BRITISH MUSEUM GENERAL 13 JUL 1978 LIBRARY NATURAL HIS

The anatomy and relationships of the cyprinid fish *Luciobrama macrocephalus* (Lacepède)

G. J. Howes
Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Contents

Synopsis

The osteology and cranial myology of the long-headed cyprinid fish, *Luciobrama macrocephalus*, is described and aspects of its cranial functional morphology are considered. On the basis of shared derived characters the closest relatives of *Luciobrama* are identified as *Aspiolucius*, *Pseudaspius*, *Aspius* and *Elopichthys* which together form a monophyletic assemblage termed the aspinine group. It is suggested that this group is related to an as yet unidentified monophyletic aggregate of the 'Leuciscinae'. The osteological characters of many other cyprinid genera are compared and commented upon in the light of their usefulness as indicators of relationship and in terms of function. The cranial myology of *Elopichthys bambusa* and *Barilius bola* is described and figured.

Introduction

Although the Cyprinoidei display a great degree of diversity in their morphology and trophic specializations, there appear to be fewer piscivorous taxa than amongst their presumed sister group of ostariophysans, the Characoidei. This is undoubtedly due, in part at least, to the fact that jaw teeth are lacking in cyprinoid fishes. On the other hand, a characteristic of cyprinoids is the protusile mechanism of the upper jaw and the correlated development of a suction method of feeding (see Alexander, 1964, 1966 & 1967). Because of this particular type of jaw mechanism, the evolution of pike-like piscivores, a habitus (of piscivore) so prevalent amongst the characoids and other teleost groups, has been severely limited. To my knowledge, only one such fish has evolved amongst the cyprinids, namely, *Elopichthys* (which is discussed in this paper). The reasons for the absence of this type of predatory facies, and those which account for the other types manifest in present day old-world cyprinid lineages, are presented on page 61.

Bull. Br. Mus. nat. Hist. (Zool.) **34** (1): 1-64 Issued 29 June 1978

In a previous paper (Howes, 1976) I described, in part, the cranial anatomy of a piscivorous cyprinid, *Macrochirichthys macrochirus*. From this initial study my attention was drawn to other piscivorous cyprinids and in particular to *Luciobrama macrocephalus*. Because *Luciobrama* is so obviously specialized, it seemed that it might offer clues to the recognition of primitive and advanced character states in other groups of cyprinids. In order to detect these and to find the closest relatives of *Luciobrama* on the basis of shared specializations, comparisons have been made with a number of other cyprinid genera (see p. 25).

As pointed out later (p. 61) the classification of cyprinid fishes is in an unsatisfactory state and it would be futile and pretentious at this stage to offer any phylogenetic scheme for subfamilial classification. What has become clear during this study is that few of the presently recognized cyprinid subfamilies are monophyletic groups.

List of study material

Species	BMNH register number	Type of preparation and standard lengths (mm) of alcohol preserved specimens	Locality
Abramis brama	1864.4.2:12	Skeleton	Holland
Abramis brama	Unregistered	Skeleton	Unknown
Alburnus alburnus	Unregistered	Alizarins; 37, 40, 58	Thames
Aspidoparia morar	1872.4.17:81	92	Bengal
Aspiolucius esocinus (Types)	1897.7.5:31–32	244, 107	Amu-Daria
Aspiopsis merzbacheri (Type)	1914.3.2:1	166	Central Asia
Aspius aspius	Unregistered	Two skulls	Danube
Aspius aspius	1860.3.7:34	225	Danube
Aspius aspius	1976.4.1:1	110	Mures R.
Aspius vorax	1920.3.3:127–146	235	Basra
Aspius vorax	1874.4.28:30	Skeleton	Tigris R.
Barbus altianalis	Unregistered	Skeleton	Lake George
Barbus altianalis	Unregistered	142	Lake George
Barbus altus	1882.2.11:314	145	Thailand
Barbus argenteus	1907.6.29:217	Skeleton	Angola
Barbus aspilus	1909.4.29:14	Skeleton	Ja R.
Barbus barbus	Unregistered	Skeleton	England
Barbus barbus	1908.12.28:123	Skeleton	England
Barbus callensis	1869.1.29:4	Skeleton	Algeria
Barbus callipterus	1975.1.17:201–210	53	Togo
Barbus camptacanthus	Unregistered	Skeleton	W. Africa
Barbus canis	1864.8.23:24	Skeleton	Jordan
Barbus capensis	Unregistered	Skeleton	Burg R.
Barbus fritschii	1904.11.18:59	Skeleton	Morocco
Barbus gonionotus	1974.10.10:823–824	144	E. Java
Barbus guirali	1902.11.12:119	Skeleton	Kribi R.
Barbus harterti	1902.7.28:35	Skeleton	Morocco
Barbus harterti	1903.10.29:16	Skeleton	Morocco
Barbus holotaenia	1902.11.12:122	Skeleton	Kribi R.
Barbus intermedius	1902.12.13:291	Skeleton	Errer R.
Barbus kersteni	1961.12.1:156	Skeleton	Aswa R.
Barbus longiceps	Unregistered	Skeleton	Galilee
Barbus mariae	1936.12.22:35–39	370	Athi R.
Barbus nasus	1902.1.4:22	Skeleton	Morocco
Barbus natalensis	1862.8.28:8	Skeleton	Natal
Barbus orphoides	1974.10.10:865–872	90	Java
Barbus oxyrhynchus	1893.12.2:31	Skeleton	Thikathike R.

Species	BMNH register number	Type of preparation and standard lengths (mm) of alcohol preserved specimens	Locality
Barbus paludinosus	1902.1.4:72	Skeleton	Morocco
Barbus perince	1907.12.2:3745	Skeleton	Nile
Barbus progenys	1903.7.28:155	Skeleton	Cameroon
Barbus radiatus	1961.12.10239	Skeleton	Aswa R.
Barbus reinii	1903.10.29:10	Skeleton	Morocco
Barbus rocadasi	1911.6.1:26	Skeleton	Angola
Barbus sarana	1889.9.26:99–103	94	Deoli
Barbus setivemensis	1869.1.29:21	Skeleton	Unknown
Barbus somereni	1971.1.5:96–99	Alizarins; 76, 60	Ruimi R.
Barbus tor	1889.2.1:523	Skeleton	Assam
Barbus trimaculatus	1907.4.9:98	Skeleton	Transvaal
Barilius bendelisis	1889.10.29:37	Skeleton	Dehra Dun
Barilius bola	1889.2.1:1205	Skeleton	Assam
Barilius bola	1889.9.26:118–127	235	Deoli
Barilius bola	1867.5.12:20–22	135	Norar R.
Barilius gatensis	1889.2.1:1135–1139	107	Nilgherriss
Barilius loati	1907.12.2:1503–1512	132	Gondokoro
Barilius loati	1907.12.2.3748	Skeleton	Nile
Barilius microcephalus	1906.9.7:4	Skeleton	L. Malawi
Barilius microcephalus	1974.1.15:25–26	210	L. Malawi
Barilius moori	1974.3.19:1–5	102–137	L. Kivu
Barilius niloticus	Unregistered	Alizarins; 23·5–40	L. Rudolf
Barilius niloticus	1907.12.2:3764–3767	Skeletons	Nile
Barilius ornatus	1893.6.30:61–70	75–93	Shan States
Barilius ubangensis	1902.11.12:142–148	88	Kribi R.
Barilius ubangensis	1903.7.28:165	Skeleton	Kribi R.
Barynotus luteus	1874.4.28:23	Skeleton	Tigris R.
Catla catla	1908.12.28:122	Skeleton	Hooghly R.
Catostomus teres	1866.12.13:5	Skeleton	Montreal
Chela laubuca	1889.2.1:1356–1359	60	Madras
Chelaethiops sp.	Unregistered	Alizarins; 20·5–30·0	L. Rudolf
Chondrostoma nasus	1976.4.1:4–6	148	Romania
Chondrostoma polylepis	1885.1.29:30	Skeleton	Coruna
Ctenopharyngodon idellus	1888.5.15:25	Skeleton	Tchang
Culter brevicauda	1891.1.31:28	Skeleton	China
Cyprinus carpio	Unregistered	122	Lincolnshire
Cyprinus carpio	Unregistered	Skeleton	Unknown
Cyprinus carpio	Unregistered	Skeleton	Amoy
Cyprinus carpio	Unregistered	Skull	Unknown
Danio aequipinnatus	1894.5.21:56–60	72	Byingi
Elopichthys bambusa	1889.6.24:51	Skeleton	Kiu Kiang
Elopichthys bambusa	1936.10.19:20	Alizarin; 116	Tatung
Elopichthys bambusa	1936.10.19:13–19	185, 250	Tatung
Elopichthys bambusa	Unregistered	220	China
Erythroculter ilishaeformis	1936.10.19:31–34	176	Hankow
Erythroculter mongolicus	1889.6.24:57	Skeleton	Kiu Kiang
Esomus danricus	1863.12.8:108–114	85	Madras
Garra blandfordi	1902.12.13:420	Skeleton	Jerrer R.
Garra lamta	Unregistered	Skeleton	Unknown
Hemiculter leucisculus	1938.12.1:26	54	Chusan
Hemiculterella polylepis	1921.7.26:21–23	132	Yunnan Lake
Hypophthalmichthys molitrix	1895.5.31:22	Skeleton	China
Labeo bata	1889.2.1:206	Skeleton	Assam

Species	BMNH register number	Type of preparation and standard lengths (mm) of alcohol preserved specimens	Locality
Labeo coubie	1907.12.2:3744	Skeleton	Kosheh, Nubia
Labeo coubie	1911.3.31:21–29	Alizarin; 52	Aboina R.
Labeo chrysophekadion	1898.11.8:115	Alizarin; 63	Menam R.
Labeo cylindricus	1902.5.26:23	Skeleton	Tana
Labeo diplostomus	1889.2.1:163	Skeleton	Hardwar
Labeo macrostoma	1904.5.2:158–160	140	Angola
Labeo niloticus	1907.12.2:975–980	122	L. Menzaleh
Labeo rohita	1889.2.1:138–139	143	Calcutta
Labeo rohita	1858.8.15:50	Alizarin, 83	India
Labeo stoliczke	1891.11.30:286	Skeleton	Sittang R.
Leuciscus cephalus	1867.4.2:15	Skeleton	Holland
Leuciscus idus	1867.4.2:6	Skeleton	Holland
Luciobrama macrocephalus	1889.6.24:48	Skeleton	Kiu Kiang
Luciobrama macrocephalus	1928.4.24:15	273	Nanking
Luciobrama macrocephalus	1896.6.24:46	420	Kiu Kiang
Luciobrama macrocephalus	1888.5.15:31–32	458	Tchang
Luciosoma bleekeri	1898.11.8:114	Skeleton	Menam R.
Macrochirichthys macrochus	1898.11.8:121	Skeleton	Menam R.
Macrochirichthys macrochus	1898.4.2:243	212	Menam R.
Megalobrama bramula	1936.10.19:21	111	Hankow
Megalobrama macrops	Unregistered	Skeleton	Formosa
Myxocyprinus chinensis	1889.6.24:10	Skeleton	Kiu Kiang
Notropis hudsonius	1925.2.3:121–125	68	Mississippi R.
Ochetobius elongatus	1936.10.19:35–38	147	Tatung, China
Ochetobius elongatus	1889.6.8:56	330	Kiu Kiang
Opsariichthys uncirostris	1901.3.6:9	Skeleton	Ningpo
Opsariichthys uncirostris	1923.3.5:6–12	152	Seoul
Oreinus sinuatus	1889.2.1:64–72	177–205	Simla
Oreoleuciscus pewslowi	1975.1.17:259–265	118–178	Mongolia
Oreoleuciscus potanini	1891.10.7:26–27	174	Mongolia
Oxygaster anomalura	1881.3.21:3	195	Sarawak
Parabramis pekinensis	1936.10.19:22–23	125	Hankow
Parabramis pekinensis	1889.6.8:46–53	235	Kiu Kiang
Parapelecus argenteus	Unregistered	166	China
Pelecus cultratus	1879.11.14:36	Skeleton	Syr Darya
Pelecus cultratus	1966.2.22:1–2	174, 175	Romania
Phoxinus lagowskii	1974.8.6:21–30	81	Onon R. Mongolia
Phoxinus phoxinus	1967.12.18:1–13	66	Kysuka R.
Pseudaspius leptocephalus	1925.8.6:28	137	Amur R.
Pseudolaubuca sinensis	1889.6.24:61	Skeleton	Kiu Kiang
Pseudolaubuca sinensis	1889.6.24:59–60	195	Kiu Kiang
Pseudoxygaster gora	1934.10.7:54	137	Allahabad
Rasbora argyrotaenia	1974.10.10:1801–1805	50–79	Bali
Rutilus friesii	Unregistered	Skeleton	L. Derkus
Rutilus rutilus	Unregistered	Skeleton	England
Rutilus rutilus	Unregistered	Alizarins; 66, 76, 77	England
Salmostoma bacaila	1889.9.26:145–154	90, 107	Rajputana
Salmostoma sardinella	1891.11.30:374–383	85, 98	Sittang R.
Saurogobio dumerili	1889.6.24:21	Skeleton	Kiu Kiang
Scardinius erythropthalmus	1867.4.2:7	Skeleton	Holland
Schizothorax esocinus	1870.11.30:40	Skeleton	Kashmir
Schizothorax esocinus	1870.11.30:39	260	Kashmir
Schizothorax grahami	1969.4.15:118	184	Kuan Hsien

Species	BMNH register number	Type of preparation and standard lengths (mm) of alcohol preserved specimens	Locality
Semiplotus macclellandi	1889.2.1:869	Skeleton	Assam
Squaliobarbus curriculus	1889.6.8:34–38	138	Kiu Kiang
Squaliobarbus curriculus	1888.5.15:29	Skeleton	Tchang
Varicorhinus beso	1968.7.24:18–19	Alizarins; 80, 114	L. Tsana
Varicorhinus steindachneri	1910.11.28:158	Skeleton	Lucalla R.
Varicorhinus tanganicae	1906.9.6:11	Skeleton	L. Tanganyika
Zacco platypus	1865.5.2:30	Skeleton	China
Zacco platypus	Unregistered	80	Locality unknown
Zacco spilurus	1939.3.23:14–16	74	Kowloon
Zacco spilurus (Types)	1956.2.25:1–5	34·5–46	Hong Kong
Zacco temmincki	1905.6.7:61–65	150	Japan

In addition to being dissected, all the alcohol preserved specimens were radiographed.

Abbreviations used in text figures

Skeletal elements

AA	Anguloarticular
AHY	Anterohyal
APTE	Autopterotic
BB 1–4	Basibranchials
BO	Basioccipital
BSR	Branchiostegal rays
C 1–5	Ceratobranchials
CIM	Cranial intermuscular bones
CL	Cleithrum
CLA	Claustrum
COR	Coracoid
D	Dentary
DHY	Dorsohyal
DPT	Dermopterotic
DSP	Dermosphenotic
E	Ethmoid
ECT	Ectopterygoid
ENT	Entopterygoid
EP	Epural
EPI 1–4	Epibranchials
EPO	Epioccipital
ES	Extrascapular
EX	Exoccipital
F	Frontal
H	Hyomandibula
HB 1–4	Hypobranchials
HF	Hyomandibular fossa
HY 1–6	Hypurals
IC	Intercalar
IF	Infrapharyngobranchial
INC	Intercalarium
IO	Infraorbitals
IOP	Interoperculum
KE	Kinethmoid
LE	Lateral ethmoid

LF	Lateral foramen
LP1	Lateral process of the 1st vertebra
LP2	Lateral process of the 2nd vertebra
MAX	Maxilla
MC	Mesocoracoid
MET	Metapterygoid
METP	Metapterygoid process
N	Nasal
NC	Neural complex of Weberian apparatus
NP2	Neural plate of 2nd vertebra
NP3	Neural plate of 3rd vertebra
OP	Operculum
OS	Orbitosphenoid
OSS	Os suspensorium
PA	Parietal
PAL	Palatine
PE	Preethmoid
PC	Postcleithrum
PH	Parhypural
PHY	Posterohyal
PMX	Premaxilla
PO	Preoperculum
PP	Pharyngeal process
PR4	Lateral process of 4th vertebra (modified pleural rib)
PRO	Prootic
PS	Parasphenoid
PTF	Posttemporal fossa
PTS	Pterosphenoid
PTT	Posttemporal
PU1+U1	Fused preural and ural centra
Q	Quadrate
RA	Retroarticular
SCA	Scaphium
SCP	Scapula
SE	Supraethmoid
SN	Supraneural
SO	Supraoccipital
SOR	Supraorbital
SP	Autosphenotic
STF	Subtemporal fossa
SUB	Suboperculum
SY	Symplectic
TR	Tripus
UN	Uroneural
V	Vomer
VHY	Ventrohyal

Muscles and soft tissues

A1, A2, A3	Divisions of the *adductor mandibulae* muscle
aap	*Adductor arcus palatini*
ah	*Adductor hyomandibulae*
ct	Connective tissue
do	*Dilatator operculi*
hh	*Hyohyoidei*
im	*Intermandibularis*
km lig	Kinethmoid–maxillary ligament
lap 1, 2	Divisions of the *levator arcus palatini*
lig	Ligament
lo	*Levator operculi*

lsa	Ligamentous sheet connecting supraneural to supraoccipital
lsb	Ligamentous sheet connecting neural complex to supraoccipital
obv 1–3	*Obliqui ventrales*
pce	*Pharyngoclavicularis externus*
pci	*Pharyngoclavicularis internus*
ph	*Protractor hyoidei*
rv 1–3	*Recti ventrales*
sb	Swimbladder
sth	*Sternohyoideus*
tf	Tendinous fascia of *adductor mandibulae* A3
tlap	Ventral tendon of *levator arcus palatini*
tv	*Transversus*

Luciobrama macrocephalus (Lacepède)

(Fig. 1)

Synodus macrocephalus Lacepède, 1803, *Hist. Nat. Poiss.* **5** : 322, pl. IX, fig. 1 (described from a Chinese drawing).
Luciobrama typus Bleeker, 1870, *Versl. Meded. K. Akad. wet. Amst.* (2) **4** : 252 (Yangtse-Kiang).
Luciobrama macrocephalus: Bleeker, 1873, *Ned. Tijdschr. Dierk* 4 : 89 (re-description).

Luciobrama is a monotypic genus (see p. 60) of east Asian and Chinese piscivorous cyprinids (see Nichols, 1925 & 1943 for a general account of this habit in the cyprinids). Stomach contents that I have examined have revealed the remains of small (*ca* 80–100 mm SL) cyprinid fishes. Specimens of *Luciobrama macrocephalus* grow to large size; Kimura (1934) records total lengths of over 700 mm and weights of 1000 g.

The external morphology of this fish has been described adequately by Bleeker (1873), Rendahl (1928), Kimura (1934) and Lin (1935). Kimura (*op. cit.*) also cited all references to the species up to that date. Since then the following accounts have been published. Chu (1935) gave an account of scale morphology and described the pharyngeal bones and teeth; Nichols (1943) and Wu (1964) both gave descriptions and noted the distribution of the species. It is unnecessary to repeat the detailed descriptions of external characters given by these authors, save to note the absence of barbels, the ellipsoid shape of the orbit and the small scales (up to 155 in the lateral line). Nuptial tubercles have not been detected in any specimens examined, but have been reported as occurring in this species (see review by Wiley & Collette, 1970).

Osteology

Circumorbital series (Fig. 2)

The first *infraorbital* (lachrymal) is an almost square plate bearing 12 pores of the lateralis canal along its ventral border.

The second infraorbital is very narrow and borders the entire ventral margin of the orbit. It is joined to the third just below the posterior border of the eye.

The third infraorbital is lamellate, the lateralis canal bearing 6–7 pores. It is an elongate bone extending in an almost horizontal plane to a point well beyond the posterior margin of the eye before joining the fourth infraorbital.

The fourth infraorbital is reduced to the canal tube. It diverges from the third at an angle of about 45° across the postorbital part of the head.

The fifth is minute and is sometimes fragmented. It consists of only the canal tube.

(See page 26 for further discussion of these bones.)

The *supraorbital* (SOR, Figs 3 & 5) is large being bordered anteriorly by the lateral ethmoid and latero-posteriorly by the frontals.

Ethmo-vomerine region

The *kinethmoid* (KE, Fig. 7) is a short columnar bone, the dorsal surface bears a wedge-shaped groove and the ventral surface is rounded. It is connected by two ventral ligaments to the heads of the vomer and by laterally extending ligaments to the maxillary ascending processes.

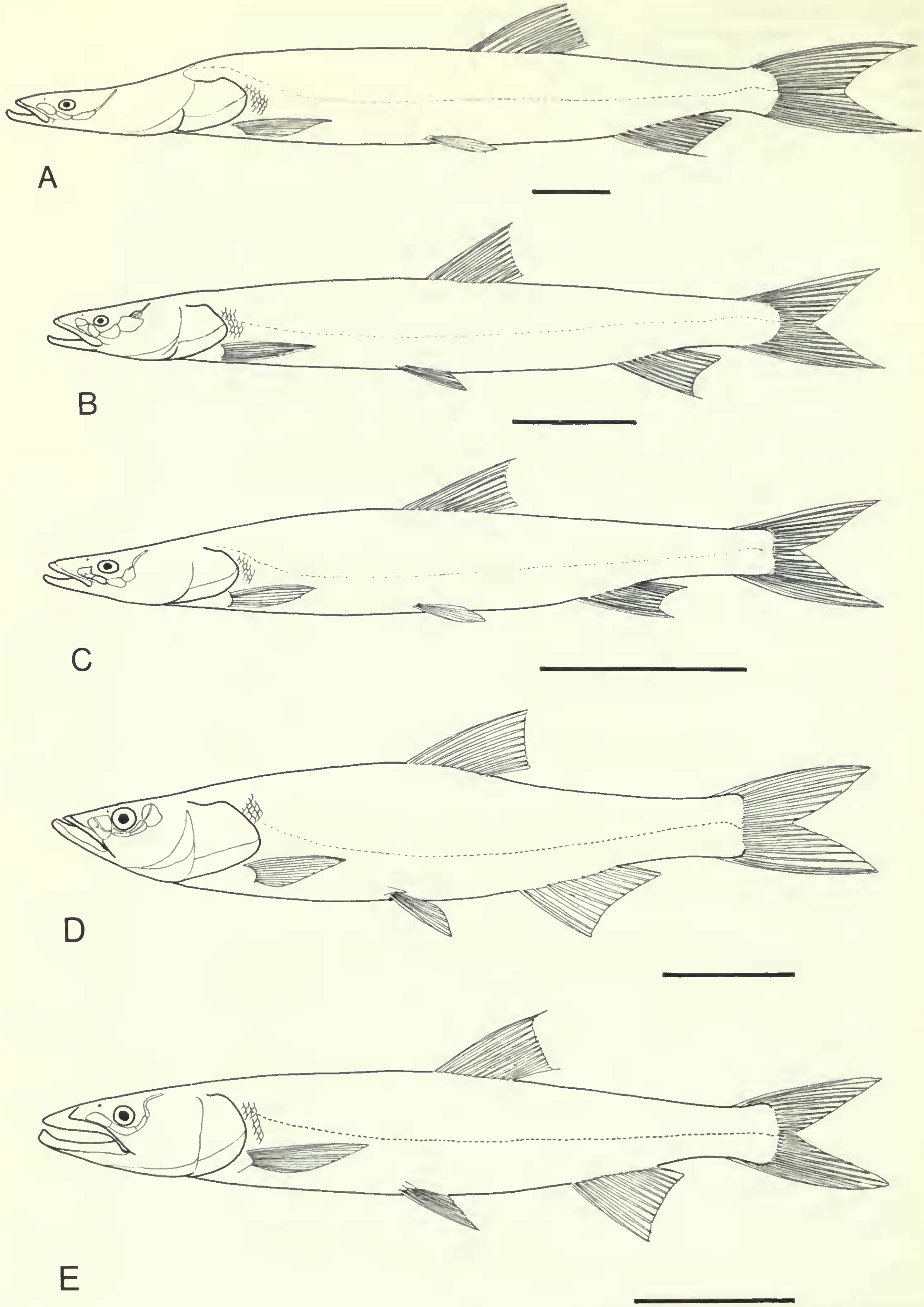

Fig. 1 Outline drawings of: A. *Luciobrama macrocephalus*, B. *Aspiolucius esocinus*, C. *Pseudaspius leptocephalus*, D. *Aspius vorax*, E. *Elopichthys bambusa*. Scale = 5 cm.

The *supraethmoid* (SE, Figs 3, 4 & 5) is narrow with thin wing-like extensions posteriorly. Laterally the bone is bordered by the nasals and posteriorly by the frontals. The anterior border is rounded with a median notch.

The *ethmoid* (E, Figs 3 & 4) underlies the supraethmoid and overlies the vomer. It is bifurcated anteriorly, the two short arms provide the medial surfaces of the fossae for the preethmoids. Antero-dorsally there is a small foramen separating the bone from the supraethmoid. Posteriorly there is a wide synchondrosis with the lateral ethmoid.

The *lateral ethmoids* (including fused prefrontals; LE, Figs 3, 4 & 5) extend to protrude well beyond the lateral margins of the cranium. Basally each bone is triangular, supporting anteriorly a thick, curved ascending wall which connects the supraorbital. Posteriorly it extends as a thin wall meeting the orbitosphenoid in a synchondrosis. Dorsally, each bone is overlain by its corresponding frontal; ventrally, contact is made with the parasphenoid. Medially, the lateral ethmoids are in contact.

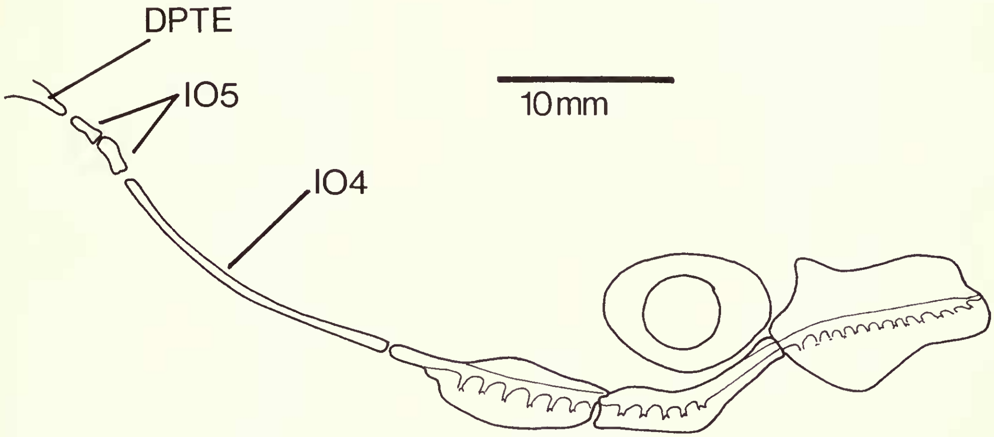

Fig. 2 *Luciobrama macrocephalus*, infraorbital series.

The *vomer* (V, Figs 4 & 5) is a thin, lamellate bone extending posteriorly to a point well beyond the centre of the orbit. It is overlain by the parasphenoid and the ethmoid. Anteriorly it flares into the shape of a double club, the arms of which provide the lower surfaces of the preethmoid fossae.

The *preethmoids* (PE, Figs 3 & 4) are irregular ovate bones articulating with the ethmoid and the vomer. They are covered by the cartilage upon which rest the autopalatines.

The *nasals* (N, Figs 3 & 4) border the supraethmoid anteriorly and the frontals posteriorly. They are in the form of long tubes bearing 9–10 pores. Laterally each nasal is attached by skin to the first infraorbital.

The *frontals* (F, Figs 3, 4, 5 & 6) are extremely long and narrow, sutured for their entire length. Anteriorly their lateral borders slope downward to contact the supraorbitals. The canal tube runs along the lateral edge of each bone from the anterior edge of the pterotic in an almost straight line to the nasal. It bears 22 pores.

Orbital region

The *orbitosphenoids* (OS, Figs 4, 5 & 6) are greatly depressed bones 'sandwiched' between the frontals and the parasphenoid. Contact with the parasphenoid is along a third of that bone's orbital length. Anteriorly, the orbitosphenoids join the lateral ethmoids by a wide synchondrosis. Dorso-posteriorly, each bone extends as a long arm which diverges slightly from its fellow. These arms contact similar anterior extensions of the pterosphenoid. Posteriorly, the lower part of each orbitosphenoid is directed medially and meets its partner in the midline to form a narrow, wedge-shaped septum. (This is not the 'orbitosphenoid septum' referred to later in this

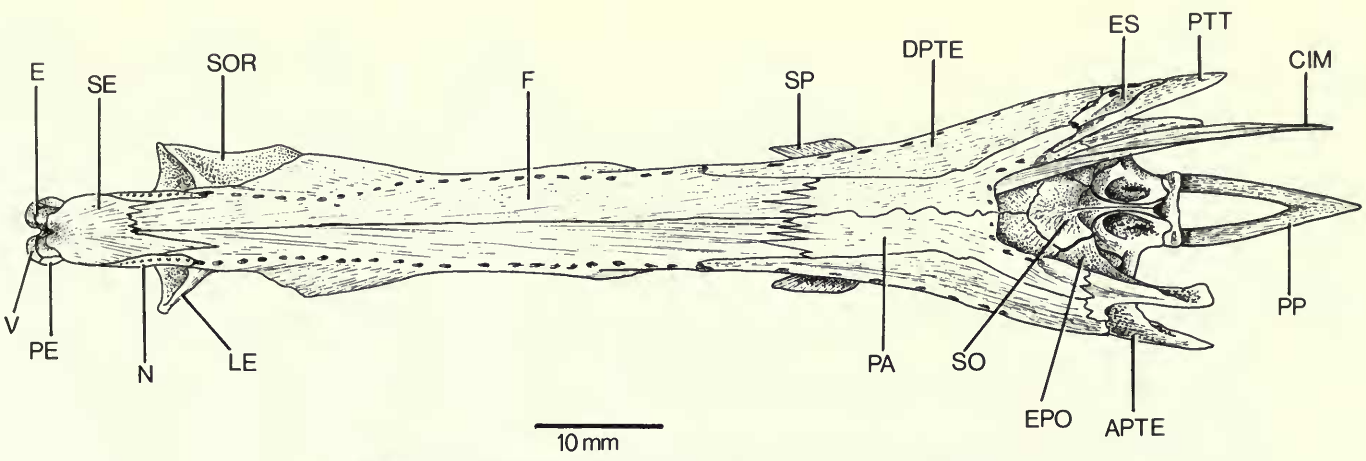

Fig. 3 *Luciobrama macrocephalus*, neurocranium, dorsal view.
Some bones are removed from the left-hand side of the skull to show the underlying elements.

