae (the spiny fins of N. American plagopterin fishes is regarded as an independent development (Miller and Hubbs, 1960)), elongate ventral keel in Cultrinae, Hypophthalmichthyinae, and some Xenocyprininae, eggs which develop while drifting downstream in Cultrinae some Gobioninae, Hypophthalmichthyinae and Xenocyprininae (the eggs of some Danioninae and Leuciscinae

are also said to be pelagic (Banareescu, 1973b)), large modified scales in the anal region of Schizothoracinae, the unique coalescing gill rakers, suprabranchial organ and large, low set eyes of Hypophthalmichthyinae and possibly the regenerated scale nucleus with anastomosing lines in Cyprininae and some Leuciscinae. The N. American Hybopsis resemble Gobioninae but this is probably convergence. Certain Gobioninae genera possess such characters as skull roof fontanelles (the fontanelle in N. American Iotichthys is regarded as independent), the swimbladder enclosed in a bony capsule, smooth dorsal fin spine, anus positioned well in front of the anal fin and more than one pair of barbels. Common ancestry is possible but unlikely and could only be determined by a careful survey of all the Gobioninae.

The Leuciscinae and Danioninae seem to present the most likely sub-families in which the Nearctic cyprinids can be placed by default. There are no obvious shared derived characters which would provide a definite link except those exhibited by Notemigonus (Abramidini) and Chrosomus (Phoxinus).

The Eurasian Leuciscinae may share common ancestry with the S.E. Asian Danioninae being a northern derivative of them which spread west into Europe and east into N. America.

This remains highly speculative at present.

TABLE 14

CYPRINID SUB-FAMILIES AND INCLUDED GENERA¹

Banarescu (1967b, 1971, 1972a, 1972b, 1973a, 1973b) and
Banarescu and Nalbant (1965).

Acheilognathinae²

Acanthorhodeus, Acheilognathus, Rhodeus.

Barbinae (including Schizothoracinae³)

Acrosssocheilus, Barbus, Bertinius, Caecobarbus,
Capoeta, Carassobarbus, Catla, Catlocarpio, Cirrhinus,
Cyprinion, Diptychus, Discogobio, Epalzeorhynchus, Garra,
Hemigarra, Hemigrammocapoeta, Iranocypris, Kosswigobarbus,
Labeo, Leptobarbus, Lobocheilus, Mesopotamichthys,
Mystacoleucus, Onychostoma, Osteochilus, Percocypris,
Phreatichthys, Poropuntius, Pseudogyrinocheilus, Ptychidio,
Puntius, Rohtee, Scaphiodontella, Schizocypris, Schizopy-
gopsis, Schizothorax, Semilabeo, Sinibarbus, Sinocyclo-
cheilichthys, Spinibarbus, Tor, Tylognathoides, Typhlogarra,
Varicorhinus.

Cultrinae⁴

Ancherythroculter, Chela, Culter, Erythroculter,
Hemiculter, Hemiculterella, Ischikauia, Longiculter,
Macrocheirichthys, Megalobrama, Oxygaster, Parabramis,
Parachela, Paralaubuca, Pelecus⁸, Pseudolaubuca,

Pseudoxygaster, Rasborichthys, Rasborinus, Salmostoma,
Siniichthys, Toxabramis.

Cyprininae

Carassius, Cyprinus, Puntioplites.

Danioninae (including Barilinae and Rasborinae).

All Nearctic cyprinids except Notemigonus; listing
in Appendix 2.

Aphyocypris, Atrilinea, Barilius, Brachydanio, Danio,
Elopichthys, Engraulicypris, Esomus, Fustis, Hemigrammo-
cypris, Luciobrama, Luciosoma, Nematabramis, Ochetobius,
Opsariichthys,⁸ Phoxinus,⁸ Rasbora, Squaliobarbus, Swamba,
Tanichthys, Yaoshanicus, Zacco.⁸

Gobioninae (including Gobiobotinae⁵).

Abbotina, Acanthogobio, Biwia, Coreius, Coreoleuciscus,
Gnathopogon, Gobio, Gobiobotia, Hemibarbus, Ladislavia,
Mesogobio, Microphysogobio, Pseudogobio, Pseudopungtungia,
Pseudorasbora, Pungtungia, Rhinogobio, Sarcocheilichthys,
Saurogobio, Squalidus.

Hypophthalmichthyinae

Aristichthys, Hypophthalmichthys.¹⁰

Leuciscinae (including Abramidini⁴ and Chondrostominae⁶).

