



# The anatomy, phylogeny and classification of bariliine cyprinid fishes

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## Synopsis

The osteology, external anatomical features and gross brain morphology of the cyprinid fish genera *Opsariichthys*, *Zacco*, *Luciosoma*, *Barilius* and *Engraulicypris* are described and compared. With the exception of *Zacco* a series of synapomorph characters are identified in these genera which enable them to be related as a monophyletic assemblage termed the *bariliine group*. The distribution of certain characters demands a reclassification of the considered genera. Species formerly included in *Barilius* are now referred to four genera, *Barilius*, *Opsaridium*, *Raiamas* and *Leptocypris*. *Engraulicypris* is recognized as monotypic and forming the sister group to *Leptocypris*. The identification of synapomorphies in *Luciosoma* and some species of *Rasbora* requires the establishment of a new genus, *Parluciosoma*, to contain the latter. *Megarasbora* is identified as a member of the bariliine group and as representing a plesiomorph luciosomine. The geographic distribution of the group is summarized. Relationships of the bariliines with other monophyletic groups is unresolved, but the chelines are nominated as the likely sister group. *Zacco* does not share any of the derived characters that relate the bariliine genera and it is suggested that its closest relatives are to be found amongst the alburnine cyprinids. Appendices are included which contain annotated lists of the bariliine taxa and notes on the generic allocation of those species previously included in *Engraulicypris*.

## Introduction

C. Tate Regan (1911) was the first author to consider *Opsariichthys* as a primitive or generalized cyprinid. He did so on the basis of its possessing triserial pharyngeal teeth, a 'complete series' of

circumorbitals, large posttemporal fossae, second and third vertebrae separated, a fenestra between the quadrate and the metapterygoid and on the form of the cleithrum.

Regan's opinion of the primitive nature of *Opsariichthys* has been accepted by all subsequent authors who have had cause to comment on cyprinid phylogeny (see, for example, Ramaswami, 1955; Weitzman, 1962; Greenwood *et al.*, 1966; Roberts, 1973). The characters enumerated by Regan do, indeed, appear to be plesiomorph for the Cyprinidae and as such are of little value in indicating the relationships of *Opsariichthys*.

In an earlier paper (Howes, 1978) I described and commented upon some anatomical features of *Opsariichthys* and compared them with similar characters in other cyprinid genera. It is now possible to present a more detailed description of osteological and other anatomical features of *Opsariichthys* and to evaluate them in terms of their plesiomorphy and apomorphy. From my earlier studies (Howes, 1978) I formed the opinion that *Opsariichthys* was related to *Barilius* and, furthermore, that *Luciosoma* also shared characters linking it with these taxa. (It must be pointed out here that my earlier remarks concerning *Barilius* (Howes, 1978) mostly refer to *B. bola* and *B. microcephalus*, taxa which this present study shows to be derived members of the genus.) As this study progressed it became evident that *Engraulicypris sardella* was also allied to *Barilius* but that it had no relationship with other species assigned to *Engraulicypris*. Thus an anatomical description of this taxon is also included.

Previous authors had regarded *Zacco* as the closest relative of *Opsariichthys*. Contrary to their opinion, the studies reported herein show that *Zacco* does not belong to the same monophyletic assemblage as *Opsariichthys*; in order to show why this is so, the anatomy of *Zacco* is described along with that of the other genera.

The data are presented in the form of character headings under which appear descriptions for each genus studied, followed by a comparative analysis at the end of each section.

An annotated list of the taxa comprising the bariliine group is given in Appendix 1 (p. 195), and a list of those taxa formerly included in *Engraulicypris* in Appendix 2 (p. 196).

## Specimens examined

Skeletal and alizarin material of representatives of all bariliine genera has been examined. Dissections have been made on a total of *c.* 50 species and all specimens have been radiographed. All the type specimens of species currently assigned to *Engraulicypris* and *Chelaethiops* have been examined. A complete list of specimens used in this study is deposited in the Fish Section of the British Museum (Natural History).