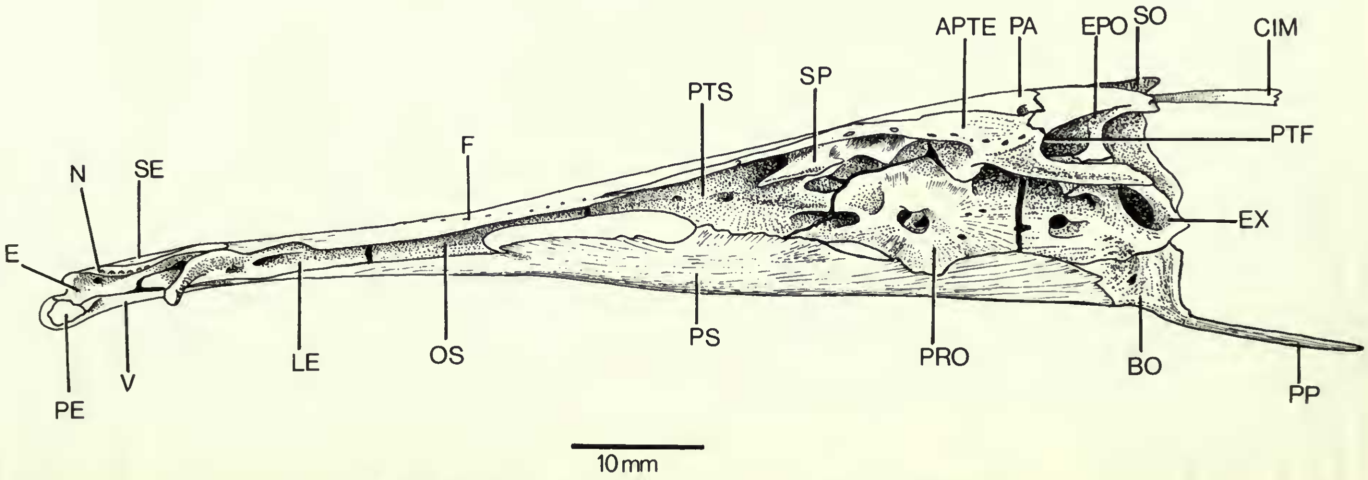

Fig. 4 *Luciobrama macrocephalus*, neurocranium, lateral view.

paper as occurring in other cyprinids (p. 32), in those cases the septum extends from the ventral surfaces of the bones.)

The *pterosphenoids* (PTS, Figs 4, 5 & 6) are extensive, forming almost half the length of the orbito-otic region. Each bone is produced into an anterior process along the ventral surface of the frontal which contacts the corresponding posterior extension from the orbitosphenoid. The posterior dorsal margin is sutured to the autosphenotic. Latero-posteriorly the bone extends as a wide branch which forms the anterior wall of the leading hyomandibular fossa. Below this the pterosphenoid border is concave, this concavity forming part of the border of the trigemino-facialis foramen; the lateral surface at this point is deeply grooved to allow for the nerve pathways. Ventrally, there is an extensive connection with the wide ascending wing of the parasphenoid. The pterosphenoids are narrowly separated from each other leaving only a small optic foramen.

The *parasphenoid* (PS, Figs 4, 5 & 6) is wide anteriorly, the ventral surface below the lateral ethmoids is flat but becomes concave below the orbitosphenoids; beyond this point the bone narrows and deepens, the sides becoming thin walls which rise gradually until, as wide ascending processes, they contact the ventral margins of the pterosphenoids. The posterior border of the ascending process is separated from the pterosphenoid and prootic by an extensive hypophysial foramen. The dorso-posterior part of the parasphenoid is first overlapped by, and then runs abutted with, the prootic, followed by the anterior part of the exoccipital. The posterior border of the parasphenoid is sutured against the basioccipital. The ventral surface of the parasphenoid is rounded below the ascending processes, flaring slightly and becoming flattened below the prootic with a slight medial groove developing posteriorly. This groove leads into the aortic foramen of the basioccipital. The posterior part of the parasphenoid forms the floor and walls of the myodome.

Otic region

The *prootics* (PRO, Figs 4, 5 & 6) are large, forming long dorsal connections with the autosphenotics. Anteriorly, the border of each prootic with the parasphenoid is interrupted by the large trigemino-facialis foramen. Postero-ventrally, part of the prootic extends to overlap the parasphenoid. Anteriorly, each bone is in the form of a wedge-shaped arm which inserts partly between the pterosphenoid and the parasphenoid; dorso-posteriorly, it contacts the pterotic. The area between the sphenotic and pterotic is bevelled and forms part of the hyomandibular facet. Postero-medially, the prootic forms the lower medial wall of the subtemporal fossa. Its posterior border is sutured to the epioccipital.

A posterior myodome is present (ascertained by radiographs) and appears similar to that described for *Aspius* by Oliva and Skořepa (1968).

The *pterotics* (APTE, Figs 3, 4, 5, 6 & 32) dorsally border the parietals and the frontals extending forward as narrow triangles overlying the autosphenotics. The outer margin of each bone bears the canal which contains 13 pores. Posteriorly, the pterotic is recessed as a facet for the hyomandibula (a continuation of that feature on the autosphenotic and prootic). Ventrolaterally, the surface is arched, the posterior foot of the arch joining the epioccipital and forming the outer roof of the subtemporal fossa (STF, Fig. 5). The lateral border continues posteriorly as a thick spine. Medially, the pterotic meets the epioccipital to form the high vaulted subtemporal fossa.

The pterotic also contributes substantially to the formation of the posttemporal fossa (PTF, Figs 4 & 32) where it provides the lateral wall, part of the roof and the floor.

The *basioccipitals* (BO, Figs. 4, 5 & 32) are sutured to the parasphenoid anteriorly and to the epioccipitals dorsally. Medially they extend forward between the prootics and form part of the roof of the posterior myodome. There is no obvious bulla acoustica lagenaris.

From the ventral surface of each bone there extends posteriorly two processes which fuse distally to form the pharyngeal process (PP, Figs 3, 4 & 5). The 'masticatory plate' is virtually absent.

The *supraoccipital* (SO, Figs 3, 4 & 32) is bordered anteriorly by the parietals and laterally by the epioccipitals, the whole area forming an almost flat platform. Medially, the bone rises as a low ridge which extends posteriorly as a thin plate-like process. This supraoccipital process barely rises above the highest level of the skull roof.

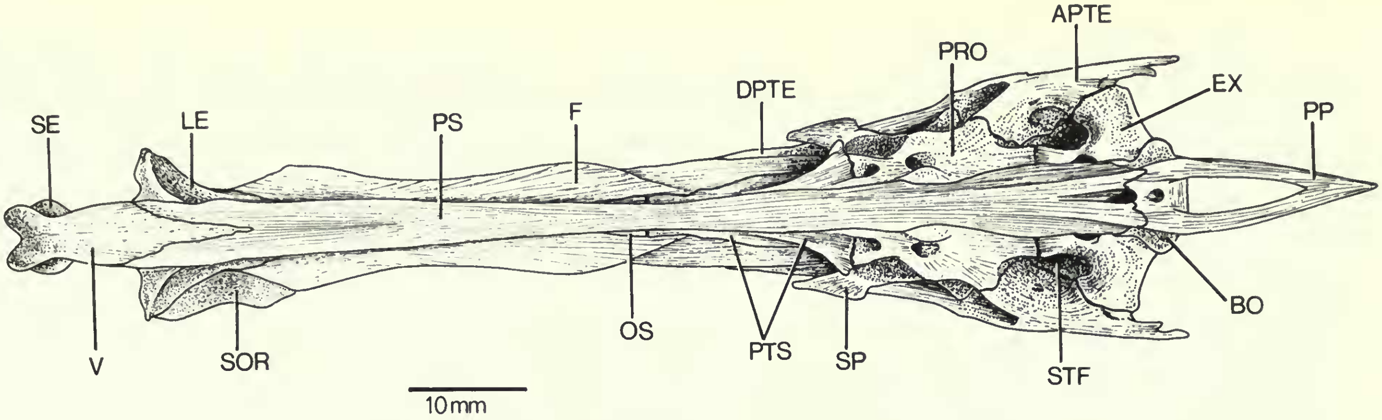

Fig. 5 *Luciobrama macrocephalus*, neurocranium, ventral view.

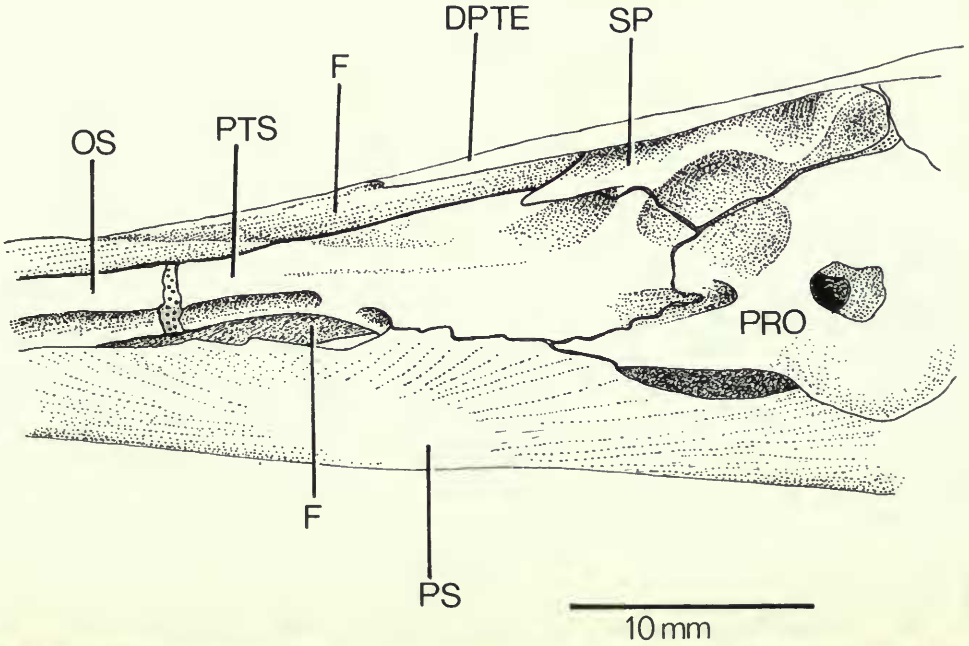

Fig. 6 *Luciobrama macrocephalus*, neurocranium, ventro-lateral aspect of the orbito-otic region.

The *intercalar* is absent.

The *parietals* (PA, Figs 3 & 4) are elongate and join the frontals anteriorly. Laterally they are bordered, for part of their length, by the pterotics. Posteriorly, the parietals are deeply recessed, the roof of this recess providing insertion for the epaxial musculature, and the lateral border origin for the cranial intermuscular bones.

The parietals gently slope posteriorly to join the supraoccipital. The presence of the transverse occipital sensory canal is indicated by four pores on the surface of each bone.

The *posttemporals* (PTT, Fig 3). Each is a paddle-shaped bone, the stem of which extends dorso-anteriorly at an angle of 45° to rest along the epioccipital. The lamellate 'paddle' of the bone is joined to the supracleithrum. Ventrally, between the posttemporal and the pterotic border, there lies a long narrow *extrascapular* (ES, Fig 3).

The *autosphenotics* (SP, Figs 3, 4, 5 & 6) are long depressed bones overlain by the pterotics. The anterior part of each sphenotic projects laterally from beneath the cranial border as a sloping shelf. Posteriorly, the dorsal surface of the bone presents two undulations which form a lateral cavity roofed by the pterotic. From this cavity arises the *dilatator operculi* muscle. The undulations of the bone also provide, ventro-laterally, the roofs of two deep facets for the hyomandibular condyles. The posterior facet is continued onto the pterotic and ventrally onto the prootic.

No *dermosphenotic* can be identified. (See page 28 for comments on this bone.)

The *exoccipitals* (EX, Figs 3, 4, 5 & 32) are seen laterally as almost square bones. Dorso-medially, each bone is in contact with the epioccipital and forms the inner surface of the subtemporal fossa. Posteriorly, the arm containing the semi-circular canal is compressed and is directed laterally to contact the descending arch of the pterotic. Medially, the exoccipital is curved around to form the border of the lateral occipital foramen. Its dorsal border is sutured to the epioccipital and supraoccipital. Ventrally, it is bordered by the epioccipital and the basioccipital. The glossopharyngeal foramen is situated in the centre of the bone's lateral face.

The *epioccipitals* (= epiotic; see Patterson, 1975) (EPO, Figs 3, 4 & 32). The lateral face of each bone forms the medial wall of the posttemporal fossa. Dorso-medially, it is suturally united with the supraoccipital and together the bones form a platform posterior to the parietal. Ventrally, the epioccipital contacts the exoccipital and prootic. Dorso-laterally, it joins the pterotic and forms the roof and the upper part of the lateral wall of the subtemporal fossa.

The upper jaw (Fig. 7)

Each *premaxilla* (PMX) is in the form of a slender rod with a large anterior ascending process which is ligamentously connected to the kinethmoid. Each premaxilla is curved gently mesad to meet its counterpart, to which it is attached by a thick band of ligamentous tissue.

Each *maxilla* (MAX) is a large triangular bone. Anteriorly, it is produced into a large knob-like process which fits into a concavity on the premaxilla. Ventrally there is a process which runs mesad below the premaxilla to contact its fellow from the opposite side.

The dorsal border of the maxilla is expanded into a large plate-like process (termed here the palatine process). Between this and the anterior ascending process runs the ligament joining the maxilla and the palatine. The posterior margin of the bone is concave, ventrally it contacts the premaxilla.

The lower jaw (Fig. 8)

Each *dentary* (D) is a long canoe-shaped bone curving gently mesad to join its partner. The coronoid process is deep with a narrow convex border. Ventrally the mandibular lateral line canal bears 20 pores.

The *anguloarticular* (AA) is a large bone sloping gently dorsad to meet the coronoid process of the dentary. The articular surface for the quadrate is almost rectangular. The anguloarticular bears 5 pores of the mandibular canal.

The *retroarticular* (RA) is a very thin wedge of bone lying ventrally.

Hyopalatine arch (Fig. 9)

The *hyomandibula* (H) is broad and flat dorsally, the border shaped into two broad articular

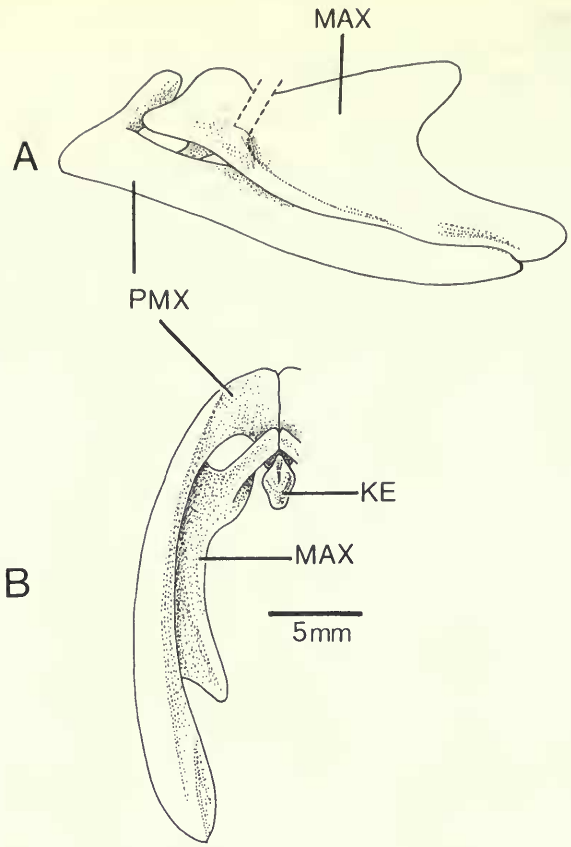

Fig. 7 *Luciobrama macrocephalus*, upper jaw. A. Lateral view. B. Ventral view.

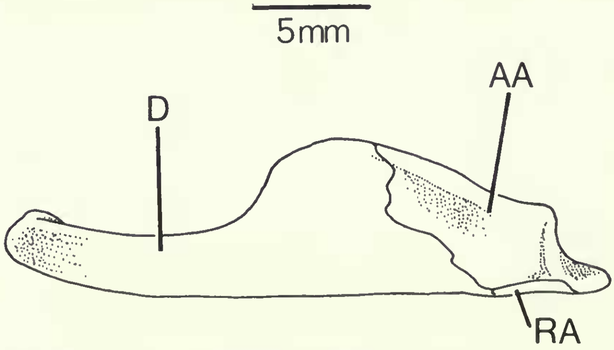

Fig. 8 *Luciobrama macrocephalus*, lower jaw, lateral view.

heads. The anterior of these heads fits into the facet formed by the sphenotic, posterior part of the pterosphenoid and the dorsal margin of the prootic. The posterior head fits into the facet formed by the sphenotic, the prootic and the pterotic.

The lower limb, or shaft, is long and broad, directed at an angle of 45° to the vertical.

The anterior border of the hyomandibula is concave, the posterior is produced into a small condyle which articulates with the operculum. The lateral face bears a weak depression.

The *quadrate* (Q) is a low elongate bone which is produced ventro-posteriorly into a triangular extension covered partially by the symplectic and preoperculum. The dorsal margin is horizontal and extends anteriorly to above the anguloarticular. Just posterior to the articulation with the anguloarticular is a large foramen. There appears to be no nerve or vessel of any kind passing through this aperture but only fibres of the connective tissue which line the floor of the branchial cavity.

There is a wide synchondrosis between the posterior border of the quadrate and metapterygoid.

The *symplectic* (SY) is a lanceolate bone and lies between the metapterygoid and the quadrate. The lateral surface bears a ridge from which originate some of the fibres of the *adductor mandibulae* muscle complex (see p. 21).

The *autopalatine* (PAL) is a thick rod-shaped element, forked anteriorly. The lateral fork provides the insertion for the maxillary ligament, the mesial process contacts the cartilage overlying the preethmoid.

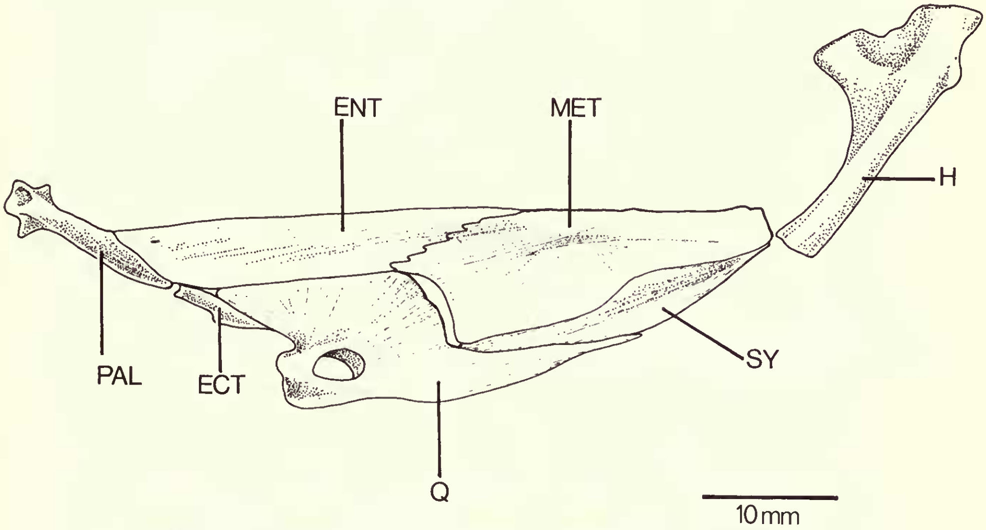

Fig. 9 *Luciobrama macrocephalus*, hyopalatine arch, lateral view.

No *dermopalatine is present.*

The *ectopterygoid* (ECT) is a thin gutter-like bone applied to the anterior border of the quadrate. Dorsally it contacts the entopterygoid. It is separated from the palatine by a wide area of cartilage.

The *entopterygoid* (ENT) is an extensive sheet of bone, the dorsal border of which is horizontal. Laterally it is overlapped by the quadrate and metapterygoid.

The *metapterygoid* (MET) overlaps the entopterygoid and ventrally partially overlaps the symplectic. The dorsal border is horizontal. The bone slopes mesad to the parasphenoid and a ridge is produced along the lateral face of the bone at the base of the slope.

The opercular series (Fig. 10)

The *preoperculum* (PO) is a large, broadly crescentic bone overlapping the anterior edge of the operculum and most of the interoperculum. There are 10 pores of the opercular–mandibular lateral line canal visible along its lower margin with 3 or 4 along the posterior border.

The *interoperculum* (IOP) is shaped like a broad knife blade. Its posterior border is rounded and overlaps the anterior margin of the suboperculum.

The *suboperculum* (SOP) is a narrow curved sheet of bone, its dorsal edge, apart from the posterior point, covered by the operculum.

The *operculum* (OP) is extensive. The dorsal margin is long and concave and is produced anteriorly into a long finger-like process to which is attached the *dilatator operculi* muscle. Mesially a thin strut, pierced ventro-anteriorly by three large foramina, extends caudal from the articular facet.

Hyoid arch (Fig. 11A)

The *interhyal* (IH) is a short flat element with a concave posterior border. The head bears a dorsally extended projection from which runs a ligament which passes between the symplectic and the shaft of the hyomandibula to insert on the ventro-posterior tip of the metapterygoid. This ligament is overlain by the connective tissue extending between the symplectic and the hyomandibula.

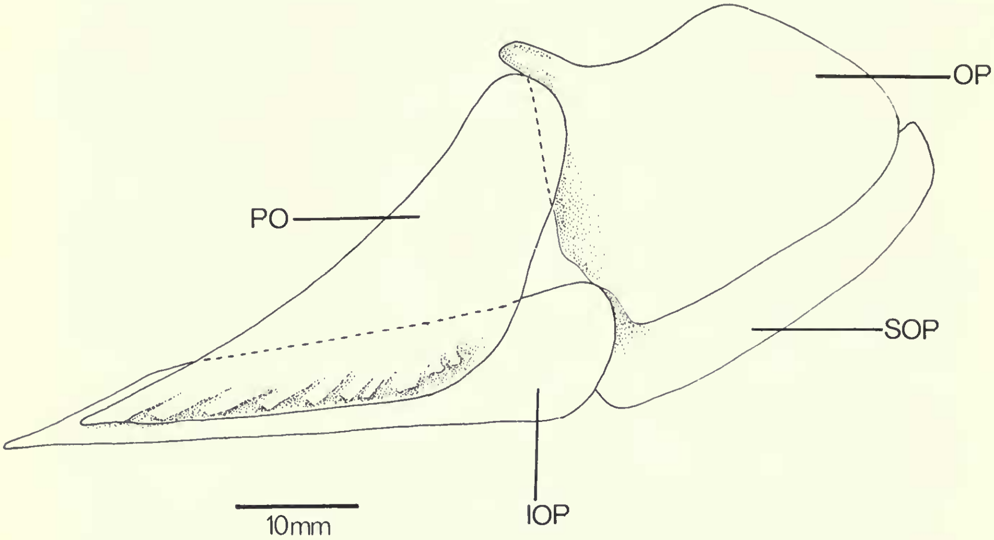

Fig. 10 *Luciobrama macrocephalus*, opercular series, lateral view.

Another ligament runs from the anterior edge of the interhyal to join the medial face of the preoperculum.

The *posterohyal* (PHY) is a thick triangular bone bearing one branchiostegal ray.

The *anterohyal* (AHY) is a thin-waisted element articulating anteriorly with the dorso- and ventrohyals. It bears two branchiostegal rays.

The *dorsohyal* (DHY) is small, and is in contact with the first basibranchial (basihyal); the *ventrohyal* (VHY) is thick, its lower surface bearing a fossa for the ligament connecting the urohyal. Its medial surface is joined to that of its opposite member by a ligament.

The *urohyal* (Fig. 11B) is extremely elongate, the ventral surface is flat, but bears a slight ridge posteriorly. A shallow vertical plate runs along the midline of the dorsal surface. Anteriorly the bone narrows into a neck from which arise two heads; these are connected to the ventrohyal by thick ligaments.

The *branchiostegal rays* (BSR 1, 2 & 3) are long lamellate bones, the first of which is thin and articulates with the ventral medial surface of the anterohyal; the second is expanded proximally into an anteriorly directed process. Articulation is on the lateral face of the anterohyal. The third is also expanded proximally and articulates with the lateral face of the posterohyal.

The branchial arches (Fig. 12)

There are two ossified *infrapharyngobranchials* (IF 2, 3), recognized as infrapharyngobranchials 2 and 3 (see Nelson, 1969). Cartilaginous elements are present between the first epibranchial and the second infrapharyngobranchial and between the fourth epibranchial and third infra pharyngobranchial. These elements most probably represent the 1st and 4th infrapharyngobranchials.

The *epibranchials* (EPI 1–4) number four. The first is wide with a blade-like posterior border overlapping the second. The third epibranchial bears a dorsal process overlapping the fourth.

The *certaobranchials* number the usual five (C 1–5). The first bears 6 long finger-like gill rakers; the second 9; the third 10 plus 6 along the medial surface; the fourth 7 plus 7. The fifth is the lower pharyngeal bone which bears a single row of 4–5 curved teeth. The bone is very thin and anteriorly elongate, curving gently mesad to ligamentously join its fellow. The pharyngeal bone and teeth have been described and figure by Chu (1935).

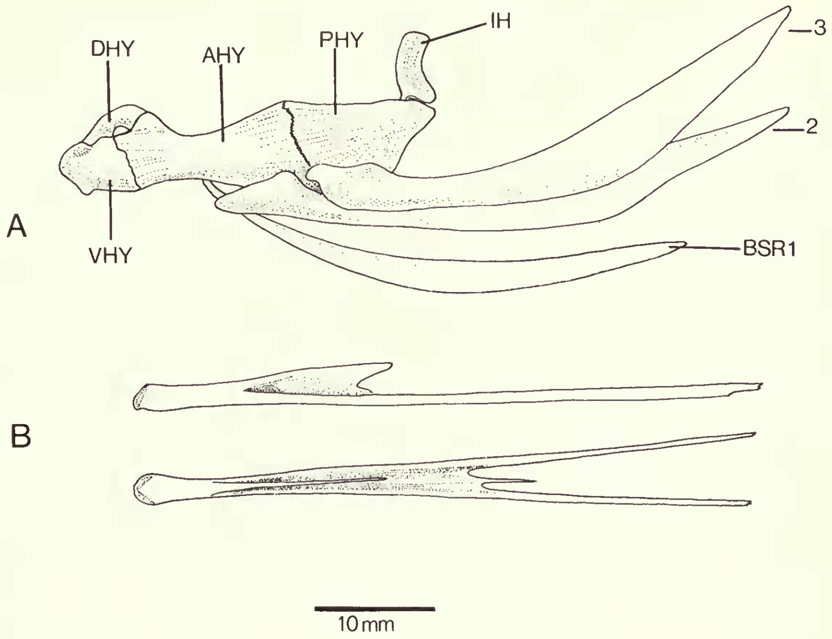

Fig. 11 *Luciobrama macrocephalus.* A. Hyoid arch, lateral view. B. Urohyal seen in (top) lateral and (bottom) dorsal views.

There are four *basibranchials* (BB 1–4). The first (basihyal) is a long thin rod in contact with the hypohyals. The second is flat and in contact with the 1st *hypobranchials* (HB1); the third is long, narrow-waisted and in contact with the 2nd hypobranchials; the fourth is thin and is curved ventrad.

Weberian apparatus and swimbladder (Fig. 13).

The 1st vertebra is a thin disc bearing lateral processes (LP1) from which a ligament extends to contact the medial face of the cleithra.

The second and third centra are fused dorsally, but ventrally they are clearly separated. The 2nd vertebra bears thick lateral processes which are inclined upward (LP2). The 3rd vertebra contains a lateral fossa for the articulation of the tripus. Extending dorsad from the second and third centra is the third neural plate (NP3). The dorsal border is triangular. On the anterior margin lies the second neural plate (NP2) which extends forward to contact the supraoccipital. Lying below the anterolateral border of the second neural plate is the *claustrum* (CLA) which is a cartilaginous cup-shaped structure. A ligament runs from each claustrum to insert upon the basioccipital.

Along the posterior margin of the third neural plate there rests part of the large neural complex (NC); see below.

The 4th vertebra bears stout lateral processes which become ventrally directed (pleural ribs, PR4). The medial surface of each extends inwards as an *os suspensorium* (OSS), a thin plate curving anteriorly so that its tip underlies the posterior edge of the 3rd vertebra. There is a short neural spine on the 4th vertebra, the dorso-anterior surface of the spine supports the posterior half of the neural complex.