Abramis, Acanthalburnus, Acanthobrama, Acanthorutilus,
Alburnoides, Alburnus, Aspiolucius, Aspius, Blicca,

Capoetobrama, Chalcalburnus, Chondrostoma, Ctenopharyngodon,
Leucalburnus, Leucaspius, Leuciscus, Mylopharyngodon,
Notemigonus, Pseudaspius, Pseudophoxinus, Rutilus, Tinca⁹,
Tribolodon, Vimba.

Xenocypridinae

Distoechodon, Plagiognathops, Pseudobrama, Xenocypris.

Wu (1964)⁷ Chinese Cyprinidae

Acheilognathinae

Acanthorhodeus, Acheilognathus, Paracheilognathus,
Pararhodeus, Pseudoperilampus, Rhodeus.

Cultrinae (as "Abramidinae"⁴)

Anabarilius, Ancherythroculter, Culter, Erythroculter,
Hainania, Hemiculter, Hemiculterella, Macrocheirichthys,
Megalobrama, Parabramis, Paralaubuca, Parapelecus,
Pseudohemiculter, Rasborinus, Rohanus, Sinibrama, Toxabramis.

Hypophthalmichthyinae

Aristichthys, Hypophthalmichthys.

Leuciscinae (including Danioninae)

Aphyocypris, Aspius, Atrilinea, Ctenopharyngodon,
Danio, Elopichthys, Leuciscus, Luciobrama, Lutiosoma,
Mylopharyngodon, Nicholsicypris, Ochetobius, Opsariichthys,
Phoxinus, Pseudaspius, Rasbora, Rutilus, Squaliobarbus,
Tanichthys, Tinca, Yaoshanicus, Zacco.

Schizothoracinae

Aspiorhynchus, Chuanchia, Diptychus, Gymnocypris,
Herzensteinia, Paraschizothorax, Platypharodon, Schizo-
pygopsis, Schizothorax.

Xenocyprininae

Acanthobrama, Distoechodon, Plagiognathops,
Xenocypris.

Nikol'skii (1961) Soviet Cyprinidae

Acheilognathinae (as "Rhodeinae"²)

Acanthorhodeus, Paracheilognathus, Pseudoperilampus,
Rhodeus.

Barbinae

Barbus, Discognathichthys, Hemibarbus, Puntius,
Tor, Varicorhinus.

Chondrostominae⁶

Chondrostoma

Cultrinae (including Xenocypridinae)

Elopichthys, Erythroculter, Hemiculter, Megalobrama,
Opsariichthys, Parabramis, Plagiognathops, Xenocypris.

Cyprininae

Carassius, Cyprinus.

Gobioninae (including Gobiobotinae⁵)

Gobio, Gobiobotia, Ladislavia, Paraleucogobio,

Pseudogobio, Pseudorasbora, Sarcocheilichthys, Saurogobio.

Hypophthalmichthyinae {

Arystichthys (sic), Hypophthalmichthys.

Leuciscinae (including Abramidini⁴ but not Chondrostominae⁶
q.v.)

Abramis, Alburnoides, Alburnus, Aspiolucius, Aspius,
Blicca, Capoetobrama, Chalcalburnus, Ctenopharyngodon,
Leucaspis, Leuciscus, Mylopharyngodon, Oreoleuciscus,
Pelecus, Phoxinus, Pseudaspis, Rutilus, Scardinius, Tinca,
Vimba.

Schizothoracinae

Diptychus, Schizopygopsis, Schizothorax.

Nichols (1938)

Acheilognathinae (as "Rhodeinae")²

Acanthorhodeus, Pseudoperilampus, Rhodeus.

Chondrostominae⁶ (including Xenocyprininae, some Barbinae
and Leuciscinae)

Chondrostoma, (Labeo), Varicorhinus, Xenocypris.

Cultrinae (as "Abramidinae"⁴) (including Abramidini⁴)

Abramis, Erythroculter, Hemiculter, Notemigonus.

Cyprininae (including some Barbinae)

Barbus, Cyprinus, Labeo, Osteochilus.

Danioninae (as "Rasborinae")

Bariluis, Danio, Opsariichthys, Rasbora.

Gobioninae

Gnathopogon, Gobio, Pseudogobio, Saurogobio.

Leuciscinae (including Nearctic Cyprinidae)

Hybopsis, Leuciscus, Phoxinus, Richardsonius.