## Abbreviations used in the figures

A1	Outer division of <i>adductor mandibulae</i> muscle	EPO	Epioccipital
AA	Anguloarticular	ES	Extrascapular
AHF	Anterior hyomandibular fossa	EXO	Exoccipital
AL	Axial lobe of pectoral fin	F	Frontal
AP	Apothysal platform	FC	Foramen for carotid artery
AS	Axial scale	FF	Frontal fossa
BO	Basioccipital	FG	Frontal groove
BOP	Basioccipital plate	FO	Optic foramen
CE	Cerebellum	FR	Frontal ring
CL	Cleithrum	FIII	Foramen for oculomotor nerve
CLA	Clastrum	FIV	Foramen for trochlear nerve
COR	Coracoid	FIX	Foramen for 9th cranial nerve
CU	Cavum utriculus	HMF	Hyomandibular fossae
EB	Epibranchial	HY	Hypural (numbered)
EM	Exit of the posterior myodome	HYP	Hypurapophysis
EP	Epurial	IC	Intercalar
		IF	Infrapharyngobranchials (numbered)

INC	Incus	OT	Olfactory tract
IO	Infraorbitals (numbered)	PA	Parietal
KE	Kinethmoid	PAP	Parasphenoid ascending process
LC	Lateral commissure	PC	Postcleithrum
LE	Lateral ethmoid	PE	Preethmoid
LJB	Lateral jugular bridge	PH	Parhypural
LKE	Ligament connecting kinethmoid to mesethmoid (divided)	PHF	Posterior hyomandibular fossa
LKM	Ligament connecting kinethmoid to maxilla	PLP	Vomerine process for attachment of palatine ligament
LKP	Ligament connecting kinethmoid to premaxillary ascending process	PMX	Premaxilla
LP1	Lateral process of 1st vertebra	PPJ	Posterior opening of pars jugularis
LP2	Lateral process of 2nd vertebra	PRO	Prootic
LPE	Ligament connecting palatine with ethmoid	PS	Parasphenoid
LPEK	Ligament connecting palatine with ethmoid and kinethmoid	PSFF	Foramen connecting posttemporal and subtemporal fossae
LPM	Ligament connecting palatine with maxilla	PTE	Pterotic
LTF	Lateral temporal fossa	PTEP	Pterotic process
LOC	Lateral occipital fenestra	PTF	Posttemporal fossa
MC	Mesocoracoid	PTS	Pterosphenoid
ME	Mesethmoid	PTT	Posttemporal
MEC	Mesencephalon	PU1 + UI	Fused preural and ural centra
MMP	Maxillary medial process	RA	Retroarticular
MX	Maxilla	RAD	Radial
MYO	Posterior myodome	SC	Supracleithrum
MYR	Posterior myodome roof	SCA	Scaphium
N	Nasal	SCP	Scapula
NC	Neural complex	SE	Supraethmoid
NP2	Neural plate of 2nd vertebra	SO	Supraoccipital
NP3	Neural plate of 3rd vertebra	SOR	Supraorbital
NS4	4th neural spine	SP	Sphenotic
OL	Olfactory lobe	STF	Subtemporal fossa
OS	Orbitosphenoid	TEL	Telencephalon
OSE	Orbitosphenoid septum	TR	Tripus
OSS	Os suspensorium	UN	Uroneural
		V	Vertebra
		VF	Vomerine foramen
		VO	Vomer

### Note on the figures

All anatomical drawings captioned *Opsariichthys* are of specimens of *Opsariichthys uncirostris bidens*. Unless otherwise stated the scale on all figures indicates 3 mm.

## Anatomical description of *Opsariichthys*, *Zacco*, *Luciosoma*, *Barilius* and *Engraulicypris*

### Osteology

#### *Ethmo-vomerine region*

#### *Opsariichthys*

The *supraethmoid* (SE, Figs 1–3) is a wide bone with a flat dorsal surface and an irregular posterior border sutured to the frontals. The lateral margin of the supraethmoid is gently concave and along this concavity lies the nasal. The supraethmoid's anterior border is thickened and bears a concave notch.