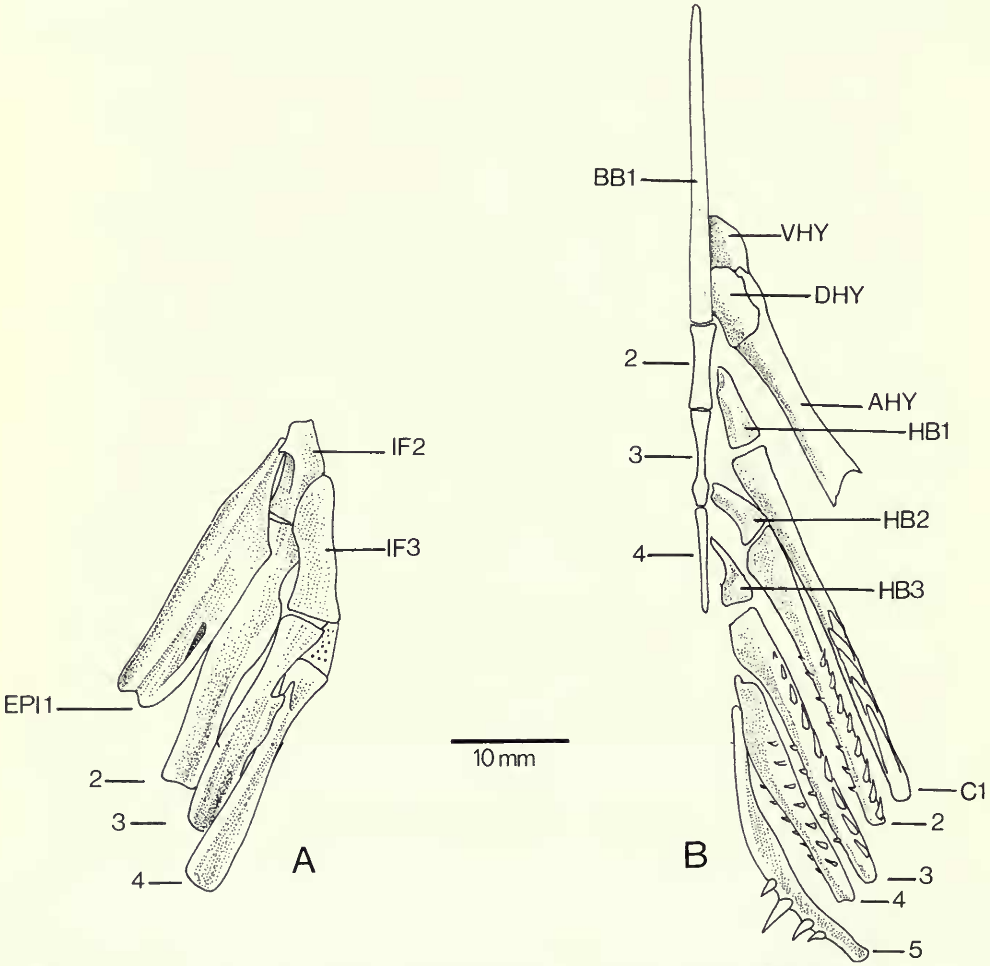

Fig. 12 *Luciobrama macrocephalus*, branchial arches. A. Upper arch, left side, dorsal view. B. Lower arch, right side and basibranchials, dorsal view.

The *scaphium* (SCA) is rounded and capped dorsally by the claustrum. Ventrally it articulates with a groove along the top of the first centrum and from a depression on its posterior face a ligament runs to connect this bone with the intercalarium.

The *intercalarium* (INC) articulates in a fossa situated below the third neural plate which overlaps the second vertebra. A ligament (a continuation of that extending from the scaphium) attaches ventrally and continues to insert upon the leading edge of the tripus.

The *tripus* (TR) is a thin triangular plate articulating with the third vertebra. Anteriorly it contacts the lateral process of the second vertebra (LP2); posteriorly its tip connects with the medial face of the process emanating from the 4th vertebra (PR4).

The *neural complex* (NC) which lies across the 3rd and 4th vertebrae is an irregularly shaped bone. The dorsal surface is grooved and posteriorly a supraneural plate (possibly two fused supraneurals) slides into the groove. This plate is connected to the supraoccipital by a ligamentous sheet (lsa) which runs across the anterior part of the grooved upper margin of the neural complex. The anterior border of the neural complex is concave and a separate ligamentous sheet (lsb) connects this to the supraoccipital.

The *swimbladder* (sb) is an elongate cigar-shaped structure extending posteriorly to above the first anal fin ray. It is bipartite.

The pneumatic duct is very long and runs along the dorsal surface of the gut from its exit at the anterior of the alimentary canal to its entry into the posterior division of the swimbladder.

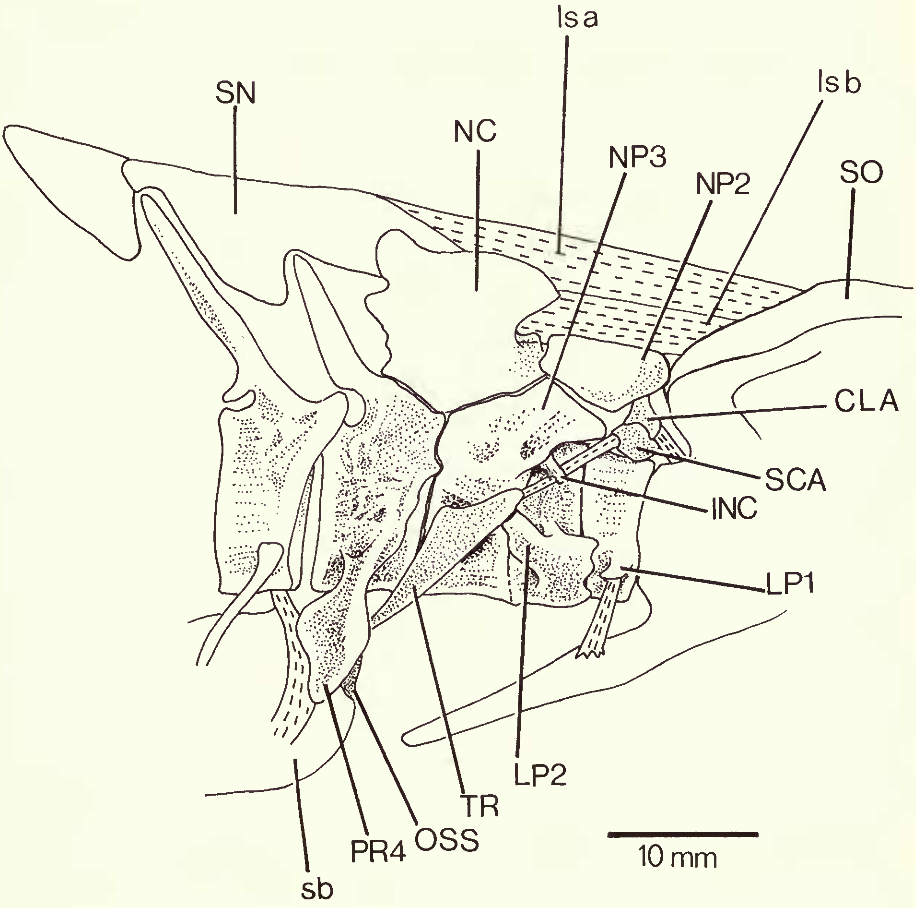

Fig. 13 *Luciobrama macrocephalus*, Weberian apparatus, lateral view.

Pectoral girdle (Fig. 14A)

The *cleithrum* (CL). The horizontal limb of the cleithrum is narrow and bifurcated anteriorly. The tip of the limb lies on a perpendicular with the posterior margin of the prootic. The ascending limb has a slightly curved hind margin; it is aligned almost vertically.

The *postcleithrum* (PC) is a short spine-like process.

The *supracleithrum* (SCL) is a small blunted crescentic element attached to the upper third of the cleithral limb. It attaches to the inner face of the posttemporal.

The *coracoid* (COR) is a narrow, flat bone posteriorly joined to the cleithrum along a flat lateral extension; anteriorly, there is a narrow area of attachment along the leading edge of the cleithrum. The coracoids diverge from each other and meet only along the anterior margin.

The *mesocoracoid* (MC) is a wide bridge of bone extending between the cleithrum and the coracoid.

The *scapula* (SCP) lies against the medial face of the cleithrum below the mesocoracoid. It joins the posterior border of the coracoid and provides an articular surface for the four plate-like *proximal radials*.

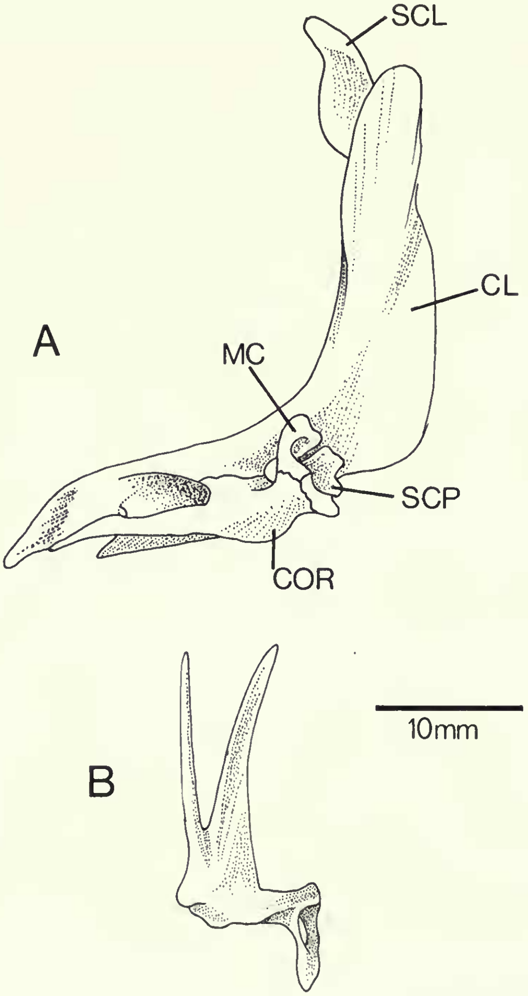

Fig. 14 *Luciobrama macrocephalus*. A. Pectoral girdle, lateral view. B. Pelvic girdle, left side, dorsal view.

Pelvic girdle (Fig. 14B)

The pelvic bones are deeply forked, the thin dagger-like arms narrowly diverging. The ischiac process is wide and is joined to its fellow along the apposed medial face.

Vertebral column

There is a total of 55 vertebrae (including the four forming the Weberian apparatus), comprising

30 precaudal (without a haemal spine), 20 caudal and the fused preural and first ural vertebrae. All the centra are of almost the same length.

There are 12 *supraneurals* lying between the neural spines of the 5th to 18th vertebrae. The first two supraneurals are expanded and contact the neural complex of the Weberian apparatus (see p. 18). The supraneurals become progressively thinner posteriorly; on a radiograph they are barely visible.

The *cranial intermuscular bones* (CIM, Figs 3 & 4) extend from the medial margin of the parietals and epioccipitals as thin rods which become lamellate and expand into 7 or 8 bones to lie above the Weberian apparatus.

The first of the *epipleurals* is associated with the 15th rib. They are exceedingly thin needle-like bones numbering 11–12. There are numerous *intermuscular bones* above the anal fin.

The first *pterygiophore* of the dorsal fin is expanded anteriorly. There are 9 dorsal and 11 anal pterygiophores. Two radials connect the pterygiophore with the fin ray (see p. 52).

Caudal fin skeleton (Fig. 15)

There are six hypurals (HY 1–6) of which the first is greatly expanded. The fused preural and ural centra (PU1 + U1) bear a knife-like neural spine. There is one large epural and a pair of small uroneurals (UN) above hypural 6. The parhypural (PH) bears only a slight hypurapophysis. The principal fin ray formula is I9 + 9I.

Cranial myology

Jaw and suspensorial muscles (Figs 16–19)

The postorbital region of *Luciobrama* is covered by thin skin, when this is removed there is exposed a large *adductor mandibulae* muscle. Two major divisions of this muscle can be distinguished, namely A1 and A2.

Adductor mandibulae A1 extends from the quadrate, symplectic and preoperculum. The anteroventral fibres run dorsad at an angle of 30°, those forming the dorsal border of the muscle run almost horizontally. Below the orbit the muscle is greatly thickened but becomes abruptly compressed prior to its insertion. The fibres insert upon a thick tendinous band which runs along the ventral border of the maxillary and is attached to that bone by connective tissue.

The maxilla has been described elsewhere (p. 13). A cartilaginous mass (car) fills the area bordered anteriorly by the concave dorsal edge of the maxilla, dorsally by the lateral ethmoid and medially by the dentary.

The large A2 extends from the lateral face of the preoperculum, the hyomandibula and the metapterygoid. The fibres running from the preoperculum and hyomandibula are orientated horizontally and form the lateral face of the muscle; those running from the metapterygoid are directed laterally at an angle of 40° to join the body of horizontal fibres. Anteriorly A2 is divided, each division inserting upon its own tendon. The tendon of the lateral division inserts upon the rim of the coronoid process of the dentary, that of the inner division on to the rim of the anguloarticular, just posterior to the outer tendon.

Adductor mandibulae Aw is absent. The medial face of the lower jaw is covered by a thick connective tissue which forms a cushion along the dorsal edge of the jaw (the lower lip), and at the articulation of the jaw is continuous with that tissue and skin covering the upper jaw.

The *levator arcus palatini* (lap) is an exceptionally well-developed muscle and to my knowledge is the most extensive described for any teleost although that of *Arapaima gigas* approaches this size (see Kershaw, 1976).

It originates from the ventral surface of the frontal, the pterotic and the sphenotic to insert upon the length of the entopterygoid, metapterygoid and on a sheet of thick connective tissue connecting the metapterygoid with the hyomandibula (ct, Fig. 17).

The ventral surface of the levator is bevelled to accommodate *adductor mandibulae* A2. The anterior border of the muscle forms the posterior border of the orbit.

When the outer layer of the muscle is removed (lap 1), two inner sections are revealed. The first (lap 2, Fig. 17) lies posteriorly and runs from a dorsal aponeurosis from which the *dilatator*

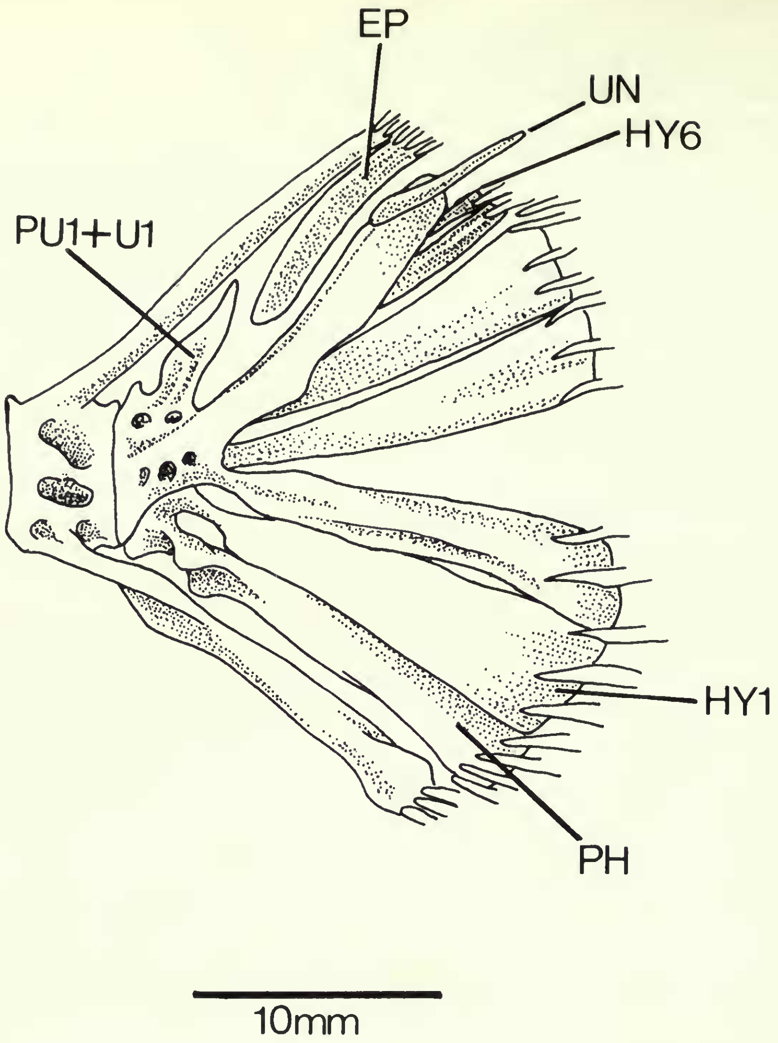

Fig. 15 *Luciobrama macrocephalus*, caudal fin skeleton, lateral view.

operculi also stems. The direction of its fibres is the same as that of the outer layer. Insertion is upon the lateral face of the hyomandibula.

The second element (ah, Fig. 17) lies against the pterosphenoid and parasphenoid. The fibres are orientated in the opposite direction to those of the other layers. Anteriorly, the muscle is bordered by a sheet of connective tissue which covers the lateral face of the pterosphenoid; posteriorly, it originates from the deep subtemporal fossa and inserts upon the medial face of the hyomandibula.

Ventral insertion of all the sections is along the medial dorsal edge of the ento- and metapterygoid.

The inner element is well differentiated from the rest of the *levator arcus palatini* and I interpret it as being the *adductor hyomandibulae* (which is also found in *Aspius* and some other genera; see p. 53).

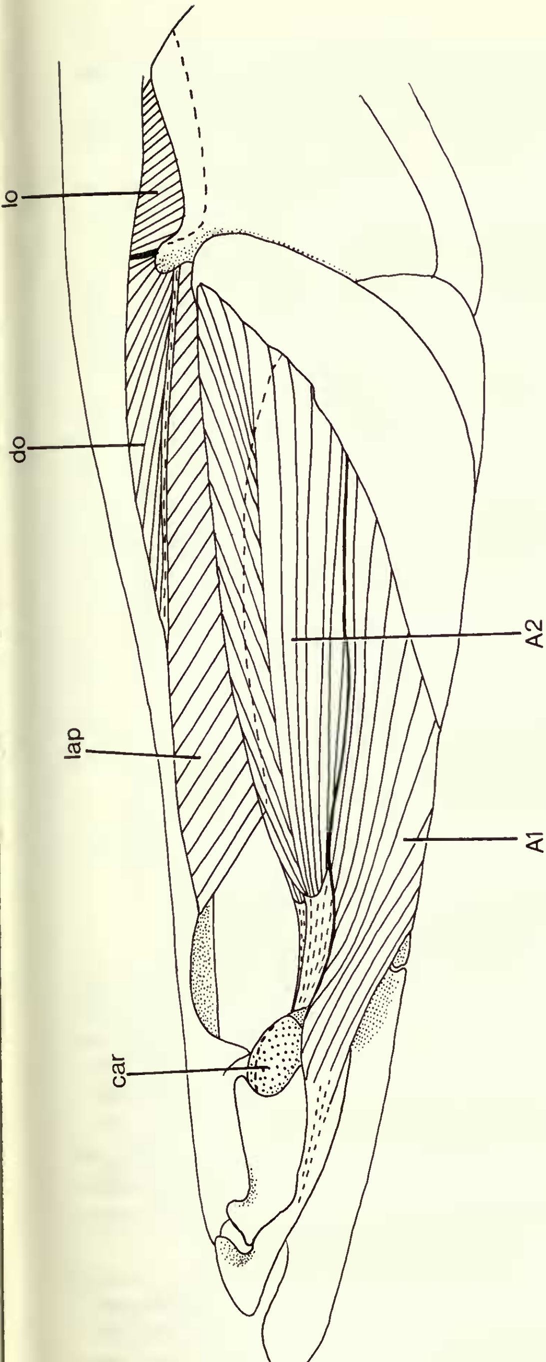

Fig. 16 *Luciobrama macrocephalus*, cranial musculature. Dotted lines indicate the ventral borders of the *levator arcus palatini* and the *levator operculi.*

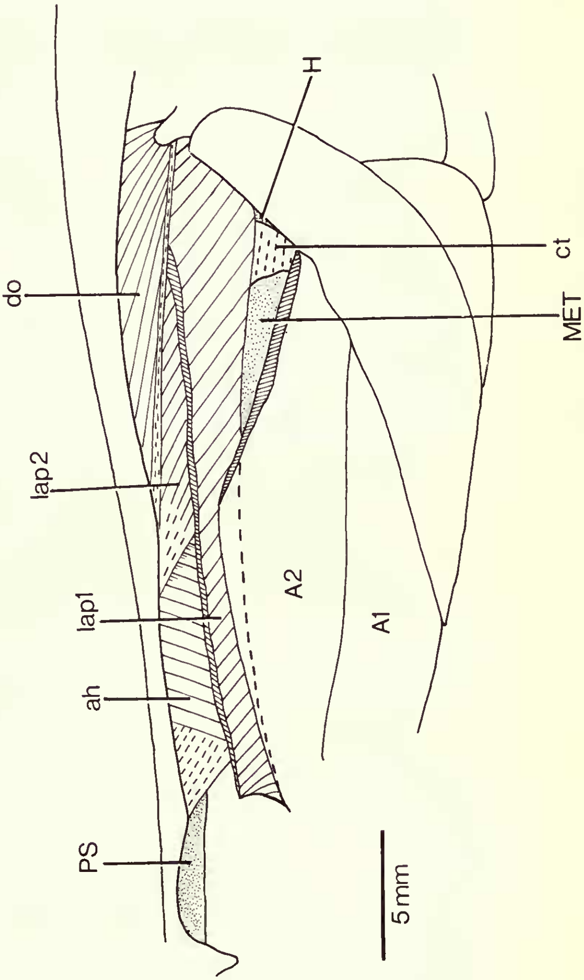

Fig. 17 *Luciobrama macrocephalus*, cranial musculature. Dissection of deeper muscle layers. The dorsal borders of the *adductor mandibulae* A1 and the *levator arcus palatini* 1 have been cut through.

The *adductor arcus palatini* is absent, but it would appear that the anterior extension of the *adductor hyomandibulae* is in fact fulfilling the function of the *adductor arcus palatini.*

The *dilatator operculi* (do) originates anteriorly from the aponeurosis which also gives rise to the inner section of the *levator arcus palatini*, and posteriorly from the lateral border of the pterotic. Some fibres also stem from the sphenotic process.

Insertion of the fibres is into a long tendon which forms the ventral border of the muscle and which joins the anterior process of the operculum. A thick band of tissue connects the lateral face of the opercular process with the pterotic.

The *levator operculi* (lo, Fig. 16) is a flat sheet of muscle running from the pterotic to the medial face of the operculum. The fibres run almost perpendicularly.

The *adductor operculi* is a thin conical muscle originating from the deep subtemporal fossa to insert upon the medial leading edge of the operculum anterior to the insertion of the *levator.*

Hyoid muscles (Fig. 18)

The *intermandibularis* (im) is very thin and ellipsoidal in cross-section. It is covered dorsally by skin and connective tissue, ventrally by the *protractor hyoideus.*

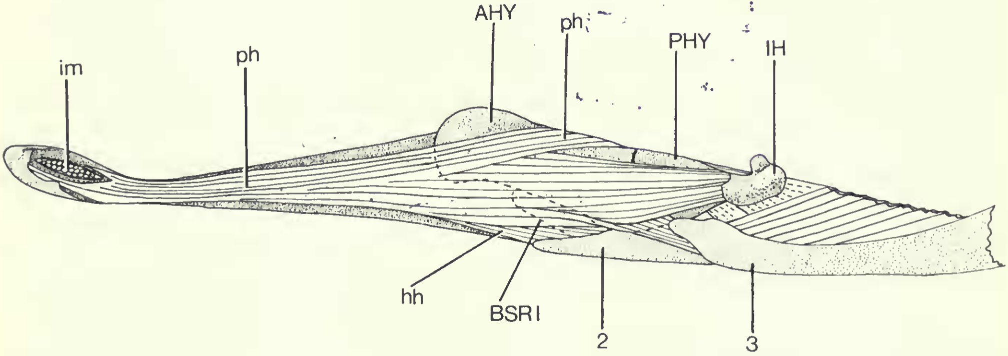

Fig. 18 *Luciobrama macrocephalus*, hyoid musculature. The hyal bones are those of the left side shown in lateral view. The first branchiostegal ray and ventral borders of other hyal bones are indicated by dashed lines. The dentary is of the right side and is shown in medial view.

The *protractor hyoidei* (ph) arise from the medial and lateral surfaces of the anterohyal and posterohyal. Those parts stemming from the internal surfaces of the bones overlap the dorsal edge of the anterohyal to pass laterally into the muscle body. The lateral origin is as far back as the interhyal. Small bundles of fibres also originate from the second and third branchiostegal rays. The two halves of the muscle join together and run as an elongate cone between the dentaries. Insertion is posterior to, and below, the *intermandibularis.*

The *hyohyoidei* (hh) are weakly developed. They lie as sheets of fibres between the branchiostegal rays. From the first branchiostegal ray the fibres run into tendinous bands which meet along a raphe below the dorso- and ventrohyals. Insertion is from the third branchiostegal ray onto the suboperculum.

It is not possible to distinguish *abductores* and *adductores* sections of this muscle and it would appear as Winterbottom (1974) noted in *Cyprinus* that the function of the *adductores* is taken over, in this case to a great extent, by the *protractor hyoidei.*

The *sternohyoideus* (sth, Fig. 19) originates from the forked leading edge of the cleithrum, the dorsal arm of the fork contributing a separate bundle of fibres which is directed ventrally into the main mass of horizontally arranged fibres. The lateral border of the muscle is marked by tendinous bands. Insertion is along the ventral and lateral faces of the urohyal.

Branchial arch muscles (Fig. 19)

I have not made a thorough investigation of the branchial arch muscles due to lack of material for deep dissection. As far as I can see, the arrangement of this musculature is essentially that described for *Opsariichthys* by Takahasi (1925).

The *obliqui ventrales* (obv1–3) are present on the first three ceratobranchials, they are very elongate well-developed muscles.

The fourth ceratobranchial bears a *transversus* muscle which meets its fellow along a median raphe into which inserts the *pharyngoclavicularis interni.*

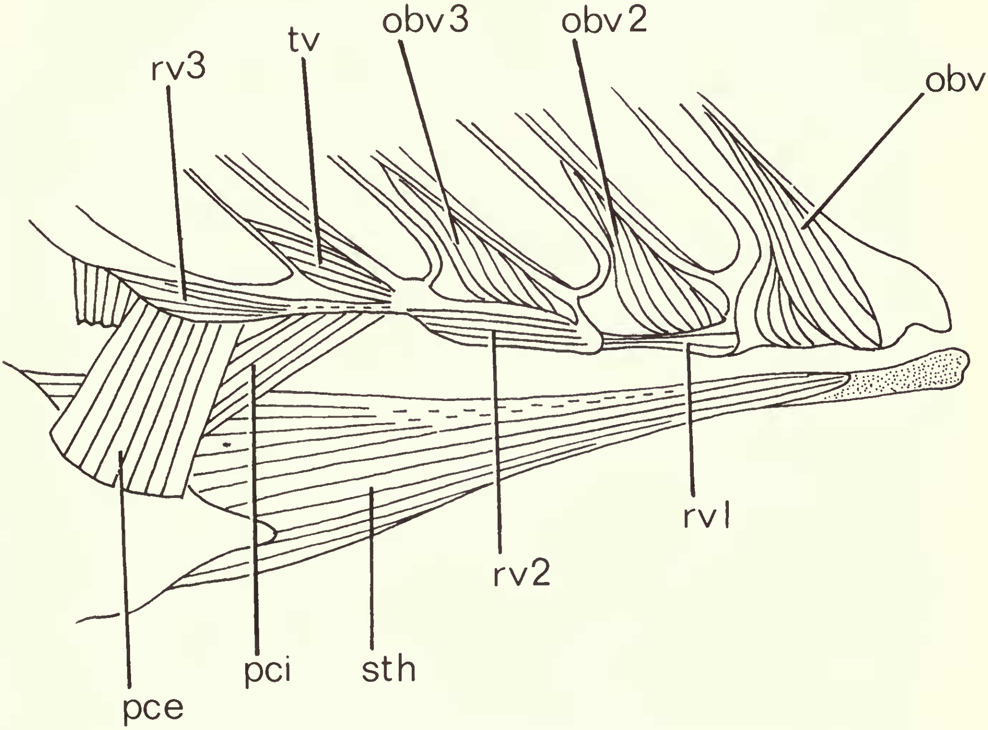

Fig. 19 *Luciobrama macrocephalus*, ventral branchial muscles of the right side shown in ventro-lateral view.

Connecting the second and third hypobranchials is a thin almost tendinous muscle, the *recti ventrales* (rv1); another larger element runs from the third to the fourth hypobranchial (rv2), a thin tendon then connecting the fourth hypobranchial to the *recti ventrales* of the fifth (pharyngeal) ceratobranchial.

These muscles are the *arcualis-hyoideus* of Takahasi (1925). Winterbottom (1974) refers to these as the *recti ventrales* and remarks that there are four to five in the cyprinids.

Comparative analysis

In order to determine the interrelationships of *Luciobrama*, it has been necessary to examine a wide range of cyprinid genera and to review a series of anatomical features to decide if they are derived or primitive characters.

The species that have been examined are listed on pages 2–5. These were chosen to represent those groups currently recognized as subfamilies (see p. 61). In referring to large genera such as *Barilius*, *Barbus* and *Labeo* it should be made clear that in the context of this paper such reference is only to those species examined and does not imply that any particular feature occurs in all congeners.

Although many genera have been examined, not all are cited in the following analysis. An initial study suggested those that could possibly be related to *Luciobrama*, those that displayed parallel features and those exhibiting marked differences. Examples of genera in all three categories have been used in this analysis.

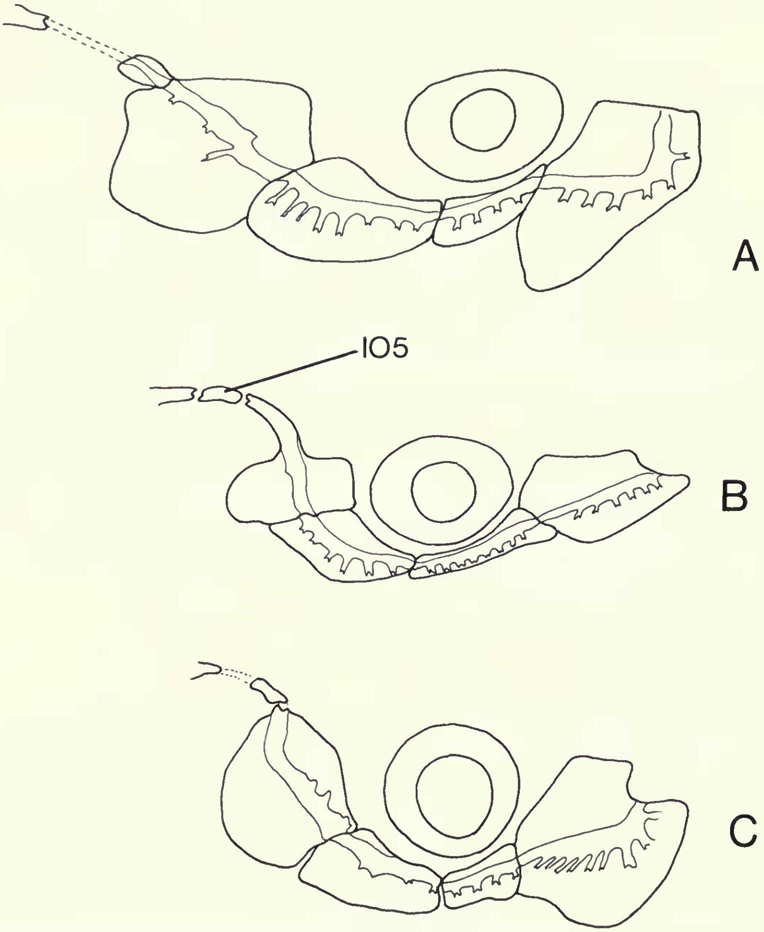

Fig. 20 Infraorbital bones of A. *Aspiolucius esocinus*, B. *Pseudaspius leptocephalus*, C. *Aspius vorax*.