Schizothoracinae

Diptychus, Schizopygopsis, Schizothorax.

Chu (1935) Chinese Cyprinidae

Acheilognathinae

Acanthorhodeus, Acheilognathus, Paracheilognathus,
Pseudoperilampus, Rhodeus.

Cultrinae (as "Abramidinae"⁴)

Anabarilius, Chanodichthys, Culter, Cultricus,
Hemiculter, Hemiculterella, Megalobrama, Metzia, Parabramis,
Parapelecus, Pseudolaucha, Rohanus, Toxabramis.

Cyprininae (including Barbinae)

Carassioides, Carassius, Cirrhinus, Cyclocheilichthys,
Cyprinus, Garra, Labeo, Lissocheilus, Onychostoma,
Osteochilus, Percocypris, Procypris, Pseudogyrinocheilus,
Ptychidio, Puntius, Semilabeo, Sinibarbus, Sinilabeo,

Spinibarbichthys, Spinibarbus, Tor, Varicorhinus.

Gobioninae

Abbotina, Chilogobio, Coreius, Gnathopogon, Gobio,
Hemibarbus, Paracanthobrama, Paraleucogobio, Pseudogobio,
Pseudorasbora, Rhinogobio, Sarcocheilichthys, Saurogobio,
Sinigobio.

Hypophthalmichthyinae

Aristichthys, Hypophthalmichthys.

Leuciscinae (including Danioninae)

Aphyocypris, Aspius, Atrilinea, Brachydanio,
Ctenopharyngodon, Danioides, Elopichthys, Leuciscus,
Luciobrama, Mylopharyngodon, Nicholsicypris, Ochetobius,
Opsariichthys, Phoxinus, Pseudaspius, Rasbora, Squaliobarbus,
Tanichthys, Tribolodon, Zacco.

Schizothoracinae

Chuanchia, Diptychus, Gymnocypris, Gymnodiptychus,
Herzensteinia, Paratylognathus, Platypharodon, Ptychobarbus,
Schizopyge, Schizopygopsis, Schizothorax.

Xenocyprininae (as "Chondrostomatinae"⁶)

Distoechodon, Plagiognathops, Pseudobrama, Xenocypris.

Rendahl (1928)

Acheilognathinae (as "Rhodeinae"²)

Acanthorhodeus, Acheilognathus, Paracheilognathus,

Pararhodeus, Pseudoperilampus, Rhodeus.

Barbinae

Barbus, Cirrhinus, Discoognathus, Hemibarbus, Labeo,
Mystacoleucus, Paracanthobrama, Paratylognathus, Semilabeo,
Sinibarbus, Tylognathus.

Cultrinae (as "Abramidinae"⁴)

Chanodichthys, Culter, Culticula, Hemiculter,
Hemiculterella, Nicholsiculter, Parabramis, Parapelecus,
Rasbora, Toxabramis.

Cyprininae

Carassius, Cyprinus.

Gobioninae (including Gobiobotinae⁵)

Ageniogobio, Chilogobio, Coripareius, Gobio, Gobiobotia,
Paraleucogobio, Pseudogobio, Pseudorasbora, Rhinogobio,
Sarcocheilichthys, Saurogobio.

Hypophthalmichthyinae

Aristichthys, Hypophthalmichthys.

Leuciscinae (including Danioninae)

Aphyocypris, Aspius, Barilius, Ctenopharyngodon,
Elopichthys, Leuciscus, Luciobrama, Mylopharyngodon,
Opsariichthys, Phoxinus, Pseudophoxinus, Squaliobarbus.

Schizothoracinae

Diptychus, Schizopygopsis, Schizothorax.

Xenocyprininae (as "Chondrostominae"⁶)

Distoechodon, Plagiognathops, Pseudobrama, Xenocypris.

Other works include Smith (1945) on Thailand cyprinids who cited Abraminae (sic) (= Cultrinae), Cyprininae (including Barbinae and Acheilognathinae), Garrinae (for Garra, Discolabeo, Epalzeorhynchus, Crossocheilus and Mekongia usually in Barbinae) and Rasborinae (= Danioninae), Kryzhanovskiy (1947) who divided cyprinids into four sub-families (sic) Barbini (including Acheilognathinae, Cyprininae and Schizothoracinae), Danionini, Gobionini and Leuciscini (including Cultrinae and Xenocyprininae) on the basis of hybridization and ecological characteristics, and Berg (1947, 1949) who listed the sub-families (sic) Cyprinini, Gobiobotiini (for the genus Gobiobotia), Hypophthalmichthyini and Psilorhynchini. Hora (1920) elevated this latter group to family rank and this is retained by Greenwood et al. (1966).