Osteological characters

Circumorbital series

In *Luciobrama* all the infraorbitals, apart from the lachrymal, are reduced to a slender ossification around the sensory canal tube. This is not an unusual condition in cyprinids and is found in many genera (e.g. *Alburnus*, *Labeo*, *Barbus*, *Notropis*, *Chrosomus*). However, in all species of three genera, namely *Aspiolucius*, *Pseudaspius* and *Aspius*, the posterior infraorbitals are of similar morphology and arrangement to those in *Luciobrama* (*cf.* Fig. 2, Figs 20A, B & C). In these three genera the first infraorbital is large, and the canal bears 9–10 pores in *Aspiolucius*, 11 in *Pseudaspius* and 9–10 in *Aspius*. The second infraorbital is short in *Aspiolucius*, but in *Pseudaspius* and *Aspius* it approaches the proportions of that bone in *Luciobrama*. The third and fourth infraorbitals are expanded, the fourth being shield-shaped. The canal carried by the fourth infraorbital is diverted across the postorbital region as in *Luciobrama.* In all these species the fifth infraorbital is minute and reduced to an ossification around the canal tube.

In *Elopichthys* (Fig. 21A), although the reduction of ossification is similar to that found in the above-cited genera, the fourth infraorbital is orientated vertically, and the fifth curved dorso-posteriorly to join the pterotic canal. This arrangement is found in a number of genera (e.g. *Leuciscus*, *Alburnus*, *Culter*, *Pelecus*, *Paralaubuca*, *Oxygaster* and *Ochetobius*; Fig. 21D). However, in *Paralaubuca* and *Oxygaster* the fourth infraorbital is expanded.

A different situation is found in *Opsariichthys*, *Zacco*, *Barilius* and some other genera (see below, p. 29). Here all elements in the infraorbital series are expanded. In *Barilius bola* the second,

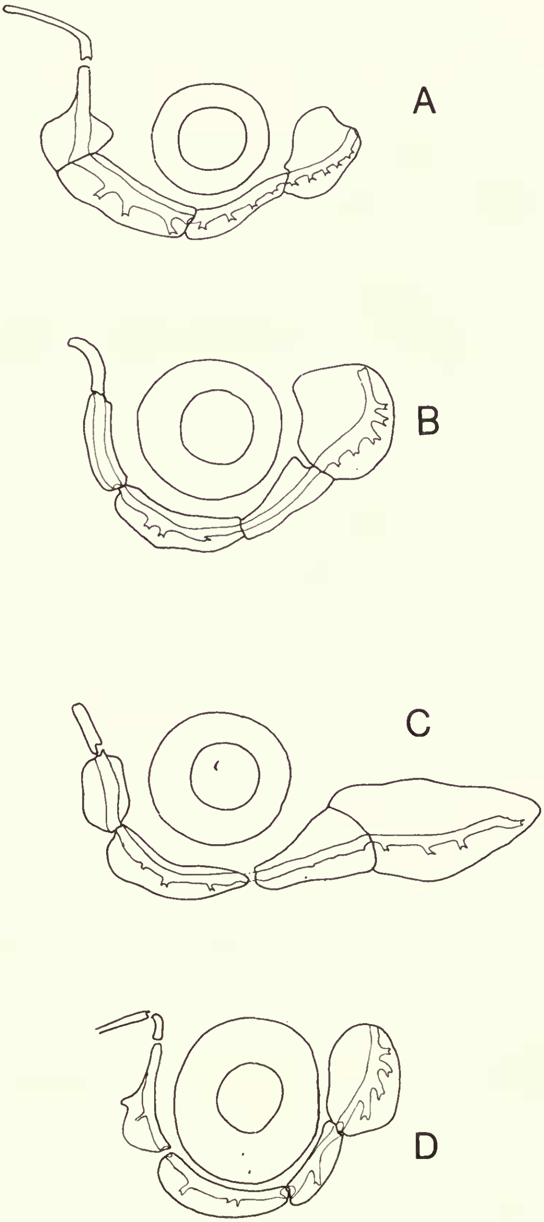

Fig. 21 Infraorbital bones of A. *Elopichthys bambusa*, B. *Erythroculter mongolicus*, C. *Schizothorax esocinus*, D. *Pelecus cultratus*.

third and fourth bones cover the entire cheek. In *Opsariichthys* the fourth and fifth infraorbitals are expanded posteriorly. Expansion of the second and third bones occurs in some *Rasbora* (Ramaswami, 1955b).

The fifth infraorbital is reduced to an ossification around the canal tube in *Opsariichthys* and is remote from the supraorbital, but in *Barilius* it is large and connected to the supraorbital. A similar arrangement is found in *Salmostoma*, *Luciosoma* and *Squaliobarbus* (see below, p. 29).

The *supraorbital* is variously developed in cyprinids (see Ramaswami, 1955b : 208). In *Aspiolucius*, *Pseudaspius* and *Aspius* (Fig. 20) it is, as in *Luciobrama*, relatively narrow, the frontal widening posteriorly to it and preventing its contacting the infraorbital series.

In narrow headed cyprinids, such as *Oxygaster*, *Pseudolaubuca* and *Macrochirichthys*, the bone is narrow and extends for almost the length of the lateral margin of the frontal but fails to make contact with the fifth infraorbital.

In most *Barbus* species the supraorbital is small and well separated from the infraorbital series by the frontal, but in *Barbus tor* the bone is very long and meets the fifth infraorbital. Gosline (1974 : 3) also noted the variability of contact in certain south-east Asian species of *Barbus*.

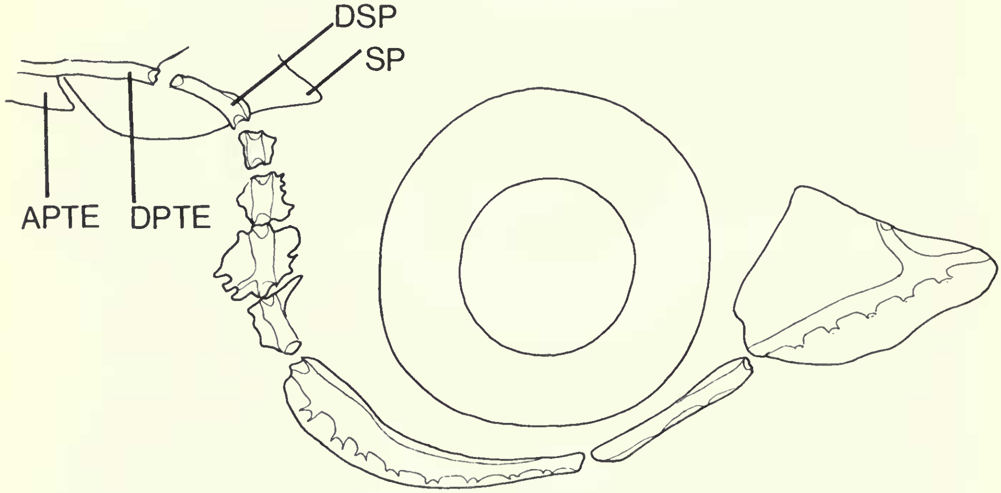

Fig. 22 Infraorbital bones of *Oreoleuciscus pewslowi.*

Comments on circumorbitals

Roberts (1973) states that in cyprinids there is an antorbital and six infraorbitals. I count only six including the first, here identified as the lachrymal (following Harrington, 1955). Gosline (1961) considered the first infraorbital in cyprinids as possibly a compound structure comprising the lachrymal and antorbital. It is not clear if Roberts considered the first infraorbital to represent two fused elements.

Harrington (1955) identified the sixth infraorbital in *Notropis bifrenatus* as the dermosphenotic, noting that it was reduced to a bony tube and was often lacking in that species.

Gosline (1975) discussed the dermosphenotic of cyprinids and thought the degree of development of this bone and its proximity to other circumorbitals could be an aid in assessing the primitive or specialized condition of a particular taxon. However, he considered that in *Aspius* there was a certain degree of difficulty in the identification of this bone. Gosline (1975 : 2; pl. 2, fig. 3) described a membranous tube connecting the fifth infraorbital with the cranium. In fact his fifth infraorbital is the fourth in the series and the 'membranous tube' is the fifth. In a series of specimens of *Aspius vorax* I have found quite some variation in the development of this bone. In some specimens there is a single completely ossified canal connecting the fourth infraorbital with the pterotic canal, in others the bony tube is fragmented into two components, the upper one of which probably represents the true dermosphenotic (sixth infraorbital) and overlies the autosphenotic. In a specimen of 110 mm SL on one side of the head there is no sign of an ossified element between the fourth infraorbital and the pterotic, although the canal is present as an epidermal tube. Yet, on the other side of the head the fifth infraorbital is well ossified.

In *Oreoleuciscus pewslowi* (Fig. 22) it is interesting to note that there is marked fragmentation of the posterior infraorbital. In one specimen the fourth infraorbital is fragmented into three separate lamellate elements and the sixth infraorbital (the dermosphenotic) is also present (see Jollie, 1975, on the fragmentation of these bones.).

In *Luciobrama* connection between the fifth infraorbital and the dermopterotic is made through an epidermal canal. This connection occurs far in front of the autosphenotic because of the forward extension of the overlying dermopterotic. Thus, there is no infraorbital bone connected with any part of the autosphenotic and which could be interpreted as a dermosphenotic.

In *Esomus*, Ramaswami (1955b) pointed out that the sphenotic occurred as a roofing bone. The bone he was referring to is, in fact, the dermosphenotic and in preparations to hand I have been able to separate this canal bearing bone from the underlying autosphenotic. Greenwood *et al.* (1966) refer to this feature in *Esomus* as being specialized, but it is probably a primitive condition for a cyprinid.

Gosline (1975) noted that in *Salmostoma* the dermosphenotic was large and contacted the supraorbital (which it also does in *Barilius*, *Cyprinus*, *Squaliobarbus*, *Luciosoma* and some other genera). He was of the opinion that contact between the dermosphenotic and supraorbital was a primitive character (Gosline, 1975 : 6) because such contact is found in the 'generalized' characoid *Brycon*.

It is so that in *Brycon* and other characoids the sixth infraorbital (dermosphenotic) is well developed and makes contact with the supraorbital (Weitzman, 1962; Roberts, 1969). However, this has little bearing on the situation in cyprinids. Indeed, if *Opsariichthys* is to be considered the 'primitive' cyprinid this argument fails because no such contact is found between the infraorbitals and supraorbital. In *Salmostoma* and other cyprinid genera in which such contact occurs, it is between the fifth infraorbital and supraorbital. No cyprinid I have examined shows any evidence of the interposition of a sixth infraorbital. This would suggest that either the dermosphenotic has been lost altogether in these genera or else it has become incorporated with the fifth infraorbital. Incorporation into another dermal head bone is suggested by an observation on *Chelaethiops*. A specimen of *Chelaethiops* sp. (29·5 mm SL) was found to possess a well-developed dermosphenotic, but in four other specimens of the same series (alizarin preparations) it was absent. However, in a fifth specimen (24·5 mm SL) a fragment of the dermosphenotic was visible, apposed to the posterior edge of the frontal (Figs 23A & B).

The dermosphenotic is also well developed in *Esomus danricus* (see above), and the fifth infraorbital, although small, maintains contact with the supraorbital; that area lying postero-dorsally to the infraorbital (i.e. above the *dilatator operculi* muscle) is covered by a 'normal' body scale, one bearing concentric radii. This scale appears to be in no way associated with any cranial bone.

The area covered by the fifth infraorbital is that which houses the *dilatator operculi* and *levator arcus palatini* muscles, and it seems likely that reduction of dermal bones in that region would be a necessary preadaptation or a response to the reorientation and expansion of the underlying musculature. It may be noted here that in some *Barilius* species where the fifth infraorbital is large, the *dilatator operculi* is covered by the *adductor mandibulae* muscle (see p. 55).

Tretiakov (1946) placed much emphasis in classifying the cyprinids on the development of the infraorbital series and suggested that those cyprinid genera with the broadest posterior bones (presumably in contact with the supraorbital) were the most primitive. He included *Cyprinus* in that category.

Gosline (1974) considered the cephalic canals of cyprinids and divided the old world genera into two groups on the basis of 'presence or absence of a gap between the supraorbital and infraorbital canals'. He stated (*loc. cit.* : 11) that all south-east Asian and African cyprinids have the supraorbital and infraorbital canals connected.

The connection between the infraorbital and supraorbital canals is dependent on the form of the last infraorbital (or dermosphenotic) already discussed above. There is always a connection between the two canal systems, be it through an ossified or an unossified tube. The 'gap' observed by Gosline is presumably the unossified condition. Such an unossified connection is found in some African *Barbus* (e.g. *B. somereni*), a group which Gosline included amongst those genera with a connection between the canal systems; whereas *Rutilus* and *Pelecus*, included in the group with a break between the canal systems, have a complete connection with the pterotic canal.

Ethmo-vomerine region

The *kinethmoid*. I have been unable to determine the condition of this bone in *Aspiolucius* and *Pseudaspius* owing to lack of material for dissection. In *Aspius* it is short and blunt as in *Luciobrama*.

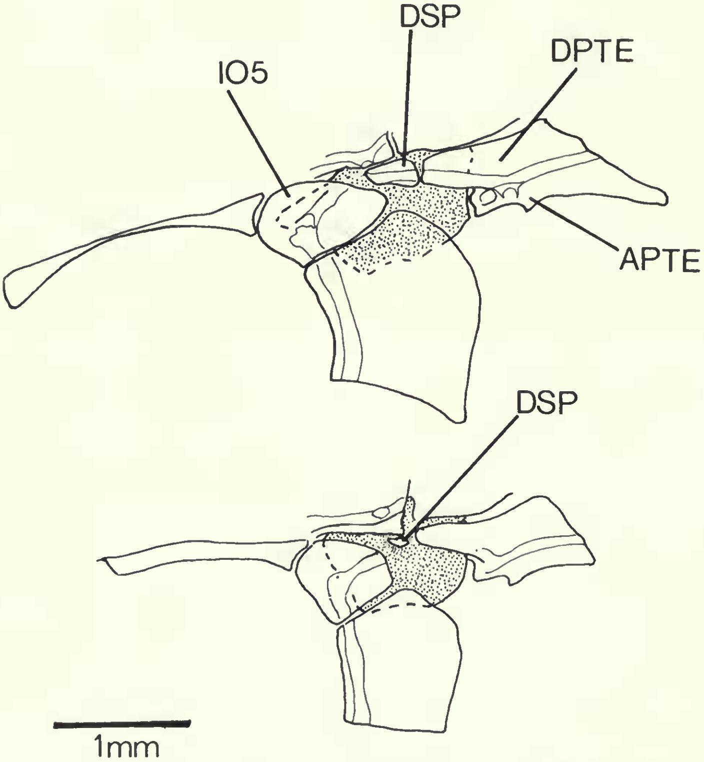

Fig. 23 Upper circumorbital bones of *Chelaethiops* sp. A. A specimen of 29·5 mm SL, B. A specimen of 24·5 mm SL.

In *Elopichthys* the dorsal surface of the kinethmoid is greatly expanded into a flat diamond-shaped plate separating the premaxillae posteriorly (Fig. 35, KE). It is attached by ligaments to the premaxillae and maxillae and rotates against the ethmoid when the jaw is opened.

In *Opsariichthys*, *Zacco* and some species of *Barilius* the kinethmoid is an elongate gutter-shaped bone the dorsal edges of which are slightly flared. However, in *Barilius bola* the dorsal surface is expanded as a solid plate similarly to that of *Elopichthys* although not as extensively (see p. 43). In other species of *Barilius* the kinethmoid is a rod-shaped structure which is notched dorsally. This is the 'usual' condition of the kinethmoid in other cyprinid genera and is probably the primitive one. Exceptionally, in the genus *Barbus*, the species *B. tor* and *B. mariae* possess very long kinethmoids, the posterior borders of which are convex, enabling the bone to rock in the anterior ethmoid groove. Current research on the genus *Macrochirichthys* has indicated an unusual feature of the kinethmoid (which is a triangular bone) whereby it articulates directly with the premaxillae.

I could only examine the features of the ethmo-vomerine region in *Aspiolucius* and *Pseudaspius* from radiographs. Both genera resemble *Luciobrama* in possessing a similar depression, elongation and contact of the lateral ethmoids with the parasphenoid.

Ramaswami (1955b) noted that in many genera including *Barbus*, *Opsariichthys* and *Aspius* the *preethmoid* articulated with the ethmoid only. However, in all the cyprinid genera I have examined the preethmoid is supported in a lateral fossa formed by the ethmoid and the vomer (the condition noted in *Labeo* by Starks, 1926 : 174). Ramaswami (1955b) also states that the preethmoid is completely lacking in, amongst other genera, *Esomus*, *Leuciscus* and *Notropis*. I can report that it is present in both the former genera and Harrington (1955) notes that it is present in *Notropis* but is supported only by the vomer. The size of the preethmoid varies considerably, being a very large laterally protruding structure in *Opsariichthys* to minute, partially ossified pads in *Chela* and *Esomus*.

The *supraethmoid* is variously developed in cyprinids. One condition appears for it to be broad and short with the anterior border notched medially; this is the type found in *Opsariichthys*, and some *Barilius* species. Although basically similar, the supraethmoid in the cultrines is narrow and the medial notch much deeper. In *Barbus* and *Labeo* the bone can become extensively developed (e.g. *Labeo cylindricus*) and the anterior border produced medially. In *Barbus tor* and *Barbus mariae* there is, however, a very deep medial groove which accepts the expanded kinethmoid; see above page 30. The usual condition is for the supraethmoid to interdigitate posteriorly with the frontals, the posterior border is mostly straight or somewhat irregular but without the long lateral forks found in *Luciobrama* and *Aspius*. However, in *Macrochirichthys*, *Chela* and some other genera the supraethmoid is overlain by the frontals. Work currently in progress suggests that this is a derived feature associated with the oblique orientation of the jaws and that it is indicative of close relationship of those genera in which it occurs.

Variability within the *ethmoid* appears to be mainly one of depth; being very deep in some genera such as *Pelecus* and shallow in others such as *Chela*. In all the cyprinids I have examined the ethmoid makes some contribution to the preethmoid fossa.

The *vomer* is usually short and wide as it is in *Opsariichthys* but in this genus and in some *Barilius* it is greatly thickened anteriorly. An extreme of this condition is found in *Elopichthys* where the ventral surface is swollen and posteriorly folds over to contact the parasphenoid (Fig. 24). The vomer in the majority of cyprinids is thin and the ventral surface is either flat or bears a shallow groove.

The *nasals* in *Aspiolucius* are long decurved bones containing 8 pores (Fig. 25); in *Pseudaspius* they are shorter, bearing 5 pores, and in *Aspius*, long with 6 pores (Fig. 26). *Elopichthys* resembles *Luciobrama* in possessing long, narrow nasals bearing 9 pores. In the majority of cyprinid genera studied the nasals are found to be short bones with 2–4 pores. In some cultrines they may be long as in *Erythroculter mongolicus* where the nasal bears a lateral flange and has 6 pores.

The *frontals* in *Pseudaspius*, but even more in *Aspiolucius*, are narrow, elongate and anteriorly are slightly separated from one another (Fig. 25). The lateral border posterior to the orbit, like that in *Luciobrama*, is markedly concave. No other cyprinid genus I have encountered has such elongate frontals as are present in *Aspiolucius* and *Luciobrama*. In most genera examined the frontals are relatively short and broad but in some *Barilius* species are narrow and elongate with a concave border above the orbit. The dorsal surface of the frontals is mostly flat or convex but in *Macrochirichthys*, *Pseudoxygaster*, *Pelecus* and some species of *Oxygaster* the frontals are medially depressed to allow for the cranial extension of the epaxial musculature (see Howes, 1976), and in *Nematabramis* there are transverse lamellate ridges across the frontal surfaces.

Orbital region

Each *orbitosphenoid* in *Aspiolucius* and *Pseudaspius* appears similar to that in *Luciobrama*; for some distance it is joined to the parasphenoid but lacks the dorsal posterior extensions seen in *Luciobrama*. (These observations were made entirely from radiographs.)

In *Aspius* the orbitosphenoids are short, deep and widely divergent (Fig. 27B). Medially, they fuse to form an interorbital septum which extends ventrally to join the parasphenoid. A similar development is found in *Elopichthys* but here the septum is reduced (Fig. 27A).

The orbitosphenoid septum is variable in its development within the Cyprinidae. Its purpose is to provide wide separation between the cranial roof and the parasphenoid. Such separation appears to have little to do with the size of the orbit but more with the angle at which the cranium is aligned to the vertebral column and the size of the buccal cavity. In piscivorous cyprinids the orbitosphenoids make direct contact with the parasphenoid without the intervention of a septum. This is also the case in those genera such as *Labeo* and *Garra* which are characterized by their depressed crania. In both cases this close union has resulted in increased rigidity of the cranium (in *Labeo cylindricus* the orbitosphenoids extend lateral wings which join similar processes from the parasphenoid), and increased area of the buccal cavity. When the orbitosphenoids are reduced in depth they often exhibit a cancellous surface and bear lateral ridges (e.g. *Labeo*, *Schizothorax*, *Barilius*).

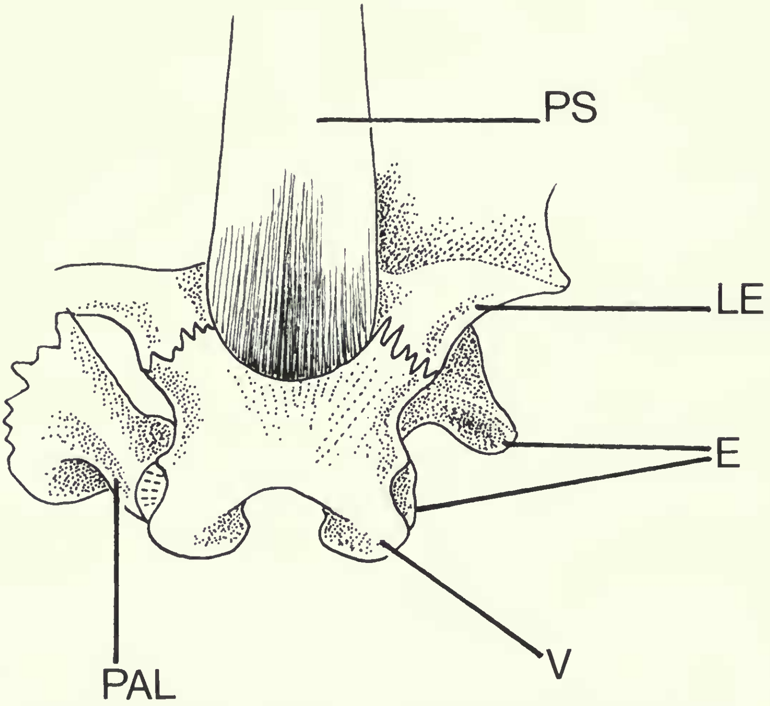

Fig. 24 *Elopichthys bambusa*, ethmo-vomerine region, ventral view.

The *pterosphenoid* in *Aspiolucius* and *Pseudaspius* is an extensive bone and is depressed as in *Luciobrama*, but in *Aspius* it is less extended antero-posteriorly, and that part of the bone forming the wall of the hyomandibular facet less well developed (Fig. 27B). The pterosphenoids of *Aspius* diverge widely and their borders are close to the lateral margins of the frontals.

In *Elopichthys* (Fig 27A, 28 & 29), the pterosphenoids present a condition not encountered in any other cyprinid. The bones are extensively developed and diverge to reach the lateral margins of the frontals. Unlike the genera mentioned above, the sphenotic is not continuous with the frontal and these two bones are separated by the intervention of the pterosphenoid, whose surface at this point is depressed to form a basin. The pterosphenoid basin provides the site of origin for the *adductor mandibulae* A3 muscle (see p. 53). As in *Luciobrama* there is an extensive connection with the parasphenoid.

The pterosphenoids of other cyprinid genera examined are generally small, almost hexagonal in outline and make contact with both the prootic and parasphenoid. However, in *Zacco*, *Cyprinus*, *Catla*, *Rutilus* and some species of *Barilius*, the pterosphenoid does not contact any

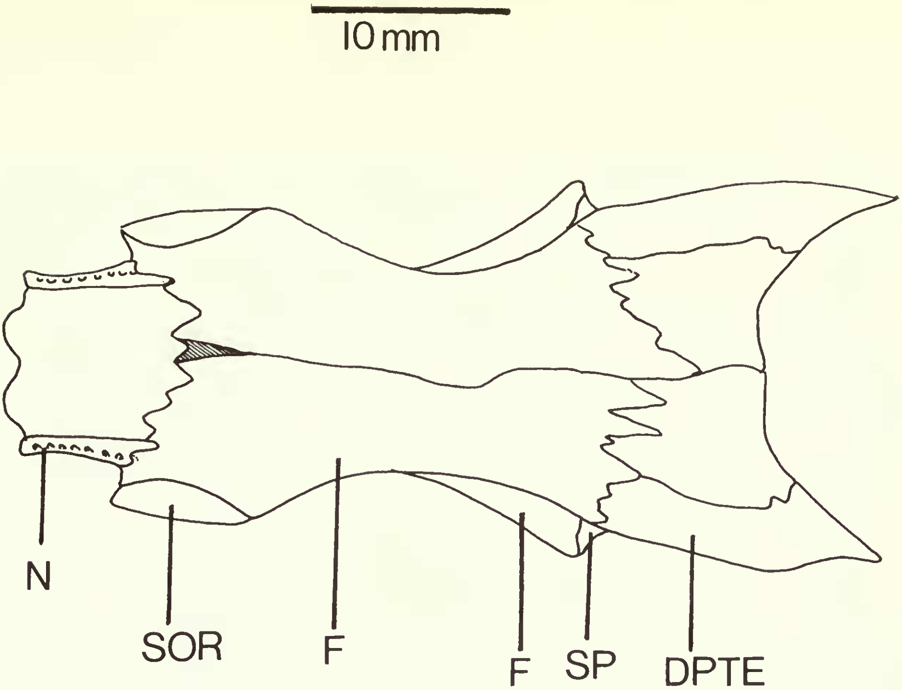

Fig. 25 *Aspiolucius esocinus*, part of the dorsal surface of the cranium. (Holotype.)

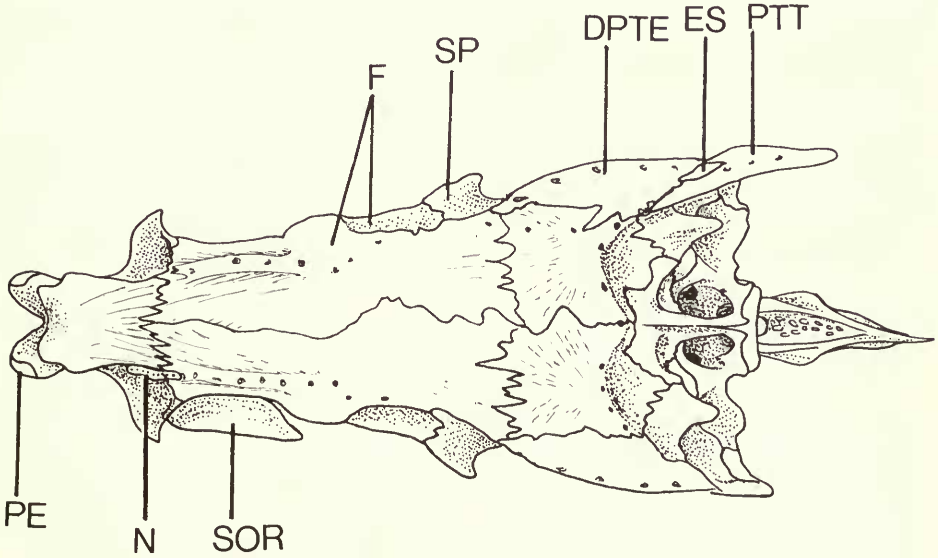

Fig. 26 *Aspius vorax*, neurocranium, dorsal view.

part of the parasphenoid but instead is sutured entirely to the prootic. (See later note on prootic, p. 35.)

The *parasphenoid* in *Aspiolucius* and *Pseudaspius* is thick and horizontally aligned, contacting the medial sections of the lateral ethmoids and the orbitosphenoids as in *Luciobrama*. In *Opsariichthys* the parasphenoid is thin, flared anteriorly, and bears a deep groove on its ventral surface. The lateral ascending wing of the parasphenoid which contacts the prootic and pterosphenoid is wide. Below the prootic the parasphenoid broadens into a triangular platform which is extended laterally by the contribution of the flattened ventral surfaces of the prootics. A similar contribution from the prootics to the parasphenoid platform is found in most *Barilius* species (Fig. 30). The lateral ascending wings of the parasphenoid in *Zacco*, some *Barilius* species, and *Leuciscus* are narrow, and as mentioned above, make contact only with the prootic and not the pterosphenoid.

Although Ramaswami (1955b) stated that the parasphenoid did not show any variation, in fact it does. In some genera the anterior part is very wide (e.g. some *Labeo* species) and there are present in others well-developed medial dorsal and ventral ridges, Again, in *Labeo* the ascending

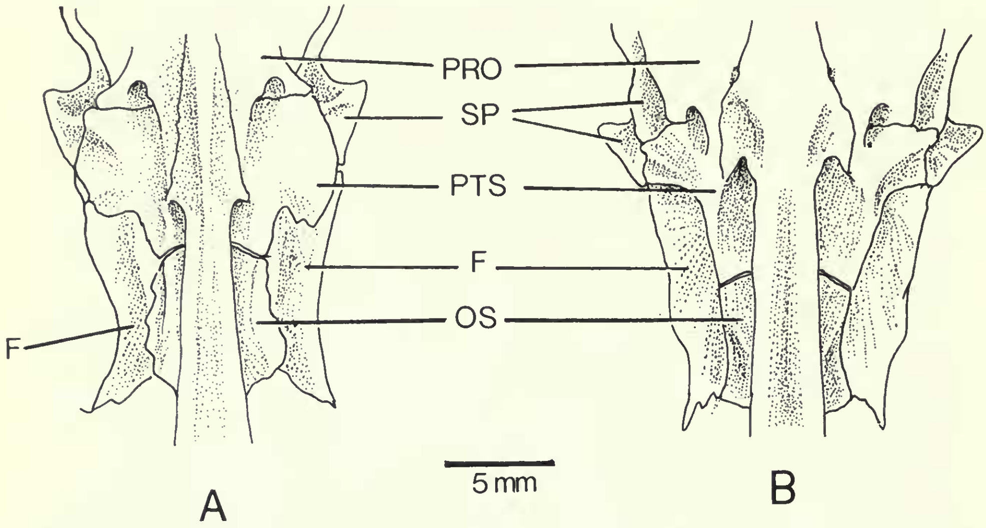

Fig. 27 Ventral views of the orbital regions of A. *Elopichthys bambusa*, B. *Aspius vorax*.

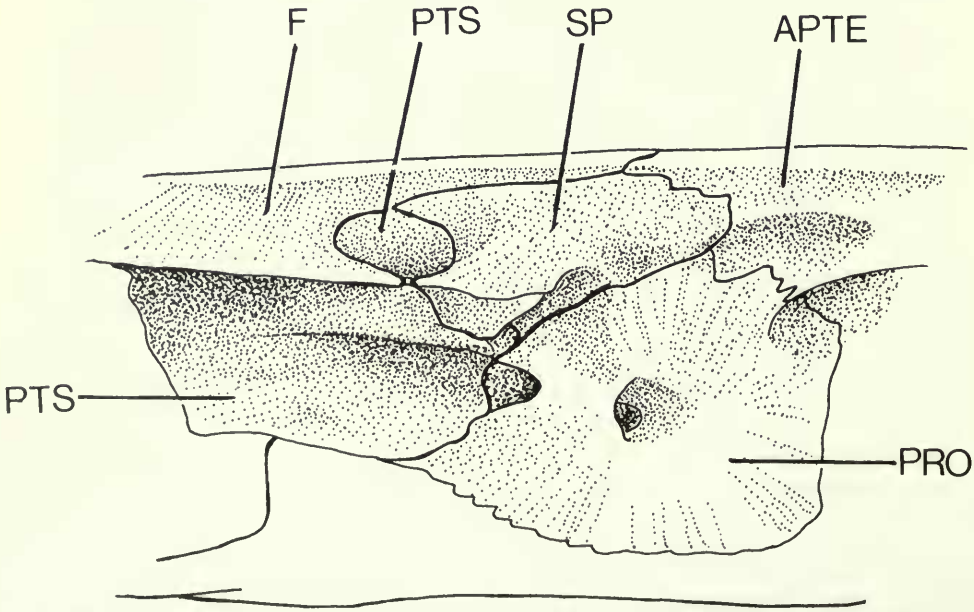

Fig. 28 *Elopichthys bambusa*. Lateral view of the orbital-otic region of the neurocranium. (Composite from three specimens.)

wing may be greatly extended laterally and there is sometimes developed a medial strut of the ascending wing which contacts the pterosphenoid. *Catla* and *Hypophthalmichthys* have the posterior part of the parasphenoid bent upwards, and the midline below the ascending wings bears a strong ventral process.

Otic region

The *prootic* in *Aspiolucius*, *Pseudaspius*, *Aspius* and *Elopichthys* is of a similar elongate shape to that in *Luciobrama* and the anterior foramen of the trigemino-facialis chamber is likewise situated on the anterior border of the bone which contacts the pterosphenoid. Also, as in *Luciobrama* the lateral commissure is wide. The large hypophysial foramen (Ramaswami, 1955b) between the parasphenoid and prootic in *Luciobrama* is absent in the above-mentioned genera.

In most cyprinid genera examined, the anterior foramen of the trigemino-facialis chamber interrupts the anterior border of the prootic, which is bounded by the pterosphenoid. However, in some species of *Barilius* the prootic bears the anterior opening of the trigemino-facialis chamber entirely in its lateral face, remote from the anterior border and in those species the lateral commissure is a narrow structure. There is much variation in the width of the lateral commissure throughout the cyprinids. Besides *Luciobrama* and the genera mentioned above, it is a wide structure in *Schizothorax*, *Erythroculter* and some *Barbus* species (all those taxa in fact, which have an elongation of the postorbital cranium). On the other hand, it is reduced to a narrow strut in *Opsariichthys*, *Zacco*, *Leuciscus* and *Labeo*.

The floor of the prootic forms the roof of the *posterior myodome* in all the genera examined. Again, the extent and depth of the myodome show great variation. As far as can be ascertained from radiographs, the myodome in *Aspiolucius* and *Pseudaspius* resembles that of *Luciobrama* which in turn bears similarity to that described in *Aspius* by Oliva and Skořepa (1968).

The topographic relationship between the prootic, parasphenoid and pterosphenoid in the cyprinids appears to have some significance in establishing phylogenetic relationships between various taxa. A particular study is being made of these bones in connection with current work on the genera *Opsariichthys*, *Zacco* and *Barilius*.

The *autosphenotic* is extensive in *Aspiolucius* and extends laterally from below the border of the cranium as a long shelf on which the *dilatator operculi* muscle originates (Fig. 25). In *Aspius* (Fig. 26) the sphenotic is not roofed by any part of the frontal or pterotic. Together with part of the frontal it extends laterally and forms the fossa for the *dilatator operculi* muscle.

The sphenotic in *Elopichthys* is bordered anteriorly by the basin-like pterosphenoid (see above, p. 32), and it extends laterally as a wide platform, the posterior ventral surface of which forms the anterior hyomandibula facet (Figs 27A, 28 & 29).

In *Opsariichthys*, *Zacco* and some *Barilius* the bone is overlapped along its medial margin by the frontal and forms a deep dilatator fossa. The anterior lateral process of the sphenotic in these genera is short and lamellate, in contrast to that of other species of *Barilius* (e.g. *bola*, *loati*) where the lateral process is long and thick.

In *Barilius microcephalus* the posterior dorsal border of the sphenotic is separated from the overlying pterotic to form a lateral foramen (LF, Fig. 31). Part of the *adductor mandibulae* A2 muscle originates from the ventral surface of the pterotic and passes through this foramen.

Some genera display a condition in which the laterally directed process of the sphenotic is separated from the overlying frontal, contact between the two bones being along their lateral margins. Thus, a foramen is formed which provides a passage for the *dilatator operculi* muscle which originates on the ventral surface of the frontal. This feature is found in *Esomus*, *Cyprinus* and *Catla*. It also occurs in some *Barbus* species and appears to be present in all European and north African species examined (*Barbus barbus*, *B. callensis*, *B. nasus* and *B. reinii*), a middle eastern species (*B. canis*), some eastern and southern African species (*B. altianalis*, *B. intermedius*, *B. oxyrhynchus*, *B. rocadasi*, *B. progenys*, *B. natalensis* and *B. capensis*) and in some Asian species (*B. altus* and *B. tor*). However, it is absent in all the other species of *Barbus* examined (see list of species on p. 2) where the dilatator fossa is of the 'usual' type (see p. 56).

In all the African and Asian *Labeo* species examined the sphenotic process is separated from the frontal in the same way as it is in *Barbus* and the other genera cited above. However, the sphenotic

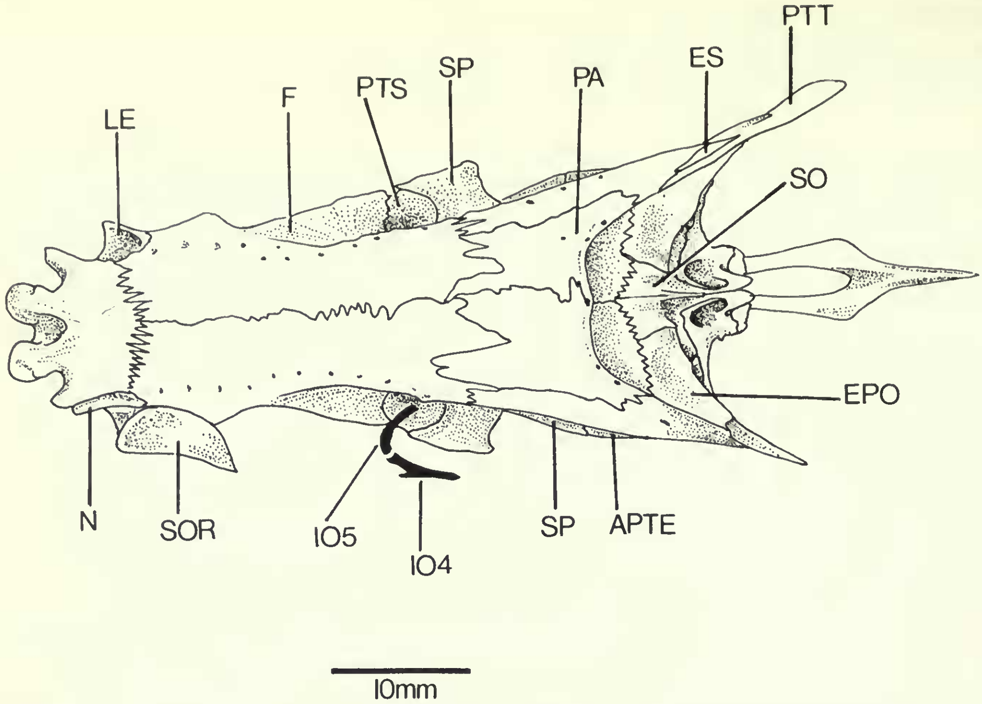

Fig. 29 *Elopichthys bambusa*, neurocranium, dorsal view. The position of infraorbitals 4 and 5 are indicated.

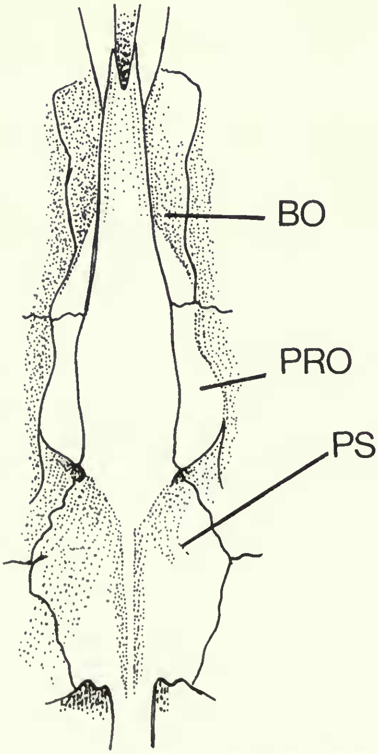

Fig. 30 *Barilius bola.* Ventral view of the parasphenoid and prootic. The parasphenoid platform is unshaded.

process, which in *Labeo* is usually reduced to a thin strut of bone, is also perforated by a foramen. These two openings allow for passage of a divided *dilatator operculi* muscle (see p. 57). A subsidiary foramen is also present in *Catla* and here too the *dilatator* muscle is divided through both apertures.

In *Squaliobarbus* the lateral process of the sphenotic is a wide platform covered for half its width by the frontal. The ventral surface of the bone provides a fossa for the articulation of the anterior condyle of the hyomandibula. Anteriorly, the sphenotic is deeply recessed, leaving only the thinnest wall between the orbital cavity and the dilatator fossa, perhaps an incipient condition for the development of this feature.

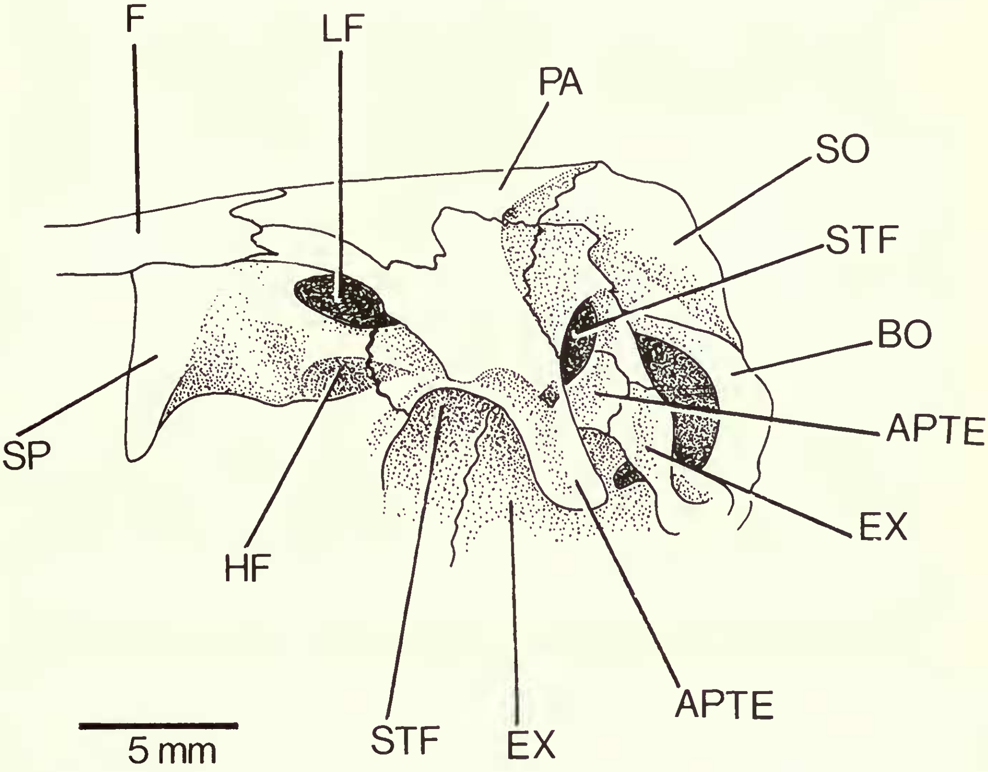

Fig. 31 *Barilius microcephalus.* Dorso-posterior section of neurocranium, lateral view.

Further discussion of the dilatator fossa is reserved until page 56.

The *pterotics* in *Aspiolucius* and *Elopichthys* (Figs 25 & 28) are wide bones contributing to the cranial surface and bordering the parietals and frontals as in *Luciobrama*. Also, as in that species, they overlie and extend anteriorly beyond the sphenotic shelf.

In *Aspius* there is only a narrow region of contact between the pterotics and the frontals. The fossa for the posterior condyle of the hyomandibular bone is almost entirely confined to the pterotics.

The cranial surface of the pterotics is narrow in *Opsariichthys* and most *Barilius* species. Medially the bones form a flat roof to the subtemporal fossa. Ventro-posteriorly their connection with the exoccipitals, through which passes the semi-circular canal, is greatly compressed. The posterior spine of each pterotic is short and is directed ventrally at an acute angle. The posterior hyomandibular fossa lies mainly in the pterotic, but the anterior third extends onto the sphenotic. In the long-jawed species of *Barilius* (e.g. *B. bola*, *B. loati*) this fossa is confined almost entirely to the pterotic.

The *posttemporal fossae* in *Luciobrama* are well developed (see p. 11 & Fig. 32A). As far as I can ascertain from radiographs such is also the case in *Aspiolucius* and *Pseudaspius*. Certainly in *Aspius* (Fig. 32B), *Elopichthys* (Fig. 33A), *Megalobrama*, *Culter*, *Erythroculter* and *Schizothorax* deep posttemporal fossae are developed. In other genera such as *Opsariichthys* (Fig. 33B) and *Pelecus* the fossae are present but are shallow. They are absent in *Leuciscus*, most *Barbus* species, *Labeo*, *Garra*, *Paralaubuca* and *Macrochirichthys*. In some *Barbus* species (*B. tor*, *B. longiceps*) 'pseudo-posttemporal' fossae are developed. That is to say, instead of the lateral wall of the fossa being formed from the pterotic, it is provided by the enlarged posttemporal, the pterotic contributing only slightly to the anterior part of the fossa (Fig. 33C).

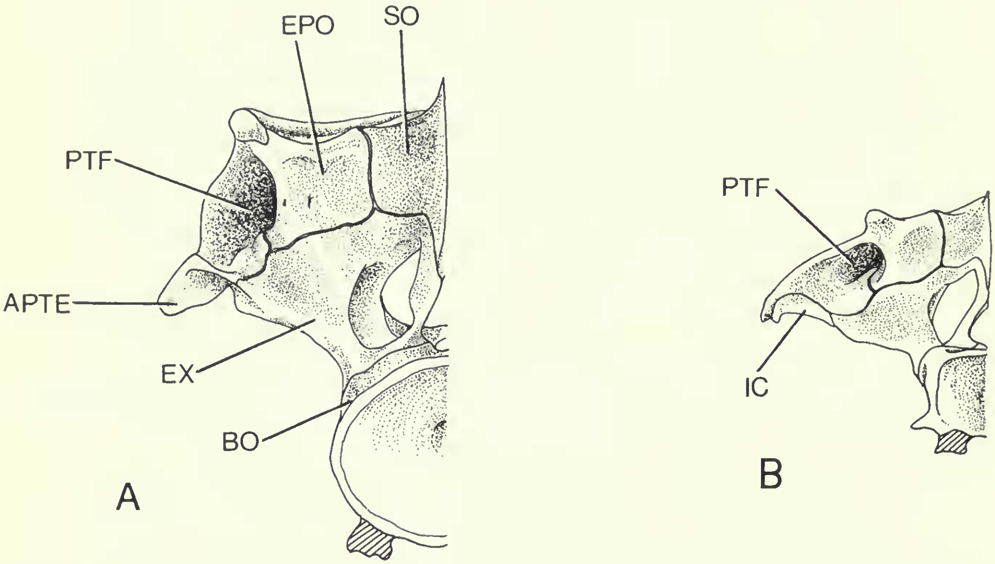

Fig. 32 Posterior views of the neurocrania of: A. *Luciobrama macrocephalus*, B. *Aspius vorax*.

A rather different situation is found in some *Barilius* species (*B. bola*, *B. microcephalus*, *B. loati*, *B. niloticus*) where there are no posttemporal fossae as such but a posterior (posttemporal) opening which invades the deep subtemporal fossa. Here, the pterotic contacts the epioccipital along the cranial surface and posterior border, forming the roof of the subtemporal fossa (Fig. 31).

Ramaswami (1955b : 222) notes that 'In some form or other all genera possess a posttemporal fossa in Cyprinidae', while Roberts (1973) stated that posttemporal fossae are entirely closed in Cyprinidae. Neither of these statements is correct.

Weitzman (1962) considered the presence of posttemporal fossae in cyprinids to be a specialized feature. Certainly the fossae take on a specialized form in *Luciobrama* and in long-headed representatives of other genera, but its presence in such relatively 'primitive' cyprinids as *Opsariichthys*, *Zacco* and *Barilius*, and the fact that this feature is much more widespread amongst the cyprinids than had previously been supposed, would indicate that it is a plesiomorph character.

The *exoccipitals* show little variation in the genera examined. In all of them the lateral occipital foramen of each bone is extensive, its border being defined by a narrow strip of bone. The lateral limb of the exoccipital is directed at an angle of 45° in *Luciobrama* (Fig. 32A) and in other long-headed cyprinids (Figs 32B & 33A).

In *Labeo* the bone is markedly modified. The lateral limb is directed horizontally (as it is in *Barbus*, Fig. 33C) and the lateral occipital foramen is reduced, being margined by a thickening of the bone.

The *epioccipital* in *Aspius* has the posterior face of this bone produced into a thick, caudally directed process. Such a feature is also noted in *Erythroculter* and *Schizothorax* but appears to be absent in *Aspiolucius* and *Pseudaspius*. Except in *Barbus tor*, where similar processes are present, such well-developed epioccipital features have not been found in the other genera examined. It is a feature no doubt associated with the elongation of the skull and the need to produce an extended surface for the attachment of epaxial muscle fibres.

The dorsal surface of the epioccipital in *Elopichthys* covers a large area which, together with the parietals and supraoccipital forms an extensive posterior cranial platform (see p. 13).

The *basioccipital* could not be examined in either *Aspiolucius* or *Pseudaspius* and the shape of the masticatory plate of the pharyngeal process cannot be ascertained. The plate is weakly developed in *Aspius* and *Elopichthys* as it is in *Luciobrama*, and the pharyngeal process itself is short and laterally compressed distally.

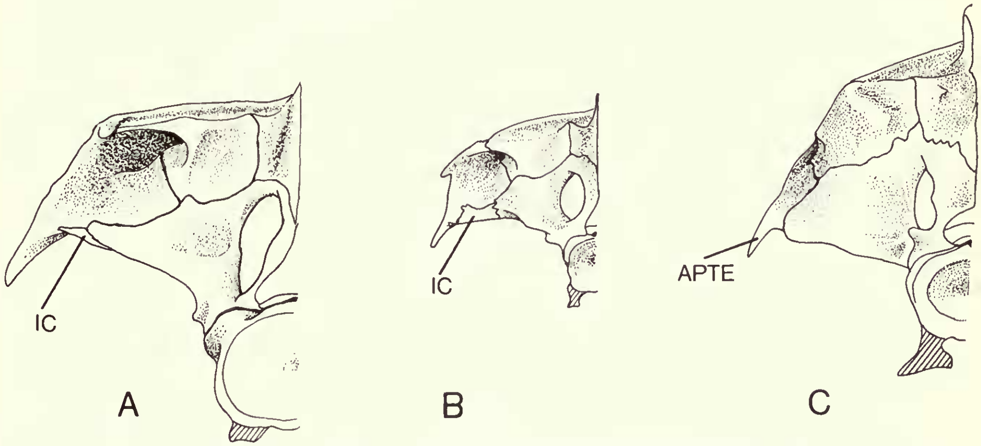

Fig. 33 Posterior views of the neurocrania of: A. *Elopichthys bambusa*, B. *Opsariichthys uncirostris*, C. *Barbus oxyrhynchus*.

Opsariichthys, *Zacco* and some *Barilius* have a pharyngeal process which is laterally compressed and steeply angled, the masticatory plate being moderately developed. The masticatory plate is particularly well-developed in many *Barbus* and *Labeo* species and in *Hypophthalmichthys* (see Ramaswami, 1955b), which in some cases, completely hides the aortic foramen. It appears that in those taxa which possess slender pharyngeal bones and teeth the masticatory plate is weakly developed (e.g. *Pelecus*, *Macrochirichthys* and long-jawed *Barilius* species).

The bulla acoustica is not well developed in any of the genera studied.

The *supraoccipital* is basically similar in all genera examined. The crest of the bone is variously developed; for example in *Labeo coubie* there are two diverging wings arising from the medial lamellae; in *Pelecus* the bone forms a high point to the cranium but the medial crest is virtually absent and in *Chela* the entire crest is truncated. Direct contact of the supraoccipital with the neural complex appears to occur only in *Labeo* (Reid, pers. comm.), connection normally being effected by ligamentous sheets (see p. 19).

The *intercalar* was said by Ramaswami (1955b : 216 -as opisthotic) to be 'normally absent'. However, in *Aspius* (IC, Fig. 32B) and *Erythroculter* the intercalar is extremely well developed and covers the area between the pterotic and epioccipital both dorsally and ventrally. Each intercalar in *Schizothorax* is reduced to a discoid bone lying ventral to the junction of the pterotic and epioccipital. The bone is also present in *Opsariichthys*, *Barilius*, *Squaliobarbus*, *Culter*, *Leuciscus* and some *Barbus* species. I have not found it in *Labeo*, *Pelecus* or *Macrochirichthys*.

The *parietals* are especially elongate in *Luciobrama*, *Aspiolucius* and *Pseudaspius*, a condition also encountered in *Hypophthalmichthys*. The 'normal' condition in the Cyprinidae is for the parietals to be short and wide, and the most extreme form of this condition is to be found in some *Labeo* species. As mentioned earlier (p. 39) the parietals in *Aspius*, *Elopichthys* and *Erythroculter* contribute to the formation of a posterior cranial platform (Figs 26 & 29).

The *posttemporals* in *Aspius*, *Pseudaspius*, *Aspiolucius* and *Elopichthys* are like those in *Luciobrama* (Figs 3, 26 & 29), namely, lamellate ventrally with a long anterodorsal extension, bordered ventrally by the lateral extrascapula.

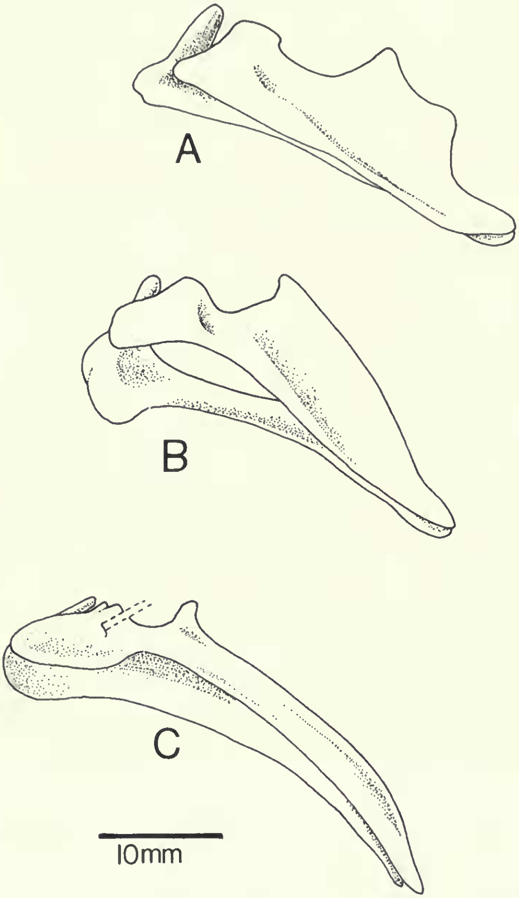

Fig. 34 Upper jaws, in lateral view of: A. *Aspius vorax*, B. *Opsariichthys uncirostris*, C. *Barilius bola*.

The *extrascapula* is variously developed in the cyprinids (noted by Ramaswami, 1955b : 218 -as supratemporal). I have found it as an ellipsoid bone in *Aspius*, thin and elongate in *Elopichthys* and varying from a plate-like element lying over the posterior part of the pterotic (as in *Squaliobarbus*) to a lamellate bone running between the posttemporal and pterotic (as in *Paralaubuca*).

The jaws

The *upper jaw* in *Aspiolucius* and *Pseudaspius* appears, from radiographs, to be similar to that of *Luciobrama* (Fig. 7). In *Aspius* the premaxilla is thin with a large plate-like ascending anterior process.

The premaxillae of *Elopichthys* are massive beak-like structures sutured along their midlines, except for a small anterior foramen. The ventral border of the bones is very sharp edged. The maxillae possess very long anterior medial processes, but the palatine processes are much reduced. The ventral border of the maxilla lies medial to the premaxilla and posteriorly it curves to project ventrally beyond the end of the premaxilla (Fig. 35).

The premaxillae in *Opsariichthys* are very slender bones. At the symphysis the ventral border is rounded. The dorsal border of the maxilla displays a marked concavity anteriorly which is the point of insertion of the maxillary-palatine ligament. The anterior medial process of each maxilla contacts its fellow from the opposite side along a narrow face. The maxilla is separated quite widely for part of its length from the premaxilla. The bones contact each other at their anterior and posterior margins.

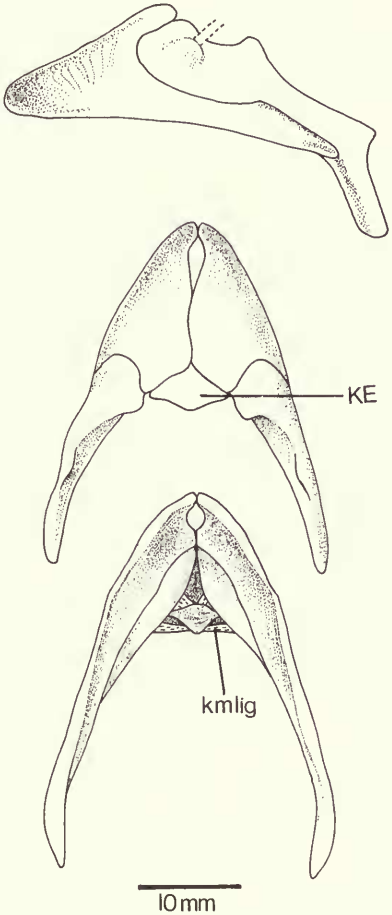

Fig. 35 *Elopichthys bambusa*, upper jaw. Lateral, dorsal and ventral views.

In *Barilius* the anterior tip of each maxilla is extended forward and curved medially so as to almost contact its counterpart. The medial process of each bone, which underlies the anterior ascending process of the premaxilla, meet each other along the midline and maintain contact along a wide surface. These medial processes (maxillary rostral process of Ramaswami, 1955b) do not appear to contact each other in other cyprinid genera examined but are connected across the midline by a ligament.

The upper jaw of *Barilius bola* is greatly elongate when compared with that of *Opsariichthys* (Figs 34B & C). The premaxilla is extremely long and thin, and dorso-laterally is overlapped for almost its entire length by the maxilla. The anterior ascending process of the premaxilla is beak-like and resembles that of *Elopichthys* (*cf.* Fig. 35) but is not so extensively developed.

Another cyprinid which is characterized by its long jaws is *Macrochirichthys* (see Howes, 1976). Here the upper jaw has a complex symphysial joint, mesial extensions being developed on the maxillae which serve to separate the two halves of the jaw to allow for the accommodation of the symphysial knob of the dentary when the jaws are closed.

In most *Barbus* and *Labeo* species examined the maxilla possesses a wide palatine process. The mesial processes are short and are connected with each other by a long ligament. The ventral border of the maxilla overlaps the premaxilla for only part of its length.