Notes on Table

1. No attempt was made to assess generic status; some may only be sub-genera or synonyms.
2. Acheilognathinae has priority over Rhodeinae (see Duyvene de Wit, 1962).
3. In Banarescu (1973b) the Schizothoracinae are separated from the Barbinae but this translated work was first published in 1968. A later assessment placed Schizothoracinae as "only a group, perhaps less than a tribe, within the Barbinae (Banarescu, 1972b).
4. The Cultrinae are sometimes called the Abramidinae. The Abramidini are a tribe of the Leuciscinae sometimes elevated to sub-family rank but not related to the Cultrinae (Banarescu, 1967a, 1967b).
5. Nikol'skii (1961) considers placement of Gobiobotia into a sub-family of its own solely on the basis of having 8 barbels as inexpedient.
6. Chondrostominae has been used to delineate the genus Chondrostoma of Europe, now usually considered as a tribe or less of the Leuciscinae. The name has also been used for the Asian Xenocyprininae.
7. This work is incomplete and the sub-families Barbinae,

Cyprininae, Gobiobotinae, and Gobioninae are referred to but not described. According to the translation at hand another sub-family, (transliterated as Yarlonae) containing Aphyocypris and Yaoshanicus, exists. It is referred to in the section on Abramidinae but not in the keys to sub-families, and these genera are referred to the Leuciscinae later.

8. Pelecus was previously placed in the Leuciscinae as were Opsariichthys, Phoxinus and Zacco. Makayeva and Ryabov (1973) place Opsariichthys in the Leuciscinae rather than the Cultrinae in which Nikol'skii (1961) had placed this genus.
9. Tinca has been placed in the Cyprininae by e.g. Sorescu (1968).
10. Ryabov (1973) places Hypophthalmichthys close to Leuciscinae in agreement with Kryshanovsky (1947).

APPENDIX 4

On the nomenclature of the genus name Endemichthys

The genus name Endemichthys was first used by Hopkirk (1967) in describing a new species of cyprinid, E. grandipinnis, from Clear Lake, California. Since this work was a doctoral dissertation the name was not published. A nomen nudum was created by publication of an abstract of the thesis without a genus description (Hopkirk, 1968). A subsequent publication issued 30 November 1973 (Hopkirk, 1973) described the new genus and species in an acceptable manner but Endemichthys had been coined as a genus name for a fossil dictyopygid, Endemichthys likhoeli (Order Redfieldiformes), from Lesotho, South Africa in a publication issued 23 March 1973 (Forey and Gardiner, 1973). The latter use of the genus name has priority and a replacement name for Endemichthys grandipinnis is required. It should be noted that the status of this species is in dispute (Hubbs, 1974) and that the 12 extant specimens collected in 1939-1940 have been referred to Lavinia exilicauda (10) and Orthodon macrolepidotus (2) or as hybrids between these two species.