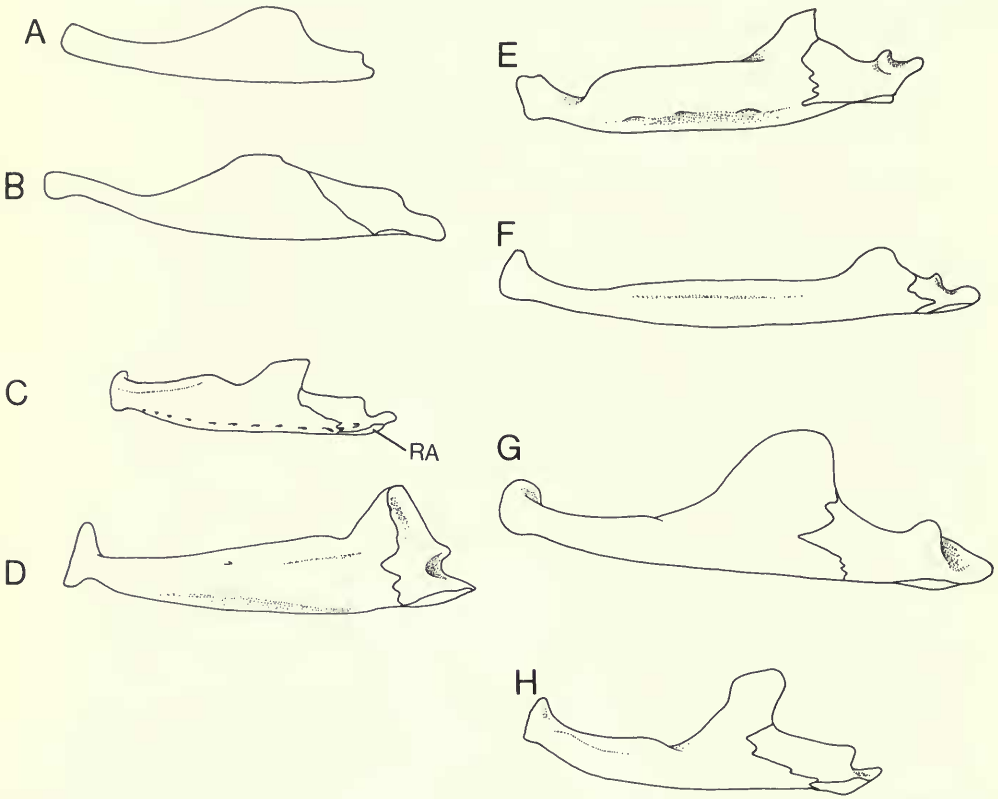

Fig. 36 Lower jaws of: A. *Pseudaspius leptocephalus*, B. *Oreoleuciscus pewslowi*, C. *Aspius vorax*, D. *Elopichthys bambusa*, E. *Opsariichthys unicirostris*, F. *Barilius bola*, G. *Schizothorax esocinus*, H. *Erythroculter mongolicus*.

The *lower jaw* in *Aspiolucius* and *Pseudaspius* is of the same narrow, canoe-shape as in *Luciobrama*. There are 14 pores in the mandibular canal on the dentary, plus 2 on the anguloarticular.

In *Aspius* (Fig. 36C) the dentary is proportionately thicker with an expanded symphysial process. The posterior border of the coronoid process is almost perpendicular, with the anguloarticular extending backwards from it at right angles. The dentary-anguloarticular junction in *Aspius* most closely resembles that of *Erythroculter* and *Opsariichthys* (Figs 36E & H).

In *Elopichthys* (Fig. 36D) the dentary is very thin, the tapered and hammer-shaped symphysial process fiting into the corresponding curvature of the upper jaw when the mouth is closed. Posteriorly the coronoid process rises steeply to meet the anguloarticular. Like *Luciobrama*, the dorsal border of this process is continuous and not broken as it is in the other genera.

The dentary of *Opsariichthys* (Fig. 36E) bears a strong symphysial process followed by a notch and then a curved thin wall which rises gradually to form the ascending process. A similar notch can be found in *Paralaubuca* and *Macrochirichthys* (see Howes, 1976 : 244).

In *Barilius bola* (Fig. 36F) the dentary is exceedingly thin and gently concave just before it enlarges to form the symphysial knob. There is a low ascending process. The other *Barilius* species examined exhibit a lower jaw similar to that of *Opsariichthys*. The number of mandibular pores ranges from 6 to 12 in both genera.

The dentary of *Leuciscus*, *Barbus* and *Labeo* is invariably short and narrow, tapering anteriorly in *Barbus* and *Leuciscus* but expanded in *Labeo*. In these genera the jaws curve sharply medially, whereas in all those genera mentioned previously the curve is a shallow one (see below).

The dentaries of *Luciobrama*, *Aspiolucius* and *Pseudaspius* have weakly developed symphysial processes; posteriorly the curve of the dorsal margin of the coronoid process is continued by the anguloarticular instead of there being an abrupt discontinuity as noted in *Aspius* (Fig. 36C). This form of articulation of the dentary with the anguloarticular is encountered in many 'primitive' teleosts (*Elops*, *Esox*, *Hoplias* and most of the characoids). In the case of *Luciobrama*, etc. it is likely that this type of lower jaw has been derived from the condition found in *Aspius* and *Opsariichthys*, the larger adductor mandibulae muscles requiring a greater area of bone for insertion. It is of interest to note that the posterior part of the lower jaw of *Oreoleuciscus* (Fig. 36B) greatly resembles that of *Luciobrama*, although the anterior part of the jaw is narrowed and curved like that of a 'typical' leuciscine.

Matthes (1963) and Liem (1970) pointed out that the presence of a high coronoid process on the lower jaw increased the power and speed at which the jaws could be closed. Only in *Elopichthys*, *Schizothorax*, *Erythroculter*, *Pelecus*, *Leuciscus* and some species of *Barbus* and *Labeo* can the coronoid process be considered as relatively high. In such exclusively piscivorous cyprinids as *Luciobrama*, *Barilius bola* and *Macrochirichthys* the process is low. In this respect it is probably the distance and angle of the coronoid process from the point of articulation with the quadrate which is more important. It will be noted by referring to Fig. 36 that in the long-jawed species in which the jaw is aligned at an angle (represented here by *Barilius bola*), the coronoid process is placed well posteriorly and is relatively low, whereas in *Elopichthys*, where the jaw is aligned horizontally, the coronoid is high, although still placed well back.

In some cyprinids the coronoid process is placed close to the anterior tip of the jaw. This apparent forward movement is due in part to the greater mesial curvature of the dentary and its subsequent foreshortening, seen particularly in *Labeo* and *Barbus* species where it is correlated with the broadening of the head. In these fishes the higher the coronoid region the greater the area available for the adductor mandibulae muscles which operate at a greater angle than those in the long-jawed species, where the muscle fibres lie partially horizontally. Dr Keith Banister has pointed out to me that in some species of *Barbus* this forward movement of the coronoid process is more real than apparent, and that it seems correlated with a definite shortening of the ethmoid region.

Ramaswami (1955b : 223) remarks that the upper jaw bones of cyprinids show a uniform morphology. Generally speaking this is true. Most cyprinids rely on protrusion of the upper jaw and employ suction feeding (Alexander, 1964, 1966, 1967 & 1969), and this requires a particular association between the maxilla and the premaxilla.

The extent of movement of the upper jaw in *Luciobrama* appears to be rather restricted. The ascending processes of premaxillae are not particularly long, and manipulation of preserved material shows that the upper jaw is not very protractile.

From measurements of the bones and manipulations of the jaws of *Barilius* it would seem that the shorter jawed species possess more mobile upper jaws than do the longer jawed species such as *B. bola* where, like *Macrochirichthys*, there appears to be very restricted movement of the premaxilla.

It must be emphasized that these observations have been made on preserved material only and so must be open to doubt.

In *Elopichthys* the upper jaw is so modified that the only kind of movement possible is rotation against the ethmoid (see p. 41), and jaw action here must be centred upon fast snapping action (an almost parallel jaw action can be seen in the African characoid, *Phagoborus*).

Greenwood (1974) noted that in piscivorous cichlids the long lower jaw is accompanied by a highly protrusile upper jaw (this is particularly noticeable in the South American cichlid genus *Petenia*). But in the long-jawed piscivorous cyprinids the reverse seems to be the case. Here the elongation of the jaws has been by posterior extension and this has necessitated a correlated movement of the hyopalatine arch so that the shaft of the hyomandibula is perpendicular and the jaw articulation is moved backward and downward to below the orbit. There has been no great extension of the anterior ascending process of the upper jaw nor of the ethmoid–vomerine region of the cranium. Only in *Elopichthys* has any marked modification been achieved in the forward extension of the upper jaw. However, I consider this fish to be a 'long-headed' rather than a 'long-jawed' cyprinid and in these species the hyopalatine arch is differently orientated (see further discussion on p. 61).

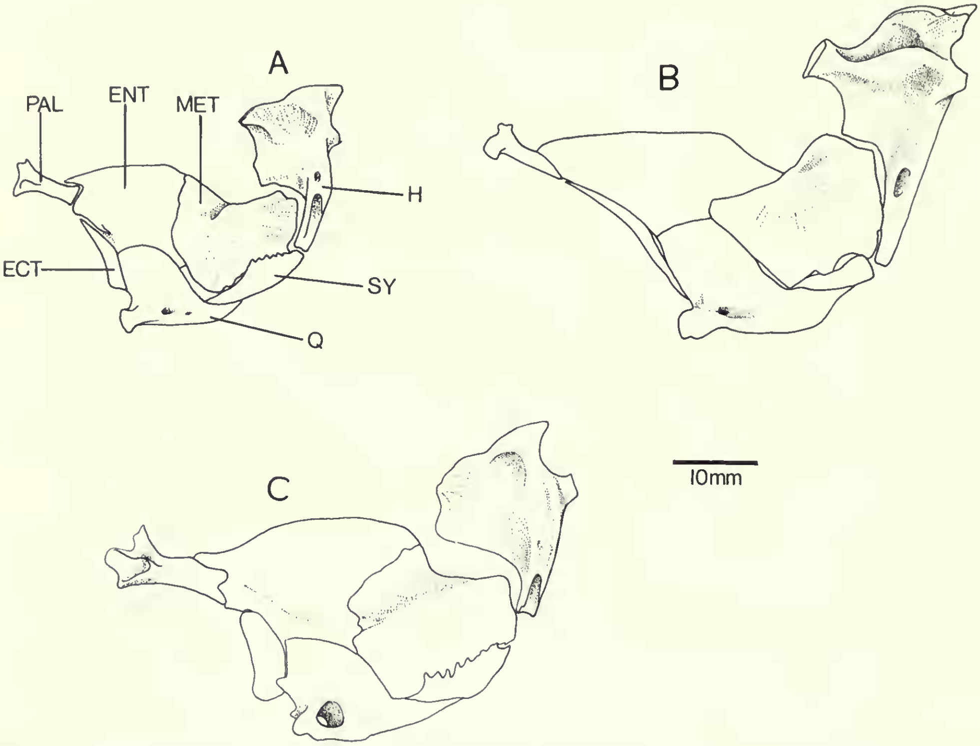

Fig. 37 Hypopalatine arches shown in lateral view of: A. *Aspius vorax*, B. *Elopichthys bambusa*, C. *Erythroculter mongolicus*.

Hyopalatine arch (Figs 37 & 38)

I am unable to determine the precise nature of the elements constituting the hyopalatine arch in *Aspiolucius* and *Pseudaspius*. From radiographs it is possible to follow the outline of the bones, and these closely resemble the description given below for *Aspius*.

In *Aspius* (Fig. 37A) the ventral limb of the *hyomandibula* is short, the posterior border of the bone is convex and the lateral face bears a shallow depression. By contrast, the hyomandibula of *Elopichthys* (Fig. 37B) has a well-developed flange in this position.

The hyomandibula in *Opsariichthys* and *Barilius* (Figs 38A & B) is vertically aligned; the ventral limb is thick and long. Here too the lateral face bears a wide flange along which the *dilatator operculi* muscle runs.

A lateral flange is also present on the hyomandibula of *Barbus tor* but is absent in other species of *Barbus* I have examined.

In *Macrochirichthys* the hyomandibula has a lateral process on which is inserted the *levator arcus palatini* muscle (see Howes, 1976). Similar lateral processes serving for muscle attachment are present in *Pseudolaubuca*.

In *Hypothalmichthys* the lateral surface of the hyomandibula is strongly curved outward so that the suspensorium lies beyond the cranial border.

The *quadrate* of *Aspius* (Fig. 37A) is a short high bone separated by a wide area of cartilage from the metapterygoid. The anterior border is perpendicular, the dorsal border curved. A small foramen is present posterior to the articulatory condyle, a feature shared with *Luciobrama* (see p. 15). I have found such a foramen in four other genera: *Elopichthys* and *Erythroculter*, in which it is large (in the skeleton of *Elopichthys* examined, the foramen is present only in the right quadrate); *Pseudoxygaster* and *Macrochirichthys*, in which it is minute.

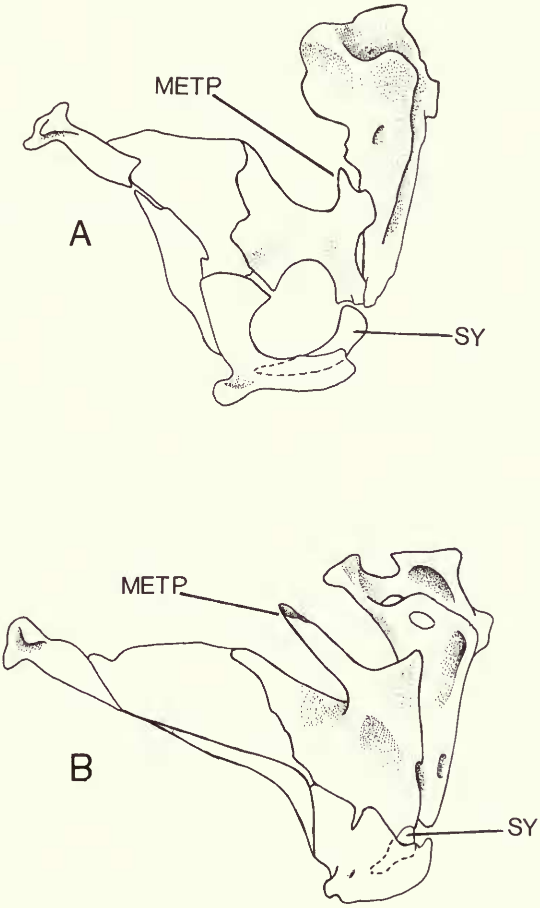

Fig. 38 Hyopalatine arches shown in lateral view of: A. *Opsariichthys uncirostris*, B. *Barilius bola.*

The quadrate of *Opsariichthys* is a thin, curved bone, the dorsal border being concave and forming the margin of a large fenestra. This feature is shared with *Zacco*, where the fenestra is not so well developed, with *Macrochirichthys*, in which it is about equally developed, with *Pseudoxygaster* and with *Salmostoma.* Further discussion of the metapterygoid–quadrate fenestra appears on page 46.

The *symplectic* is an extensive bone in most of the genera examined. Medially it overlaps the posterior extension of the quadrate. In *Opsariichthys* the symplectic forms the postero-ventral border of the metapterygoid–quadrate fenestra. In *Barilius* it is a small element lying medial to the quadrate (Fig. 38B). Ramaswami (1955b : 224) comments on the symplectic in other cyprinid genera.

A *dermopalatine* has not been found in any of the genera examined.

The *autopalatine* varies little in the genera examined. Differences involve the degree of development of the articular head with the ethmoid; it may be very wide and flat in this region as in *Hypophthalmichthys* or rod-shaped as in *Luciobrama*. The medial face of the palatine is almost always concave. There is also variation in its articulation with the entopterygoid. Usually this is by way of a right-angled indentation in the entopterygoid bnt sometimes as in the case of *Barilius bola* (Fig. 38B) and *Elopichthys* (Fig. 37B) the edge of the palatine may be sloped and partly overlapped laterally by the entopterygoid. In both *Opsariichthys* and *Barilius* the palatine is laterally compressed and in the former genus bears a ventral keel.

The *ectopterygoid* in most cyprinids is a thin sheet which partly underlies the medial face of the quadrate and the ventral margin of the entopterygoid. The 'generalized' condition of this bone appears to be wide with a slightly concave to convex anterior mrgin. In the long-jawed taxa such as *Elopichthys*, *Macrochirichthys* and *Barilius bola* the ectopterygoid is very narrow with a markedly concave anterior border, *Figs* 37B & 38B. Only in *Luciobrama* (and possibly in *Aspiolucius*) does the ectopterygoid appear to be rod-shaped.

The *entopterygoid* is generally short and deep, its dorsal border rounded. In *Luciobrama*, *Aspiolucius*, *Pseudaspius* and *Elopichthys* the bone is narrow and long with a straight dorsal margin. In broad-headed species of the genera *Barbus* and *Labeo* the entopterygoid is markedly medially directed and often bears a thick ridge along the fold for the insertion of the *adductor arcus palatini* muscle.

Ramaswami (1955a) notes the presence in *Labeo macrostoma* and *Cyprinus carpio* of a mesial facet on the entopterygoid which articulates with the lateral ethmoid. Other *Labeo* species I have examined have this facet variously developed and it seems to be well developed in those species with a long ethmoid but is virtually absent in those with a short ethmoid. In other cyprinid genera this part of the entopterygoid is usually a wedge-shaped platform and varies considerably in size.

The *metapterygoid* of almost all genera examined is deep with the lateral ridge developed to varying degrees depending on the angle at which the bone is directed mesially toward the parasphenoid. The dorsal border is invariably concave (the one exception to this rule being *Luciobrama*). In *Opsariichthys* (Fig. 38A) the metapterygoid is narrow and axe-shaped, its ventral border forming the dorsal margin of the metapterygoid–quadrate fenestra. Posteriorly it is sutured to the hyomandibula. There is a small ascending process on the dorso-posterior edge of the bone (METP). *Barilius bola* has a similar metapterygoid process but in this case it is developed as a long anteriorly directed spine which serves both as the point of origin for the *adductor mandibulae* A3 and for the insertion of the *levator arcus palatini* muscles. Posteriorly, the metapterygoid has a long perpendicular border in contact with the hyomandibula (Fig. 38B). A metapterygoid spine appears to be present in all the species of *Barilius* I have examined but in none it is developed to the same degree as in *B. bola*. There is no metapterygoid spine in *Zacco*.

The significance of the metapterygoid–quadrate fenestra has been discussed by Regan (1911)[1] and remarked on again by Ramaswami (1955b), Weitzman (1962), Gosline (1973, 1974 & 1975) and Howes (1976). Most authors, including Regan (1911), have assumed it to be a generalized or primitive character. Gosline (1973), however, expressed doubts about this, and was inclined to attach more significance to the state of the entire pterygoid complex.

In those genera with a long postorbital cranium (*Luciobrama*, *Aspiolucius*, *Pseudaspius*) the hyomandibula has a short ventral limb which is directed anteriorly, and there is also an increase in the length of the pterygoid bones but not in their depth. In the majority of cyprinids the hyomandibula is a deep bone with its shaft aligned almost perpendicular to the skull. The pterygoid bones are also short and deep and in those genera with wide and depressed crania the metapterygoid is often acutely directed mesad toward the parasphenoid (e.g. *Labeo*) thus providing a large space to accommodate the thick *adductor mandibulae* muscles.

---

[1] Regan (1911) stated that a fenestra is present in *Chela* but he did not designate the species. I have been unable to detect it in any species now assigned to the genus *Chela* (Bănărescu, 1968) and I suspect that Regan was in fact referring to *Macrochirichthys*, which he knew as *Chela macrochir*. It would seem that the skeleton of *Macrochirichthys macrochirus* in the BMNH collection which was available to Regan was the only skeleton bearing the generic name *Chela* at the time he would have examined it.

If a comparison is made with the situation in characoids where the metapterygoid–quadrate fenestra is widespread the following points emerge.

In the majority of characoids there does not seem to be the same degree of dorsal extension of the pterygoid bones as occurs in cyprinids. The ectopterygoid and overlying entopterygoid are long (a correlate of the generally more elongate snouts and jaws of characoids). However, in broad-headed characoids such as *Erythrinus*, *Lebiasina*, *Citharinus*, and in some leporinids and prochilodontids the pterygoid bones are deep and directed acutely mesad as in the broad-headed cyprinids. In these cases the metapterygoid–quadrate fenestra is either absent or reduced. Furthermore, it is noted that the *adductor mandibulae* and *levator arcus palatini* muscles in the characoids do not utilize the surfaces of the pterygoid bones to the same degree as in the cyprinids and in those characoids where the *adductor mandibulae* muscles are particularly extensive (*Hepsetus*, *Ctenolucius*, *Acestrorhynchus*, *Salminus*) there has been a forward extension of the hyomandibula along the dorsal margin of the metapterygoid thereby providing the additional surface area of attachment (see Roberts, 1969).

The fenestra between the quadrate and metapterygoid is certainly a functional device which would seem to serve either to relieve stresses by directing forces generated in the lower jaw around the perimeter of the pterygoid bones and into the cranium or perhaps, more importantly, it acts as a type of hinge which enables the pterygoid bones to undergo lateral rotatory movements. Again, it is noted that those characoids in which the fenestra is reduced are those in which there is little or no development of the symphysial articulation of the lower jaw – as in most of the cyprinids. There are also differences in the articulation of the palatine with the ento- and ectopterygoids in the broad-headed and narrow-headed cyprinids which indicate different degrees of lateral rotation.

The exact functional significance of this fenestra is not obvious and may only be realized when all the vectors have been analysed. Whatever its use as a stress-relieving or force-directing device, one possible advantage of this feature seems that in *Macrochirichthys*, *Pseudoxygaster* and *Salmostoma* its presence has allowed the jaw articulation to move further forward than in other cyprinids. The jaws of *Macrochirichthys* are proportionately as long as those of *Barilius bola* and it might be supposed that retention of such a fenestra would also have been an advantage to this bariliine. However, in *Barilius* there is a well-developed *adductor mandibulae* A3 muscle extending from the dorsal process of the metapterygoid (see p. 55), whereas in *Macrochirichthys* and *Pseudoxygaster* A3 originates from the hyomandibula (see Howes, 1976 : 242). The development of this muscle and bone in *Barilius* as a functional unit could account for a ventral expansion of the hyomandibula so as to occlude any opening that may have been present in the ancestral form. Some confirmation of this comes from my current studies on *Salmostoma* in which there is a reduction in the size of the metapterygoid–quadrate fenestra in those species with the longer jaws.

My current researches on *Macrochirichthys* indicate that neither it, *Salmostoma* nor *Pseudoxygaster* are at all closely related to *Opsariichthys* or *Zacco* and so the metapterygoid–quadrate fenestra cannot therefore be regarded as a synapomorph feature. I conclude that it represents a primitive cypriniform character (widespread occurrence in the Characoidei) and that in *Opsariichthys* and those genera in which it occurs it should be considered as plesiomorph. Possibly the potentiality for its development was inherited in several lineages and was realised (as in *Macrochirichthys*) under the necessary combination of selective pressures.

Opercular series

In *Aspiolucius*, *Pseudaspius* and *Aspius* the morphology of the opercular elements closely resembles that in *Luciobrama*; the pre-, inter- and subopercula are extensive bones. The operculum has a long concave dorsal border and a well-developed anterior extension for the insertion of the *dilatator operculi* muscle. The medial strut contains two ventral foramina. The preoperculum has 9–10 pores along the ventral border.

In *Elopichthys* the vertical limb of the preoperculum is longer and the horizontal limb shorter, than in the genera mentioned above. The ventral border bears 6 pores. The medial strut of the operculum is feeble and contains a single large foramen.

In *Opsariichthys* and the majority of *Barilius* the lower limb of the preoperculum does not extend so far forward and the ascending process of the limb is almost vertical. Three pores of the mandibular lateral line canal are present on the ventral border. The operculum is deep, with a short dorsal border; it lacks the prominent anterior extension for the *dilatator operculi* muscle. The interoperculum in *Barilius bola* has been greatly reduced in length, a change in proportion correlated with the backward shift of the jaw articulation (see above, p. 43).

Most *Barbus* and *Labeo* species have a wide, vertically orientated preoperculum which has a short ventral limb. The operculum generally is deep, with a short dorsal border, but *Barbus tor*, *B. longiceps* and *B. barbus* all have a long dorsal border.

A large operculum with a long dorsal border appears characteristic of some predatory cyprinids, e.g. *Pelecus*, *Macrochirichthys* and *Erythroculter*, where it is associated with a shallow, acutely angled preoperculum. This is the situation encountered in *Luciobrama*, *Aspiolucius*, *Pseudaspius* and *Aspius* in which are present noticeably elongate pre-, inter- and subopercula. There is an opposite situation in the long-jawed *Barilius* species where an operculum with a short dorsal border is associated with deep and narrow opercular elements.

Hyoid and branchial arches

HYOID ARCH. There is little variation in the morphology of the elements comprising the hyoid arch in the genera studied.

All the branchiostegal rays, apart from the first, are expanded proximally.

The urohyal is variously developed, sometimes being channelled ventrally as in *Aspius* and *Opsariichthys*, or flat, as in *Barilius* and *Barbus*. The medial plate can be short and high as in *Schizothorax* or reduced to a slight ridge as in *Elopichthys*.

The basihyal is greatly elongated in *Luciobrama* (p. 17), a condition also encountered in *Aspiolucius* and *Elopichthys*.

THE BRANCHIAL ARCHES. Intergeneric comparison reinforces Ramaswami's (1955b) opinion that there is a general uniformity in the branchial elements of cyprinids.

I have not found either first or fourth infrapharyngobranchials represented as an ossified element.

There is some variation in the development of the dorsal processes on the epibranchials.

The *pharyngeal teeth* of *Aspiolucius* are arranged in two rows with 3–5 teeth, those of *Pseudaspius* in two rows (2–4), of *Aspius* in two rows (3–5) and of *Elopichthys* in three rows (5–3–2 or 5–4–2).

The whole problem of what constitutes a primitive pharyngeal dentition in the cyprinids has been discussed at length by numerous authors (see Nelson, 1969 : 513). In the case of *Luciobrama* it seems evident that a single row of pharyngeal teeth is a derived condition.

Weberian apparatus and swimbladder

In *Aspius*, *Elopichthys* and, as far as I can tell from radiographs, in *Aspiolucius* and *Pseudaspius*, the os suspensorium is curved anteriorly, the lateral processes of the fourth centrum (PR4) are short and thin, and those of the second centrum (LP2) are curved slightly dorsad. In all these genera, except *Aspius*, the second neural plate contacts the supraoccipital, and the fused neural complex is in contact with a supraneural plate.

In *Luciobrama*, *Aspius* and *Elopichthys* (Figs 39A & B) the second and third centra are not completely fused. Dorsally a distinct separation can be detected; ventrally this is not so clearly defined since the suture line is always visible and there is never the complete fusion seen in other cyprinids where the division between the centra has become completely obliterated.

In *Opsariichthys* and *Barilius* (Fig. 39D) the lateral processes of the fourth centrum (PR4) are weakly developed and directed posteriorly. The lateral processes of the second centrum are greatly expanded laterally and are not curved. The tripus in these genera is very elongate. The second and third centra are separated in *Opsariichthys* but they are fused in *Barilius*.

In *Schizothorax*, *Barbus* and *Labeo*, and in the majority of genera examined, the os suspensorium is curved anteriorly and the lateral processes of the fourth centrum are well developed; those of *Barbus* are often expanded distally.

In *Macrochirichthys* and *Pseudoxygaster* the os suspensorium is very short and vertically directed; the tripus is elongate and the second and third centra are separated and in *Pelecus* (Fig. 39C) the os suspensorium is almost horizontally directed. Although *Pelecus* has been included in the Cultrinae along with *Macrochirichthys* and *Pseudoxygaster* (see Bănărescu, 1967) there are many differences in the structure of the anterior part of the vertebral column. The first and second centra of *Macrochirichthys* and *Pseudoxygaster* are greatly modified, whereas in *Pelecus* these centra are of a generalized nature. (Work is in progress on the description and analysis of these elements in the Cultrinae.)

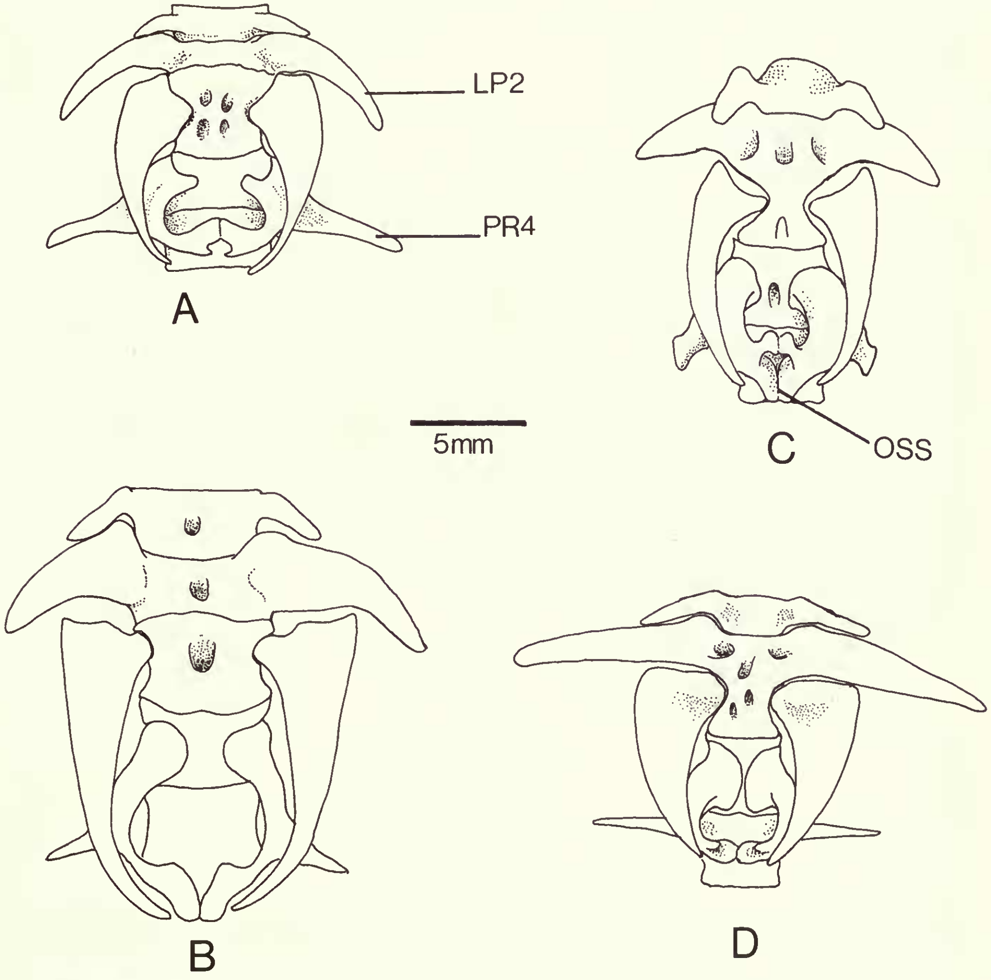

Fig. 39 Weberian apparatus shown in ventral view of: A. *Aspius vorax*, B. *Elopichthys bambusa*, C. *Pelecus cultratus*, D. *Barilius microcephalus*.

Sorescu (1972) studied the Weberian apparatus of representatives of the subfamilies Danioninae and Cultrinae. Her ideas of primitive and specialized characters exhibited by these skeletal elements are ill-defined and her conclusions concerning the relationships of the Cultrinae and Danioninae – neither of which are monophyletic assemblages – are, in my opinion, invalid.

As far as I am aware no comparative study has been made of the *swimbladder* throughout the Cyprinidae. Tchang (1933) frequently notes the condition of the swimbladder in various genera.

He mentions that the organ in *Opsariichthys* is enclosed in a bony capsule. I can find no evidence to justify this statement.

The swimbladder in most of the genera studied is a simple bipartite structure. In some genera at present included in the Cultrinae there is a further posterior division.

Pectoral girdle

In *Aspiolucius*, *Pseudaspius* and *Aspius* the pectoral girdle is similar to that of *Luciobrama*. In all these genera the horizontal limb of the cleithrum is directed forward to a point below the anterior border of the prootic, and (except in *Aspius*) it is bifurcated anteriorly. The coracoids are joined only anteriorly. The mesocoracoid in *Aspius* is a thin bridge of bone. The postcleithrum in *Aspiolucius* and *Aspius* is short, like that of *Luciobrama* but in *Pseudaspius* it is elongate. The supracleithrum is elongate in *Aspius*, while that of *Aspiolucius* and *Pseudaspius* is of a length intermediate between that of *Aspius* and *Luciobrama*.

In *Elopichthys* the anterior margin of the ventral limb of the cleithrum is very wide, the ascending limb short. The mesocoracoid is wide and the coracoids are joined medially for half of their lengths. The postcleithrum is very long and the supracleithrum as elongate as that of *Aspius*.

In both *Opsariichthys* and *Barilius* the vertical limb of the cleithrum is narrow. The coracoids are joined anteriorly, the mesocoracoids are long and narrow, the supracleithra elongate and the postcleithra very long and spine-like.

A similar kind of arrangement, but with the upright and horizontal arms of the cleithrum broadened, is found in *Barbus* and *Labeo*.

Throughout the cyprinids there appears to be considerable variation in the degree of development of the cleithral–coracoid fenestra which may, as in the case of *Chela*, be entirely lacking. The development of this feature appears to be associated with the variation of the pectoral fin muscles and ventral extension of the coracoids.

In *Salmostoma*, *Oxygaster*, *Pseudolaubuca*, *Paralaubuca*, *Pelecus*, *Pseudoxygaster*, *Chela* and *Macrochirichthys* there is a great expansion and complete, or almost complete, medial contact of the coracoids (see description of pectoral girdle of *Pelecus* by Rauther, 1950).

Regan (1911 : 28–29) states that '*Barilius*, *Danio* etc. agree with *Opsariichthys* in the form of the cleithra, rounded or pointed anteriorly, and these are connected by genera such as *Aspius* with *Leuciscus* and its allies, in which the cleithra are more expanded and truncated anteriorly . . . the *Barbus* group differs in that the cleithra are distinctly emarginate anteriorly'. Broadly speaking, the cleithra of all these genera are similar, but in *Barbus*, *Leuciscus* and *Alburnus* the curved dorso-lateral margin of the cleithral limb is raised into a blade-like ridge. Furthermore, it is not the case, as stated by Regan (see above), that all *Barbus* exhibit anteriorly emarginate cleithra. In *Barbus tor*, for example, the cleithra are forked anteriorly as in *Luciobrama*, providing two places of origin for the *sternohyoideus* muscle (see p. 19).

One variable element of the pectoral girdle is the postcleithrum. It is usually found as a long medially curved bone which reaches its most extensive development in *Macrochirichthys*. In some genera (e.g. *Salmostoma*) it is reduced to a short spike and in *Barilius* appears as a small scale-like bone, whilst in *Pseudoxygaster* it appears to be entirely lacking (although it may possibly be identified as a modified external scale above the pectoral fin).

Sorescu (1968) uses the morphology of the pectoral girdle as a principal character in differentiating cyprinid subfamilies. She has placed reliance on similarity of shape of the elements to indicate affinity. This has led, for example, to placing *Barilius zambezensis* in the Cultrinae without taking account of other *Barilius* species. Sorescu's failure to utilize other and probably more significant cranial characters, and her apparent failure to recognize parallelism, renders her conclusions doubtful.

Pelvic girdle

There is little variation in the pelvic girdle. In some genera the pelvic bone is only shallowly forked, but as far as I am aware there are no cyprinids with an unforked pelvic bone, the usual condition in characoids.

Appendicular skeleton

VERTEBRAL COLUMN. The total number of *vertebrae* in *Aspiolucius*, *Pseudaspius*, *Aspius* and *Elopichthys* ranges from 51 to 54 (*cf.* 55 in *Luciobrama*).

Of the other genera examined, only *Pelecus*, *Hemiculterella* and *Ochetobius* possess more than 50 vertebrae. It is to be noted that in *Ochetobius* the increased number is in the posterior abdominal region (i.e. between the dorsal and anal fin bases). No other member of the Cyprinidae has such a distance between the posterior ray of the dorsal and the origin of the anal fin. In all remaining genera examined the total number of vertebrae is from 41 to 49.

The more elongate cyprinid species show an increase in vertebral number (see Lindsey, 1975). The proportions of the centra in all cyprinid genera I have examined are virtually identical. Only in *Macrochirichthys* and *Pseudoxygaster* is there any appreciable elongation of the precaudal centra, but in none have the caudal centra been lengthened.

Table 1 Vertebral counts of some Cyprinid genera. These are arranged in groups of what I believe to be related genera. W = Weberian vertebrae. * = Second and third centra separate or partially separated. ? = Condition unknown. A = Abdominal. C = caudal vertebrae. T = total number. SN = Supraneurals

Genus	W	A	C	T	SN
Luciobrama	4*	30	21	55	12
Aspiolucius	4?	27	23	54	13
Pseudaspius	4?	26	21	51	11
Aspius	4*	25–26	24	51–52	13–14
Elopichthys	4*	25–27	22–23	52–54	15–16
Barilius spp	4	16	23–25	43–45	11
Barilius bola	4	22	21	48	13
Opsariichthys	4*	19	21	44	6–7
Oxygaster	4*	16	23	43	13
Pseudolaubuca	4*	17	26	47	15
Pseudoxygaster	4*	19	21	44	12
Macrochirichthys	4*	23	22	49	16
Hemiculterella	4*	17	23	44	10
Pelecus	4	24	24	52	22–23
Erythroculter	4	19	23	46	7
Parabramis	4	19	21–22	45–46	5–6
Paralaubuca	4	16	22	42	12
Schizothorax	4	22–25	19–20	45–49	11
Oreinus	4	22–24	20–21	47–48	12–13
Leuciscus	4	21–22	20–22	46–48	10–12
Abramis	4	20	22	46	10
Ochetobius	4	34	22–23	60–61	14

The total number of vertebrae in *Barbus* and *Labeo* never exceeds 48 (Banister and Reid, pers. comms).

The *supraneurals* vary considerably in their development and in their number, ranging from 5 to 6 in *Parabramis* to 23 in *Pelecus*. In *Luciobrama*, *Aspiolucius*, *Pseudaspius*, *Aspius* and *Elopichthys* they are thin rod-like structures, numbering 11–16, whereas those of *Schizothorax*, *Oreinus*, *Barbus* and *Labeo* are plate-like, numbering 10–13. In *Semiplotus* the supraneurals reach their most marked degree of development, expanding between the neural spines to form a rigid pre-dorsal septum along the vertebral column.

In *Macrochirichthys* the anterior supraneurals are horizontally aligned and are in contact with the enlarged neural spines (Howes, 1976 : 244). A similar arrangement is present in *Pseudoxygaster* and *Pseudolaubuca*.

Median fin skeleton. In all cyprinid genera examined the first proximal dorsal pterygiophore is expanded. In those with well-ossified anterior dorsal rays the corresponding proximal pterygiophores bear lateral struts.

Roberts (1973) comments on the number of radials (pterygiophores) supporting the dorsal and anal fin rays in cyprinids. He notes that there are three in *Opsariichthys* but that according to Bridge (1896) there are usually two in cyprinids. However, Bridge (*op. cit.*) did in fact identify three elements in all the cyprinids he examined, namely species of *Barbus*, *Cyprinus*, *Abramis* and *Tinca*.

In all the species I have examined there are three elements, distal, medial and proximal pterygiophores.

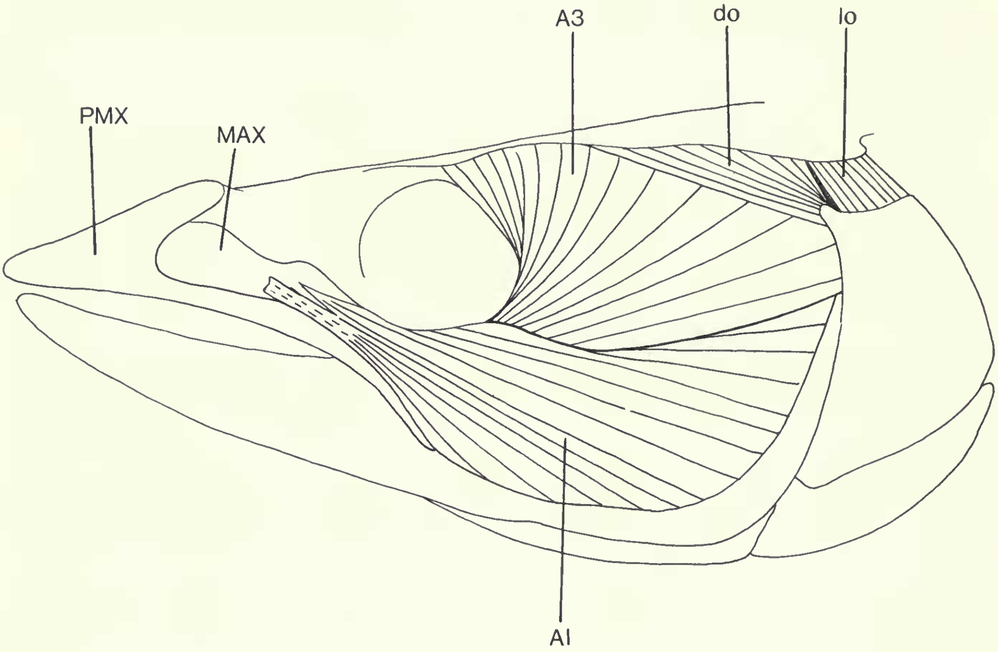

Fig. 40 *Elopichthys bambusa*, cranial musculature, superficial elements.

Caudal fin skeleton. In all the genera examined there is a marked consistency in the construction of the caudal fin skeleton. The only variation appears to be in the size of the first hypural and the number of epurals (either one or two).

Roberts (1973) gives 10+9 as the count for the principal caudal rays, but I count 9+9 in all genera examined.

Shukla & Verma (1972) have described the caudal fin skeleton of *Barilius bola*. They have, however, misidentified many of the elements and have used published descriptions of other cyprinids in their comparative treatment. Thus their conclusions concerning the 'primitive' nature of this species are very dubious.

Myological characters

Cranial muscles

Several workers have described the cranial muscles of various cyprinids (e.g. Takahasi, 1925, several genera; Ping *et al.*, 1958, *Cyprinus*; Saxena, 1960, *Garra*; Matthes, 1963, *Labeo*, *Barbus*, *Barilius* and other genera; Munshi & Singh, 1967, *Labeo* and *Cirrhina*; Meinel *et al.* 1970, *Barbus nasus*, *Ctenopharyngodon* and *Squalius*).

From a superficial dissection of the type specimen of *Aspiolucius esocinus* it would appear that the cranial muscles of this species are like those in *Luciobrama*. The *dilatator operculi* and *levator arcus palatini* are developed in the same way and the *adductor mandibulae* muscles are similarly arranged. I was unable to examine the arrangement of the deeper muscles. *Pseudaspius* and *Aspius* both exhibit the same basic arrangement as *Luciobrama*.

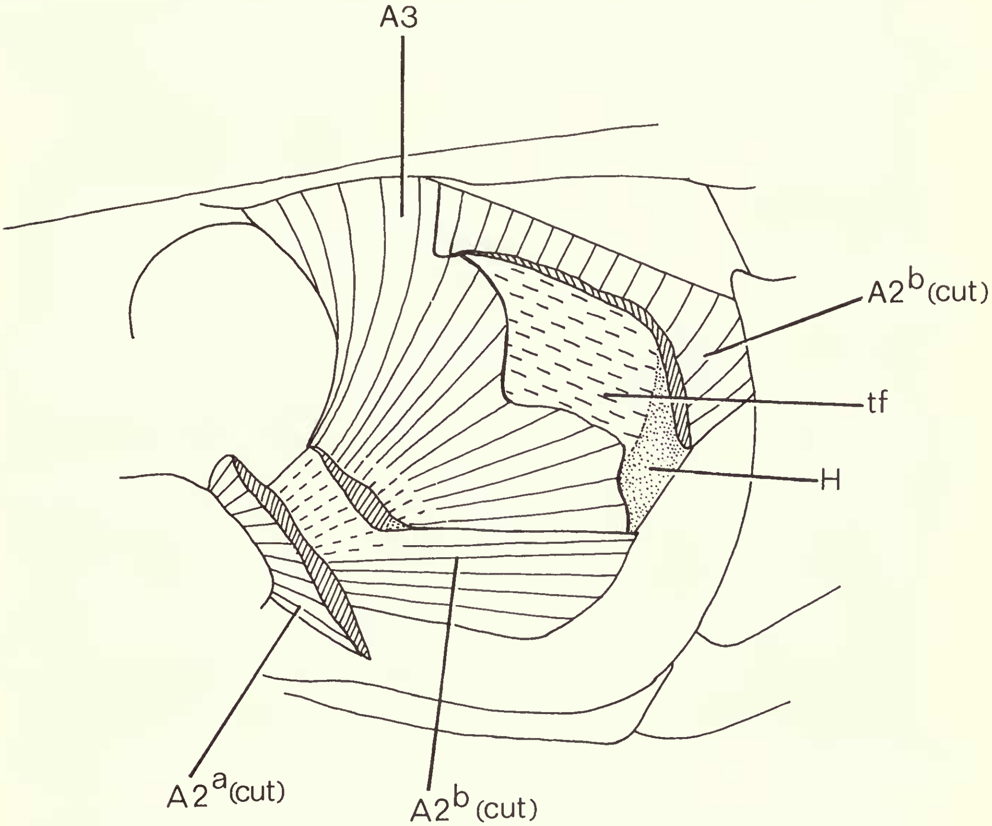

Fig. 41 *Elopichthys bambusa*, cranial musculature, deeper layers. *Adductor mandibulae* A2 is cut through to expose A3, which in turn is cut to show the tendinous fascia.

The cranial muscles of *Aspius aspius* have been described by Suslowska (1971). I have compared the muscles of *Aspius vorax* with those of *A. aspius* and find them to be of almost identical morphology. Suslowska (1971) does not recognize the conventional divisions of the *adductor mandibulae*. Although she points out that the external portion (A1) inserts on the maxilla, she does not state that it is bifurcated at this insertion.

The *levator arcus palatini* is extensive; a tendinous sheet extends through the lateral surface of the muscle to join the preoperculum and this provides a site of origin for part of the *adductor mandibulae* (A2). The *levator* is divided by A3. An *adductor arcus palatini* is present.

Suslowska (1971) noted the presence of an *adductor hyomandibulae*. The form of this and the other muscles she describes for *A. aspius* are as those in *A. vorax*.

The musculature of *Elopichthys* (Figs 40–44) resembles that of *Aspius* in that the *adductor mandibulae* is separable into its various parts only anteriorly. The *adductor mandibulae* A1 inserts via two tendons onto the maxilla (Fig. 40). A2 inserts onto the rim of the anguloarticular. Aw is poorly developed. The morphology of the inner element, A3, differs quite considerably from that described in any other cyprinid. This muscle originates partly from the frontal, partly from the pterosphenoid basin (see p. 32 & Fig. 42) and partly from the dorsal aspect of the sphenotic. Laterally it stems from the face of the sphenotic and pterotic and from a tendinous fascia covering the hyomandibula (tf, Fig. 41).

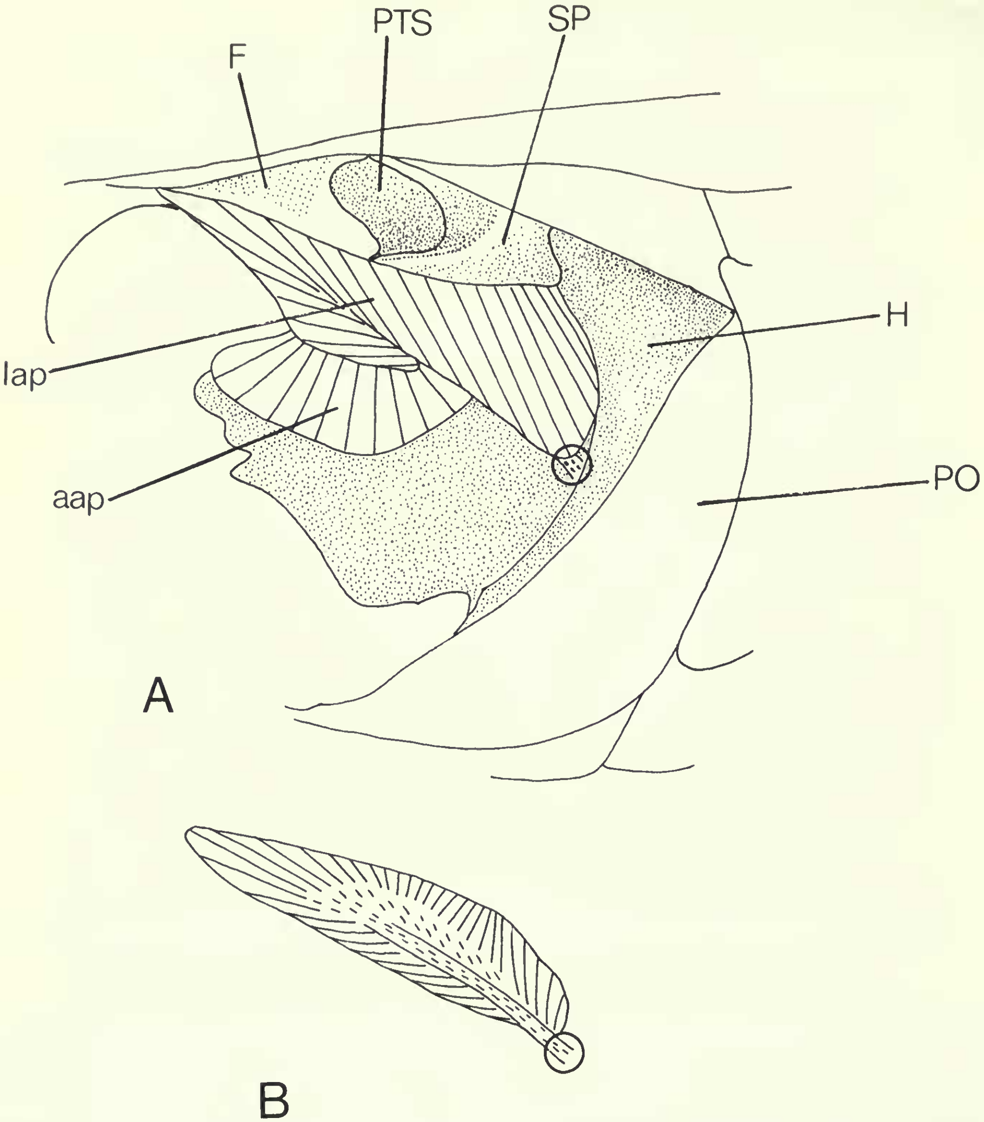

Fig. 42 *Elopichthys bambusa*, cranial musculature. A. Deep dissection to show *levator arcus palatini*; the *adductor mandibulae* muscles having been removed. B. Inner section of *levator arcus palatini*. The circle indicates that part of the tendon of the inner muscle which is visible before the outer layer is removed.

The *levator arcus palatini* in *Elopichthys* runs from the lower border of the frontal, the faces of the pterosphenoid and the sphenotic. The muscle is a complex one; the anterior bundle of fibres, which runs from the frontal, joins a medial pinnate sheet of fibres which originates from the face of the pterosphenoid and sphenotic to insert on the hyomandibula (Fig. 42A). The ventral border of this element is a stout tendon. When this outer layer is removed there is revealed a pinnate medial section with its fibres running in the opposite direction (Fig. 42B). When this medial layer is removed there is yet another, triangular sheet bordered anteriorly by a wide tendon (tlap, Fig. 43). This tendon stretches from the ventral surface of the frontal to insert upon the edge of the metapterygoid. The muscle fibres arise in part from the frontal but mostly from the sphenotic. Insertion is along the medial face of the hyomandibula. I would identify this medial element as an *adductor hyomandibulae*.

The *adductor arcus palatini* is a stout muscle which stems from the base of the prootic to insert ventrally upon the metapterygoid. The *dilatator operculi* runs across the upper border of the levator *arcus palatini* from the pterotic and sphenotic to the anterior process of the operculum. Medially the muscle originates in part from the face of the hyomandibula (a condition also found in *Pseudaspius*). Suslowska (1971) states that the *dilatator* inserts upon the hyomandibula in *Aspius*.

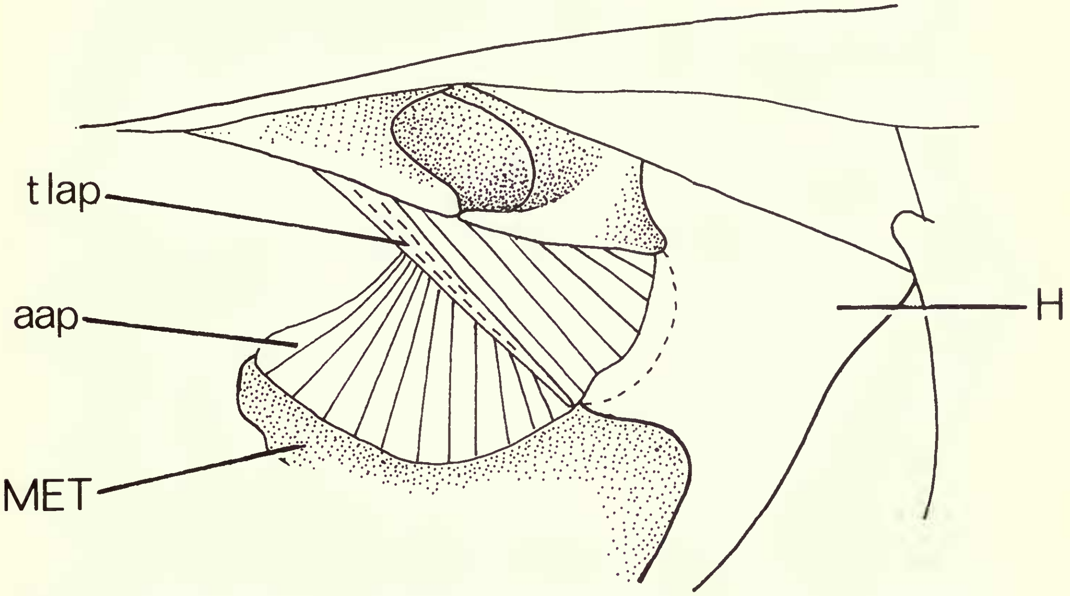

Fig. 43 *Elopichthys bambusa*, cranial musculature. The outer layers of the *levator arcus palatini* have been removed to expose the inner layer and the *adductor arcus palatini*.

In *Opsariichthys*, *adductor mandibulae* A1 is a single element inserting on the maxilla; A2 is a large muscle inserting on the anguloarticular and separated medially from A3 by the *levator arcus palatini*. Aw is present. The *dilatator operculi* originates from a discrete lateral fossa formed by the sphenotic. It is not covered by any part of the *adductor mandibulae* since this complex muscle originates below its ventral border.

In *Barilius* the *adductor mandibulae* A1 is a narrow, divided element (Matthes, 1963, recognized divisions A1a and A1b) the anterior part of which is bordered ventrally by a strong *ligamentum primordium*. It inserts along the lateral face of the maxilla. The larger element inserts via a thick tendon medial to the outer element. (In *Barilius bola* the medial section of A1 joins the maxilla along its distal border; there is no tendon of insertion, see Fig. 44.)

The A2 section of the *adductor* in *Barilius bola* and other long-jawed *Barilius* species is extensive, and originates from the preoperculum, pterotic and sphenotic; it gives rise to a reduced Aw section. A3 originates from the dorsal process of the metapteryoid (see p. 47). This process also provides the insertion area for the *levator arcus palatini* which originates from the ventral margin of the frontal and from the sphenotic. The *dilatator operculi* runs from the posterior part of the sphenotic process and is covered by A2. The *adductor arcus palatini* is well developed. In other, shorter-jawed *Barilius* species (e.g. *ubangensis*, *bendelisis*, *ornatus*) *adductor mandibulae* A2 is not as extensive, does not cover the *dilatator operculi* and does not originate from the sphenotic; the metapterygoid process is reduced and the *adductor arcus palatini* is small. In other words, the cranial muscle arrangement greatly resembles that of *Opsariichthys* (see Takahasi, 1925). Indeed, this basic type of morphology has been found in all the other cyprinid genera examined. There are, of course, modifications, as for example in *Oxygaster* and *Pseudolaubuca* where the anterior part of the *adductor mandibulae* A1 is narrowed and tubular; the dorsal part of the *levator arcus palatini* in *Pseudolaubuca* extends to insert upon the operculum together with the *dilatator operculi*; the *dilatator operculi* is divided in *Labeo*, and the *levator arcus palatini* is complexly divided, as described in this paper for *Elopichthys* and in *Macrochirichthys* (Howes, 1976).

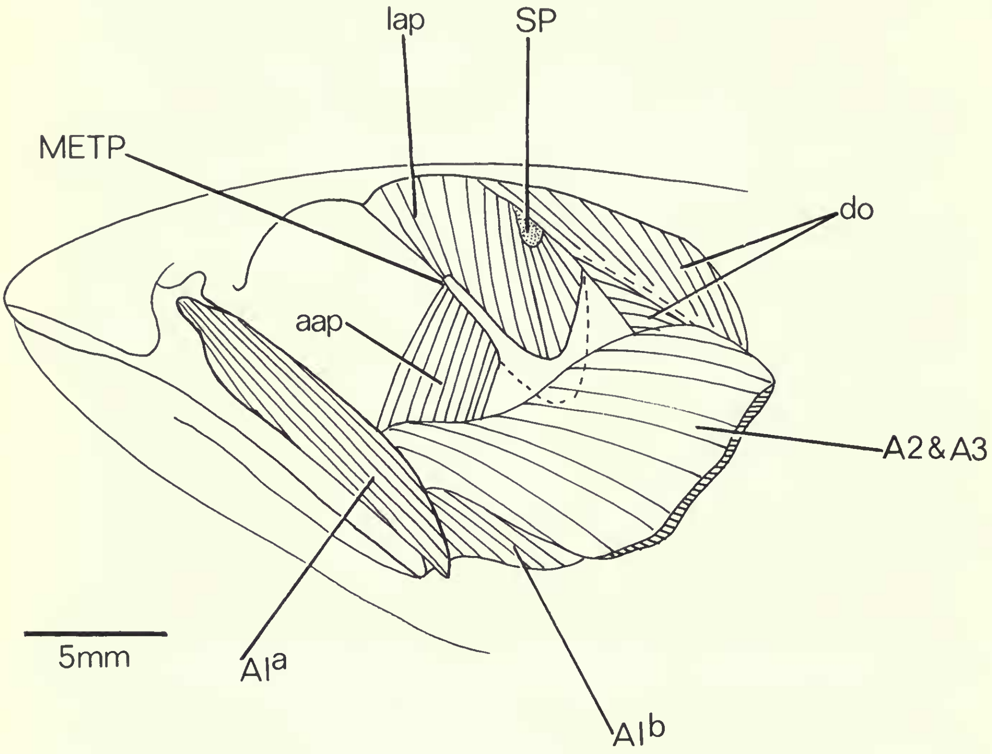

Fig. 44 *Barilius bola*, cranial musculature. *Adductor mandibulae* A2 and A3 are reflected to expose the deeper muscles.

A *ligamentum primordium* is not well developed in the syprinids studied. Only in *Barilius* have I have found it to be clearly differentiated and this not to the same extent as it is in most characoids. It may be a primitive character of cyprinids.

Earlier (p. 35), differences in the morphology of the *dilatator operculi* fossa were pointed out; four main types of fossa can be distinguished:

1. That involving mostly the sphenotic, with part of the frontal and pterotic, and lying laterally on the cranium, sometimes roofed by part of the frontal. This type of fossa is usually small and found in many cyprinid genera (e.g. *Opsariichthys*, *Zacco*, *Rasbora*, *Danio*, some *Barilius* and *Barbus* species and most cultrine species).
2. That involving a broad sphenotic process and a large area of the frontal, and which extends onto the cranial roof. This type of fossa is variously developed and can be extensive as in *Hypophthalmichthys*, where it occupies a large area of the frontal. It is characteristic of most genera currently assigned to the Leuciscinae. In Characoids a similar fossa is found in the Cynodontini (Howes, 1976).