APPENDIX 5

Program listings

```

10 REM "HNCOF3" HENNIG'S COEFFICIENT - NON-FRACTIONAL VERSION: 25SEP1975
20 REM
30 REM THIS PROGRAM CALCULATES HENNIG'S COEFFICIENT WHICH RANGES FROM 0 TO 1,
40 REM 0 INDICATING NOT RELATED, 1 INDICATING SISTER-GROUP RELATIONSHIP.
50 REM H.C. FOR A PAIR OF TAXA = D/T = NO. SHARED DERIVED CHARACTERS/
60 REM NO. CHARACTERS WHICH ARE DERIVED IN ONE OR BOTH OF THE TAXA.
70 REM PRIMITIVE CHARACTER STATES ARE CODED AS 0, ADVANCED AS 100 WITH, (IF
80 REM NECESSARY) SINGLE INTERMEDIATE STATES AS 50, DOUBLE INTERMEDIATES AS
90 REM 33 AND 67, ETC. WHERE A CHARACTER IS INAPPLICABLE IN A GROUP OR
100 REM DATA IS LACKING, CODE THE STATE AS 999. BE PREPARED TO INPUT THE
110 REM NUMBER OF TAXA AND THE NUMBER OF CHARACTERS USED. START DATA
120 REM IN LINE 900.
130 DIM AI[50,50], AS[20], BS[20], BI[50,15]
140 DISP "INPUT NUMBER OF TAXA (ROWS)"
150 WAIT 2000
160 INPUT L
170 DISP "INPUT NO. OF CHARACTERS (COLUMNS)"
180 WAIT 2000
190 INPUT K
200 FOR R=1 TO L
210 READ BS
220 TRANSFER BS TO B[R,1]
230 FOR C=1 TO K
240 READ A[R,C]
250 NEXT C
260 NEXT R
270 PRINT
280 PRINT " TAXON X TAXON HENNIG'S NUMBER DERIVED
290 PRINT " " " COEFFICIENT CHARACTERS COMPARED.
300 PRINT " " " (NON-FRACTIONAL) "
310 WRITE (15,*) "
320 PRINT "

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```

330 M=1
340 N=1
350 FOR Z=1 TO L
360 GOSUB 420
370 N=N+1
380 NEXT Z
390 M=M+1
400 IF M=L+1 THEN 660
410 GOTO 340
420 D=T=J=0
430 FOR Q=1 TO K
440 IF A[M,Q]+A[N,Q]=0 THEN 510
450 IF A[M,Q]+A[N,Q]>998 THEN 610
460 IF A[M,Q]-A[N,Q]=0 THEN 490
470 T=T+1
480 GOTO 510
490 D=D+1
500 T=T+1
510 NEXT Q
520 TRANSFER B[M,1] TO A$
530 TRANSFER B[N,1] TO B$
540 FORMAT F6.3, 10X, F3.0
550 IF J=K THEN 640
560 IF T=0 THEN 590
570 WRITE (15,540)A$, TAB21,B$,TAB50,D/T,TAB60,T
580 RETURN
590 WRITE (15,540)A$,B$,0,0
600 RETURN
610 J=J+1
620 GOTO 510
630 FORMAT 2F20.0," NO CHARACTERS CAN BE COMPARED"
640 WRITE (15,630)A$,B$
650 RETURN
660 PRINT
670 PRINT
680 PRINT "RUN COMPLETE"
690 END

```

```

10 REM "MATCOF" SIMPLE MATCHING COEFFICIENT. VERSION: MARCH 1975
20 REM CALCULATION OF SIMPLE MATCHING COEFFICIENT OF SOKAL & SNEATH (1966)
30 REM THIS COEFFICIENT = NO. MATCHING CHARACTERS/NO. OF CHARACTERS.
40 REM THIS PROGRAM CALCULATES THE SIMPLE MATCHING COEFFICIENTS FOR ALL PAIRS
50 REM OF SPECIES. CODE THE CHARACTER STATES AS 0 AND 1. WHERE DATA FOR A SPECIES
60 REM IS UNAVAILABLE OR WHERE THE CHARACTER IS INAPPLICABLE FOR THAT SPECIES
70 REM CODE THE CHARACTER FOR THAT SPECIES AS 9. IN DATA LINE 900
80 REM LIST THE CHARACTER STATES OF CHARACTERS 1 TO N FOR THE FIRST SPECIES.
90 REM DO THE SAME IN LINE 910 FOR THE NEXT SPECIES & SO ON TO THE LAST SPECIES
100 REM RUN THE PROGRAM REING PREPARED TO INPUT THE NUMBER OF THE SPECIES
110 REM THEN THE NUMBER OF CHARACTERS. THE HIGHER THE COEFFICIENT, THE MORE ARE
120 REM CHARACTERS THE TWO SPECIES SHARE AND THE MORE CLOSELY "RELATED" THEY ARE
130 REM WHERE THE NUMBER OF CHARACTERS COMPARED IS LOW, THE COEFFICIENT IS
140 REM BEST IGNORED. PROGRAM OCCUPIES ABOUT 2230 WORDS, TO RUN WITH 10
150 REM SPECIES AND 48 CHARACTERS USED 4444 WORDS WITH INTEGER PRECISION IN
160 REM DIM STATEMENT. DIM STATEMENT MAY NEED TO BE MODIFIED ACCORDING TO
170 REM CODED DATA. IF FRACTIONS SUCH AS .5 USED IN CHARACTER CODES THEN
180 REM INTEGER PRECISION CAN'T BE USED, AND SPLIT PRECISION MUST BE USED
190 REM IN THE DIM STATEMENT. FOR VERY LARGE ARRAYS RUN HALF DATA AT A TIME
200 REM OR BRING IN REST OF DATA OFF TAPE PART WAY THROUGH PROGRAM.
210 REM IF ONE INTERMEDIATE CHARACTER STATE IS REQUIRED CODE AS 0,.5, & 1
220 REM IF TWO INTERMEDIATE STATES AS 0,.33,.66 & 1, ETC. (IF INTERMEDIATE
230 REM TO SAVE SPACE: AI(V1,V2), INSTEAD SPLIT PRECISION: AS(V1,V2) MUST
240 REM BE USED. IF NEEDED DELETE REM STATEMENTS TO SAVE SPACE.
250 DIM AI(11,39), AS(20), BS(20), BI(11,20)
260 DISP "INPUT NUMBER OF TAXA (ROWS)."
270 WAIT 2000
280 INPUT L
290 DISP "INPUT NO. OF CHARACTERS (COLUMNS)"
300 WAIT 2000
310 INPUT K
320 FOR R=1 TO L
330 READ BS
340 TRANSFER BS TO B[R,1]
350 FOR C=1 TO K
360 READ A[R,C]
370 NEXT C

```

```

380 NEXT R
390 PRINT "
400 PRINT "
410 PRINT "
420 WRITE (15,*)"
430 J=0
440 M=1
450 N=1
460 FOR Z=1 TO L
470 GOSUB 530
480 N=N+L
490 NEXT Z
500 M=M+1
510 IF M=L+1 THEN 710
520 GOTO 450
530 G=0
540 FOR Q=1 TO K
550 IF A[M,Q] 8 THEN 660
560 IF A[N,Q] 8 THEN 660
570 G=G+(SQR((A[M,Q]-A[N,Q]))^2))
580 NEXT Q
590 TRANSFER B[M,1] TO A$
600 TRANSFER B[N,1] TO B$
610 FORMAT 2X,F6.3,13X,F3.0
620 IF K-J=0 THEN 680
630 WRITE (15,610)A$,TAB21,B$,TAB50,((K-G-J)/(K-J)),TAB60,K-J
640 J=0
650 RETURN
660 J=J+1
670 GOTO 580
680 WRITE (15,610)A$,B$,"NO CHARACTERS CAN BE COMPARED"
690 J=0
700 RETURN
710 PRINT
720 PRINT
730 PRINT "RUN COMPLETE"
740 END

```

NUMBER OF
CHARACTERS"

SIMPLE MATCHING

COMPARED"

COEFFICIENT

TAXON

X

TAXON

APPENDIX 6

Author and year of publication of principle genera and sub-genera of North American cyprinids referred to in this thesis. .

Acrocheilus Agassiz 1855

Agosia Girard 1856

Algansea Girard 1856

Campostoma Agassiz 1855

Chrosomus Rafinesque 1820

Clinostomus Girard 1856

Couesius Jordan 1878

Dionda Girard 1856

Eremichthys Hubbs and Miller 1948

Ericymba Cope 1865

Erimystax Jordan 1882

Evarra Woolman 1895

Exoglossum Rafinesque 1818

Extrarius Jordan 1919.

Gila Baird and Girard 1853

Hemitremia Cope 1870

Hesperoleucus Snyder 1912

Hybognathus Agassiz 1855

Hybopsis Agassiz 1854

Iotichthys Jordan and Evermann 1896

Lavinia Baird and Girard 1854

Lepidomeda Cope 1874

Macrhybopsis Cockerell and Allison 1909

Margariscus Cockerell 1909

Meda Girard 1856

Moapa Hubbs and Miller 1948

Mylocheilus Agassiz 1855

Mylopharodon Ayres 1855

Nocomis Girard 1856

Notemigonus Rafinesque 1819

Notropis Rafinesque 1818

Opsopoeodus Hay 1880

Oregonichthys Hubbs 1929

Orthodon Girard 1856

Parexoglossum Hubbs 1931

Phenacobius Cope 1867

Pimephales Rafinesque 1820

Plagiopterus Cope 1874

Platygobio Gill 1863

Pogonichthys Girard 1854

Ptychocheilus Agassiz 1855

Relictus Hubbs and Miller 1972

Rhinichthys Agassiz 1848

Richardsonius Girard 1856

Semotilus Rafinesque 1820

Stypodon Garman 1881

Tiaroga Girard 1856

Xystrosus Jordan and Snyder 1899

Yuriria Jordan and Evermann 1896