3. That in which the sphenotic is developed below the frontal as a shelf. This type of fossa occurs in *Luciobrama* and its relatives. In characoids a similar type of fossa is found in *Salminus* (Roberts, 1969) and in *Brycon alburnus* (pers. obs.).
4. That in which the frontal and underlying sphenotic have become partly separated to form a foramen. This type of fossa is found in some *Barbus* species in *Cyprinus*, in *Labeo* and what are believed to be related genera (Reid, unpublished information). In characoids a similar foramen is found in some erythrinids, Acestrorhynchinae and Ctenoluciidae (Roberts, 1969; pers. obs.).

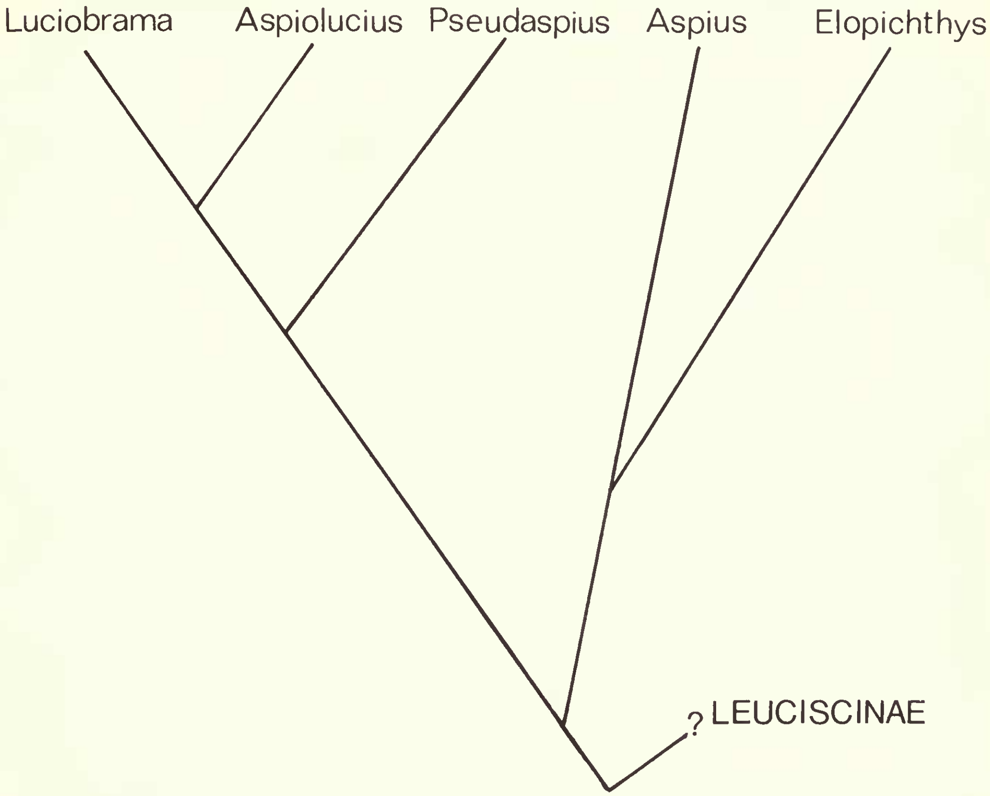

Fig. 45 Cladogram to illustrate the relationships of the aspinine genera.

There is also another condition, whereby the dilatator fossa is virtually absent. This occurs in the long-jawed *Barilius* species, e.g. *bola*, *loati*, and in *Macrochirichthys*. In these taxa the *dilatator operculi* muscle has either been so reduced (*Barilius*) or runs almost perpendicularly that the need of an inclined or horizontal shelf has been eliminated.

Roberts (1973) places little value on the condition of the dilatator fossa, believing it to be 'extremely labile'. Admittedly, we must be aware of parallelism in the formation of this as in any other character, but I believe the particular characteristics of this feature are indicators of relationships. Gosline (1975) also draws attention to the varying conditions of the dilatator fossa.

Hyoid and branchial muscles

During this present study no extensive comparison of these groups of muscles has been made. It is noted that the development of the hyoid muscles in *Luciobrama* and *Aspius* is relatively 'weak' when compared with that of the *Barbus* and *Labeo* groups of genera, where the hyohyoidei are well developed (see Matthes, 1963).

Various arrangements of the hyoid muscles are found in the cyprinids (i.e. *intermandibularis* absent; *protractor hyoidei* divided anteriorly), but the basic plan is little modified from that described in *Opsariichthys* by Takahasi (1925).

Concerning the branchial arch muscles, the only comments I am able to make at present concern the *retractor pharyngeus* of the upper branchial arches. Winterbottom (1974) points out two conditions of this muscle, one as observed in *Opsariichthys*, where it is undivided, and the other as in *Cyprinus*, where there are two divisions. In *Luciobrama*, *Aspius* and *Elopichthys* there appears to be a single element stemming from the basioccipital process and inserting along the medial edge of ceratobranchial 5.

Considerations of functional morphology in *Luciobrama*

The head of *Luciobrama* is enormously elongate, but as described in this paper, this elongation is entirely postorbital in extent. The preorbital part of the head is 'normal' and in fact greatly resembles that of *Aspius*, both in shape and proportions.

Suslowska & Urbanowicz (1957) have commented on the feeding mechanism of *Aspius*, and their comments may be of help in elucidating those of *Luciobrama*. These authors compared *Aspius* with *Cyprinus* and *Esox* and considered the morphology of the cranium and jaw in *Aspius* to be in accordance with development 'from an omnivore into a carnivore'. (See remarks on p. 61.) Suslowska (1971) again compared *Aspius* with *Cyprinus* and *Esox*. She comments that the form of the *levator arcus palatini* in *Aspius* closely resembles that of *Cyprinus*. However, there is a difference in the orientation of the fibres, those of *Aspius* being more horizontally directed (as in *Luciobrama*, see p. 21). Suslowska (*op. cit.*) also demonstrated a close resemblance between the arrangement of the *adductor hyomandibulae* in *Aspius* and *Esox*.

Woskoboinikoff (1932), Yeremeyeva (1950), Alexander (1964), Suslowska (1971) and Howes (1976) all draw attention to the form of the *dilatator operculi* and note that this muscle is developed to the greatest degree in those fishes with elongate heads in which the operculum has become greatly extended. The need for strong dilatation of the opercula is two-fold, providing an increased flow of water for respiration and enabling the prey to be moved into the buccal cavity.

In *Luciobrama*, the large operculum and long *dilatator operculi* may not necessarily be indicative of their principal role in the feeding action. The movement of the operculum at its articulation with the hyomandibula seems to be restricted and it seems likely that the muscle's action is concerned primarily with strong breathing movements (see Alexander, 1969).

The enormous elongation of the postorbital skull region in *Luciobrama* and the correlated development of both the pterygoid series and the *levator arcus palatini* suggest, as a consequence, a powerful abduction of the hyopalatine arch, which would provide a suction corridor and thus reinforce the feeding action.

Summary

The following characters in *Luciobrama* are considered to be specialized (apomorph):

1. Reduced and elongate fourth infraorbital, diverted across the postorbital face (pp. 7 & 26).
2. Elongate postorbital region (including lengthened and narrowed parietals) (pp. 11 & 35).
3. Long tubular nasals, bearing 9–10 pores (pp. 9 & 31).
4. Orbitosphenoid and pterosphenoid bearing posterior and anterior extensions respectively (pp. 9 & 31).
5. Autosphenotic underlying the frontal as a shelf (pp. 13 & 35).
6. Posttemporal fossa extending well forward (pp. 13 & 38).
7. Extensive postparietal platform (pp. 13 & 40).
8. Specialized form of the lower jaw and large number of pores in the mandibular lateral line canal (pp. 13 & 42).
9. Short, inclined hyomandibula (pp. 13 & 44).
10. Elongate pterygoids (p. 15 & 45).

11. Extensive opercular series (pp. 15 & 47).
12. Second neural plate contacting the cranium (pp. 17 & 48).
13. Total number of vertebrae 50 or more (pp. 20 & 51).
14. Enlarged and complex *levator arcus palatini* muscles (pp. 21 & 53).
15. Scales minute and numerous (p. 7).

Of these characters only 4 is confined to *Luciobrama*. Characters 2 and 10 are shared only with *Aspiolucius*. Characters 8 and 9 are shared with *Aspiolucius* and *Pseudaspius*. All the remaining characters are shared with *Aspiolucius*, *Pseudaspius* and *Aspius*.

Relationships of *Luciobrama*

Bleeker (1870) suggested that *Luciobrama* was near to *Aspius*. Since that perceptive statement was made no other worker has speculated upon the relationships of this genus.

Berg (1964) thought that *Pseudaspius* was close to *Leuciscus* but implied that *Aspiolucius* and *Aspius* were related.

Luciobrama has been placed in the Leuciscinae by Rendahl (1928), Chu (1935) and Lin (1935), and in the Cyprininae by Tchang (1933). *Aspiolucius*, *Pseudaspius* and *Aspius* are placed in the Leuciscinae by Chu (1935) and Nikolsky (1954).

From the summary of synapomorph characters presented above (p. 58) it would appear that *Luciobrama* is, as Bleeker (1870) supposed, closely related to *Aspius*, but with even closer ties to *Aspiolucius* and *Pseudaspius*. I regard *Luciobrama* and *Aspiolucius* as a sister group and *Pseudaspius* as the closest relative of those two genera. In turn, all three are the sister group to *Aspius* which, by virtue of the morphology of the jaw and relatively unmodified cranium, I consider to be the least specialized representative of this group of genera. The relationships of the aspinine group of genera are discussed below, page 61.

Relationships of *Elopichthys*

Elopichthys poses a difficult problem concerning relationships and I have included it here because I believe it belongs to the aspinine assemblage.

Gosline (1974 : 12) stated '. . . *Elopichthys* (with *Ochetobius*) and *Hypophthalmichthys* (with *Aristichthys*) seem to represent highly specialized cyprinid groups without close relatives'.

From this statement I assume that Gosline is considering *Ochetobius* to be related to *Elopichthys*. I have examined specimens of *Ochetobius elongatus*, but apart from an enlargement of the *levator arcus palatini* muscle and the numerous vertebrae (see p. 51) I am unable to find any specializations that would suggest close affinity with *Elopichthys*. The upper jaw of *Ochetobius* appears to be highly protractile, the premaxillae possess long anterior ascending processes, there is no expansion of the pterosphenoid and the lower jaw is short and deep. All these features represent marked differences between *Elopichthys* and *Ochetobius*. I believe *Ochetobius* to be a specialized leuciscine.

I agree with Gosline (1974) that *Elopichthys* is a highly specialized taxon and has diverged sufficiently from its ancestral lineage to almost 'stand alone'. Nevertheless, *Elopichthys* shares many derived characters with the aspinine genera (see list on p. 58). Particularly important are those characters shared only with *Aspius*: the lateral expansion of the pterosphenoid to the cranial borders, the close resemblance of the orbitosphenoids and the elongate supracleithrum.

I consider *Elopichthys* to be most closely related to *Aspius* and thus, together, these form the sister group to *Luciobrama*, *Aspiolucius* and *Pseudaspius*.

The aspinine group of cyprinids

For the present I do not intend to assign any formal taxonomic status to the assemblage of genera considered here as the aspinine group. The reasons for this are discussed below (p. 61).

No single character of those enumerated below will distinguish the aspinines from other groups of cyprinids but the following combination of characters will identify this assemblage.

Character	Character state
Barbels absent	? Plesiomorph
Scales small; 65–155 in lateral line	Apomorph
Vertebrae 51–55	Apomorph
Cranium elongate; in some cases the postorbital cranium is three times the length of the preorbital part	Apomorph
Sphenotic exposed as a shelf below the frontal margin	Apomorph
Orbitosphenoid making extensive contact with parasphenoid	Apomorph
Infraorbitals 2, 3, 4 and 5 narrow, the fourth elongate	Apomorph
Operculum antero-posteriorly extended with a long dorsal border	Apomorph
Posttemporal fossa present, extending well forward	Presence: Plesiomorph Condition: Apomorph
Pterosphenoid sometimes extended to the lateral margin of the frontal	Apomorph
Pterosphenoid makes extensive contact with the parasphenoid	Apomorph
12 or more pores in the mandibular lateral line canal	Apomorph
Nasals elongate with 9–10 pores	Apomorph
Second neural plate contacts the cranium	Apomorph
Levator arcus palatini muscle extensive and complex	Apomorph
Dilatator operculi muscle extended	Apomorph

The genera and species comprising the aspinine group are:

Aspius Agassiz, 1832
- *Aspius aspius* (Linn.) 1758
- Distribution: Europe
- Two subspecies are recognized by Berg (1964), *A. aspius aspius* (Europe) and *A. aspius taeniatus* (Caspian and Aral seas).
- *Aspius vorax* Heckel 1843
- Distribution: Tigris R.

Aspiolucius Berg 1907
- *Aspiolucius esocinus* (Kessler), 1874
- Distribution: Amu-Darya
- Berg (1964) and Nikolsky (1954) mention a second species, *A. harmandi* (Sauvage) from Tonkin. This is an error. The species originally described as *Gymnognathus harmandi* by Sauvage (1884) is a synonym of *Elopichthys bambusa* (see synonymy in Lin, 1935 and Wu, 1964). Tchang (1933) placed *Aspiopsis merzbacheri* Zugmayer, 1921 in the genus *Aspiolucius*. He gave no reason for this action. I have examined the type and can find no characters which would justify inclusion in this genus. I agree with Berg (1964 : 541) in treating *Aspiopsis* as a synonym of *Leuciscus* (*sensu latu*).

Pseudaspius Dybowski, 1869
- *Pseudaspius leptocephalus* (Pallas), 1776
- Distribution: Amur basin

Luciobrama Bleeker, 1870
- *Luciobrama macrocephalus* (Lacepède), 1803
- Distribution: Southern China
- *Luciobrama longiceps* Pellegrin, 1907
- Distribution: Hanoi
- Rendahl (1928) considered *L. longiceps* as possibly a subspecies or other populational variant.

Since the species is known from only a single specimen more material from a wide range of localities will have to be available before its supposed subspecific status can be evaluated.

Elopichthys Bleeker, 1859
Elopichthys bambusa (Richardson), 1844
Distribution: China

Discussion

Luciobrama is a highly specialized member of the aspinine group of cyprinids. Although this group can be seen as a monophyletic assemblage it is difficult to relate it to other groups; the crux of this difficulty is the fact that various classifications of the Cyprinidae have been made by attaching significance to superficial resemblances and by utilizing only single characters or a series of too few characters. In some cases the significance of these features has defied interpretation. For example, Saxena & Khanna (1965) in their work on the osteology of *Catla* state 'It is impossible to indicate any specific features of the osteocranium as representative of primitive or evolved conditions.'

Because cyprinids tend to present a uniformity in those characters previously analysed, several authors have concluded that the family cannot be divided readily into subfamilies or other well-defined groupings (Sagemahl, 1891; Regan, 1911; Ramaswami, 1955b; Hensel, 1970; Gosline, 1973). Hensel (1970) has presented a history of the classification of the Cyprinidae. It seems that certain genera were assigned to a subfamily on a purely arbitrary basis (see p. 59 concerning *Luciobrama*).

In view of this unsatisfactory state of affairs it is not possible to place the aspinine genera in any relevant framework of related groups. Although I suspect that the aspinines can be related to the 'Leuciscines', until the Leuciscinae can be identified on the basis of shared specializations it will not be possible to say exactly how they are related.

From the anatomical evidence presented in this paper it is apparent that the piscivorous facies characterizing the aspinines is a derived condition – derived no doubt from an ancestral form possessing a reasonably protractile jaw and narrow cranium, i.e. a 'leuciscine-type' fish. One representative of this related group may be *Oreoleuciscus* which shares affinities with the aspinines in the morphology of the lower jaw, infraorbitals and dilatator fossa; see page 43.

Some authors have considered a piscivorous or carnivorous habit to be a primitive character for the Cyprinidae (see Hubbs & Black, 1947 and Matthes, 1963). Roberts (1969) also noted this possibility in the characoids, referring specifically to *Hepsetus.* I take the contrary view to these authors and maintain that it is the omnivores of the respective cyprinid lineages which represent the 'primitive' type' Evidence for this point of view is presented in this paper where it is shown that the piscivorous facies are the result of derived anatomical features, or 'specializations'. (See also the remarks of Suslowska & Urbanowicz, 1957; quoted here on page 58.

Several lineages of old-world cyprinids have evolved as piscivores. One, the aspinines, is considered in this paper. The predatory morphology of this group has been achieved not by any marked changes in jaw structure (apart for *Elopichthys* which is considered below), but by an increase in length of the postorbital part of the cranium and modification of the hyopalatine arch so as to improve or modify the suction feeding method. Another, exemplified by *Barilius*, has evolved by the more 'usual' method of elongating the jaws but because of the particular type of protractile mechanism of the cyprinid upper jaw (involving the kinethmoid and not the median ethmoid), the jaw elements have lengthened posteriorly. This has meant a correlated deepening of the hyopalatine series coupled with a slightly increased length to the postorbital part of the cranium. *Macrochirichthys* represents another type in which there has also been a lengthening of the jaws but coupled with a forward movement of their articulation and modification to the anterior part of the vertebral column which has allowed an upward movement of the head (pers. obs.). In this case there has been no lengthening of the postorbital cranium. Some other genera such as *Erythroculter* and *Schizothorax* display attributes of both the aspinine type of morphology (increased postcranial length) and bariliine type (increased jaw length and deepening of the pterygoid series).

Only one cyprinid, the aspinine *Elopichthys*, has developed what may be termed the pike-like facies so characteristic of other teleost piscivores. This has been achieved by 'sacrificing' the evolutionary potential of the protrusile upper jaw. The 'early stages' of this particular evolutionary pathway may, however, be detected in *Barilius bola*.

Acknowledgements

I am greatly indebted to Dr P. H. Greenwood for his encouragement, advice and criticism of many earlier drafts of the manuscript.

I want to express my gratitude to Dr K. E. Banister and Mr G. McGregor Reid for so many helpful discussions concerning the phylogeny of cyprinids and for providing me with much unpublished information concerning their respective studies on the genera *Barbus* and *Labeo*.

Mr M. van Oÿen of Leiden University provided much help by discussing functional anatomical problems as did Dr Richard Vari in discussing characoids. I am most grateful to them both.

To Mr J. Chambers go my thanks for preparing so many alizarin specimens and to Mrs Margaret Clarke for assisting with radiographs and numerous other jobs.

Finally, I wish to thank Dr P. J. P. Whitehead for his helpful advice and criticism of the final draft of the manuscript.

References

Alexander, R. McN. 1964. Adaptation in the skull and cranial muscles of South American characinoid fish. *J. Linn. Soc.* (*Zool.*) **45** : 169–190.

—— 1966. The functions and mechanisms of the protrusible upper jaws of two species of cyprinid fish. *J. Zool. Lond.* **149** : 288–296.

—— 1967. *Functional design in fishes*. London. 160 pp.

—— 1969. Mechanics of the feeding action of a cyprinid fish. *J. Zool. Lond.* **159** : 1–15.

Bănărescu, P. 1967. Studies on the systematics of Cultrinae (Pisces, Cyprinidae) with description of a new genus. *Revue roum. Biol.* (*Zool.*) **12** (5) : 297–302.

—— 1968. Remarks on the genus *Chela* Hamilton-Buchanan (Pisces, Cyprinidae) with description of a new subgenus. *Annali Mus. civ. Stor. nat. Giacomo Doria* **77** : 53–64.

Berg, L. S. 1964. *Freshwater fishes of the USSR and adjacent countries*. **2**. (English translation of the fourth ed. of 1949.) 496 pp.

Bleeker, P. 1870. Nieuw vischsoorten van China. *Versl. Meded. K. Akad. wet. Amst.* **4** : 251–256.

—— 1873. Notice sur le *Synodus macrocephalus* Lac. (*Luciobrama typus* Blkr). *Ned. Tijdschr. Dierk* **4** : 89.

Bridge, T. W. 1896. The mesial fins of ganoids and teleosts. *J. Linn. Soc.* (*Zool.*) **25** : 530–602.

Chu, Y. T. 1935. Comparative studies on the scales and on the pharyngeals and their teeth in Chinese cyprinids, with particular reference to taxonomy and evolution. *Biol. Bull. St. John's Univ., Shanghai* 2 : 1–225.

Gosline, W. A. 1961. Some osteological features of modern lower teleostean fishes. *Smithson. Misc. Coll.* **142** (3) : 1–142.

—— 1973. Considerations regarding the phylogeny of cypriniform fishes, with special reference to structures associated with feeding. *Copeia*, 1973 (4) : 761–776.

—— 1974. Certain lateral-line canals of the head in cyprinid fishes, with particular reference to the derivation of North American forms. *Jap. J. Ichth.* **21** (1) : 9–15.

—— 1975. The cyprinid dermosphenotic and the subfamily Rasborinae. *Occ. Pap. Mus. Zool. Univ. Mich.* **673** : 1–13.

Greenwood, P. H. 1974. The cichlid fishes of Lake Victoria, East Africa: the biology and evolution of a species flock. *Bull. Brit. Mus. nat. Hist.* (Zool.), Suppl. 6 : 1–134.

Greenwood, P. H., Rosen, D. E., Weitzman, S. H. & Myers, G. S. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bull. Am. Mus. nat. Hist.* **131** : 339–456.

Harrington, R. W. 1955. The osteocranium of the American cyprinid fish, *Notropis bifrenatus* with an annotated synonymy of teleost skull bones. *Copeia*, 1955 (4) : 267–290.

Hensel, K. 1970. Review of the classification and the opinions on the evolution of **Cyprinoidei** (Eventognathi) with an annotated list of genera and subgenera described since 1921. *Annotnes Zool. Bot. Bratislava*, **57** : 1–45.

Howes, G. J. 1976. The cranial musculature and taxonomy of characoid fishes of the tribes Cynodontini and Characini. *Bull. Brit. Mus. nat. Hist.* (Zool.) **29** (4) : 203–248.

Hubbs, C. L. & Black, J. D. 1947. Revision of *Ceratichthys*, a genus of American cyprinid fishes. *Misc. Publs. Mus. Zool. Univ. Mich.* **66** : 1–56.

Jollie, M. 1975. Development of the head skeleton and pectoral girdle in *Esox*. *J. Morph.* **147** (1) : 61–88.

Kershaw, D. R. 1976. A structural and functional interpretation of the cranial anatomy in relation to the feeding of osteoglossoid fishes and a consideration of their phylogeny. *Trans. zool. Soc. Lond.* **33** : 173–252.

Kimura, S. 1934. Description of the fishes collected from the Yangtse-Kiang, China by the late Dr K. Kishinouye and his party in 1927–1929. *J. Shanghai Sci. Inst.* **1** (3) : 11–247.

Liem, K. F. 1970. The comparative anatomy of the Nandidae (Pisces : Teleostei). *Fieldiana Zool.* **56** : 1–166.

Lin, S. Y. 1935. Contribution to the study of cyprinidae of Kwangtung and adjacent provinces. *Lingnan Sci. J.* **14** (4) : 651–663.

Lindsey, C. C. 1975. Pleomerism, the widespread tendency among related fish species for vertebral number to be correlated with maximum body length. *J. Fish Res. Bd. Can.* **32** (12) : 2453–2469.

Matthes, H. 1963. A comparative study of the feeding mechanism of some African Cyprinidae (Pisces, Cypriniformes). *Bijdr. Dierk.* **33** : 3–35.

Meinel, W. Von, Holl, A. & Schulte, E. 1970. Vergleichend-anatomische und funktionsanalytische Untersuchungen an der splanchnischen Muskulatur einiger Cyprinidae (Teleostei). *Zool. Beit.* **16** : 93–128.

Munshi, J. S., Datta. & Singh, B. R. 1967. The cranial muscles and the natural mechanism of opening and closing of mouth in two Indian major carps. *Zool. Anz.* 178 (1–2) : 49–60.

Nelson, G. J. 1969. Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. *Bull. Am. Mus. nat. Hist.* **141** art. 4 : 479–552.

Nichols, J. T. 1925. Chinese freshwater fishes. *Nat. Hist. N.Y.* **25** (4) : 346–352.

—— 1943. *Freshwater fishes of China*. Nat. Hist. of Central Asia. **9**. American Museum of Natural History, New York. 322 pp.

Nikolsky, G. V. 1954. *Special Ichthyology*. 2nd ed. Moscow. 458 pp.

Oliva, O. & Skořepa, V. 1968. The myodome in carp (*Cyprinus carpio* Linnaeus) and Repfen (*Aspius aspius* Linnaeus). *Vest. csl. Zool. Spol.* **32** (1) : 39–45.

Patterson, C. 1975. The braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. *Phil. Trans. Roy. Soc.* B 269 (899) : 275–579.

Ping, C., Pao, S. & Yang, H. Y. 1958. The skeletal musculature of the carp (*Cyprinus carpio*). *Acta zool. sin.* **10** : 289–315.

Ramaswami, L. S. 1955a. Skeleton of cyprinoid fishes in relation to phylogenetic studies: 6. The skull and Weberian apparatus in the subfamily Gobioninae (Cyprinidae). *Acta Zool.* **36** (2) : 127–158.

—— 1955b. Skeleton of cyprinoid fishes in relation to phylogenetic studies: 7. The skull and Weberian apparatus of the Cyprininae (Cyprinidae). *Acta Zool.* **36** (3) : 199–242.

Rauther, M. 1950. Über *Pelecus cultratus* (L.) in Vergleich mit anderen 'Beilfischen'. *Zool. Anz.* **145** : 794–804.

Regan, C. T. 1911. The classification of the teleostean fishes of the order Ostariophysi. 1. Cyprinoidei. *Ann. Mag. nat. Hist.* (8) **8** : 13–32.

Rendahl, H. 1928. Beiträge zur kenntnis der Chinesischen süswasserfische. 1. Systematischer Teil. *Ark. Zool.* **20A** (1) : 1–194.

Roberts, T. R. 1969. Osteology and relationships of characoid fishes, particularly the genera *Hepsetus*, *Salminus*, *Hoplias*, *Ctenolucius* and *Acestrorhynchus*. *Proc. Calif. Acad. Sci.* (4) **36** : 391–500.

—— 1973. Interrelationships of ostariophysans. *In*: *Interrelationships of fishes*, Greenwood, P. H., Miles, R. S. & Patterson, C. (Eds) : 373–395. London and New York.

Sagemahl, M. 1891. Beiträge zur vergleichenden Anatomie der Fische, IV. Das Cranium der Cyprinoiden. *Morph. Jahrb.* **17** : 489–495.

Sauvage, H. E. 1884. Contribution à la faune ichthyologique du Tonkin. *Bull. Soc. zool. Fr.* **9** : 209–215.

Saxena, S. C. 1960. The cranial musculature of a hill-stream cyprinid fish *Garra mullya* (Sykes). *Proc. Nat. Inst. Sci. India* B (4) **26** : 176–188.

Saxena, D. B. & Khanna, S. 1965. Osteology of the freshwater teleost *Catla catla* (Ham.). Part I. Osteocranium. *Vest. csl. Zool. Spol.* **29** : 127–145.

Shukla, G. R. & Verma, S. R. 1972. Appendicular skeleton of *Barilius bola* (Ham.). (With the remark of phylogenetic consideration.) *Anat. Anz.* **130** : 560–570.

Sorescu, C. 1968. Vergleichende Untersuchungen über den Schultergürtel der Cyprinidae. *Senck. biol.* **49** (5) : 387–397.

—— 1972. Comparative studies on the Weberian apparatus in the subfamily Danioninae and Cultrinae (Cyprinidae – Pisces). *Revue roum. Biol.* (Zool.). **17** (6) : 391–398.

Starks, E. C. 1926. Bones of the ethmoid region of the fish skull. *Stanf. Univ. Public. Biol. Sci.* **4** (3) : 139–338.

Suslowska, W. 1971. A comparative study of the muscles of the head of *Aspius aspius* (Linnaeus, 1758) and *Esox lucius* Linnaeus, 1758. *Acta Zool. Cracov.* **16** (16) : 695–713.

—— **& Urbanowicz, K.** 1957. Badania prownaweze nad wybranymi elementami szkieletu szezupala – *Esox lucius* L., bolenia – *Aspius aspius* (L.) i karpia – *Cyprinus carpio* L. *Zesz. nauk. Univ. Lodz* (2) **3** : 71–93.

Takahasi, N. 1925. On the homology of the cranial muscles of the cypriniform fishes. *J. Morph.* **40** : 1–109.

Tchang, T. L. 1933. *The study of Chinese cyprinoid fishes*, Part 1. Zool. Sinica 2 (1) : 1–247.

Tretiakov, D. K. 1946. Systematic groups of Cyprinidae. *Zool. Zh.* **25** (2) : 149–156.

Weitzman, S. H. 1962. The osteology of *Brycon meeki*, a generalized characin fish, with an osteological definition of the family. *Stanford ichthyol. Bull.* **8** (1) : 3–77.

Wiley, M. L. & Collette, B. B. 1970. Breeding tubercles and contact organs in fishes: their occurrence, structure and significance. *Bull. Am. Mus. nat. Hist.* **143** art. 3 : 143–216.

Winterbottom, R. 1974. A descriptive synonymy of the striated muscles of the teleostei. *Proc. Acad. nat. Sci. Philad.* **125** (12) : 225–317.

Woskoboinikoff, M. M. 1932. Der Apparat der Kiemenatmung bei den Fischen. *Zool. Jb. Anat. Jena* **55** : 315–488.

Wu, Hsien-Wen. 1964. *Cyprinid fishes of China.* **1**. Shanghai. 228 pp.

Yeremeyeva, E. F. 1950. Zavistimost miezdu stroieniem cherepa i stroiemiem rotovogo i golotochnogo apparatov kostistich ryb. *Trudy Inst. Morf. Zhivot.* **3** : 34–41.