The *mesethmoid* (ME, Figs 1–3) underlies the supraethmoid and is composed of two lateral walls fused anteriorly bearing a sloped concavity (a continuation of the supraethmoid notch)

which accommodates the kinethmoid. Antero-ventrally the mesethmoid is produced into a wedge-shaped surface that provides part of the preethmoid fossa. The posterior border of the mesethmoid wall is deeply notched so as to form part of the olfactory foramen.

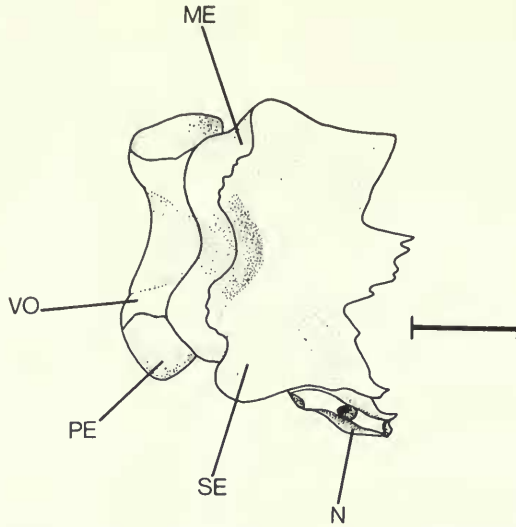


Fig. 1 *Opsariichthys*. Dorsal view of ethmoid region.

Each *preethmoid* (PE, Figs 1-3) is a large irregular hemispherical bone which lies in the fossa formed from the mesethmoid and vomer. The preethmoid does not lie flush with the edges of these two bones but leaves a wide margin of each exposed. In a dissection it is found that the cartilage which covers the preethmoid fills this surrounding area. In a specimen of 38.5 mm SL the preethmoids are small, partially ossified elements occupying only the vomerine part of the fossa.

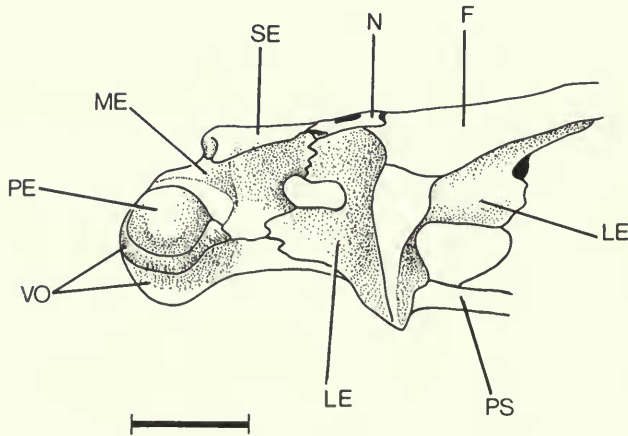


Fig. 2 *Opsariichthys*. Lateral view of ethmo-vomerine region.

Each *lateral ethmoid* (LE, Figs 2 & 3) contacts the dorsal and ventral parts of the mesethmoid, the space between the bones forming part of the olfactory foramen. Laterally, the bone is produced as a thick wall with a wide triangular base. The dorsal surface of the wall is covered by the frontal. The orbital face of the lateral ethmoid is concave and its posterior margin bears a notch through which passes the superficial ophthalmic nerve. The posterior margin of the orbital part

of the bone is sutured to the orbitosphenoid, and the dorsal part to the frontal. Medially, the lateral ethmoids meet above the parasphenoid. There is no anterior myodome.

The *kinethmoid* when viewed laterally is seen as an elongated S (Fig. 4A). The dorsal curvature expands into two heads upon which the ligaments joining the bone to the premaxillaries. A ledge along the lateral face of the bone also supports a ligament. This ligament runs from the maxilla and becomes bipartite, one part inserting on the dorsal surface of the ledge, the other, on its ventral surface (Fig. 4B). Basally the kinethmoid is strongly curved towards the ethmo-vomerine complex and it is this part of the bone which is seated in the anterior groove of the vomer. Connection with the ethmo-vomerine block is *via* a bipartite ligament which inserts on a tissue sheath that encloses the ventral half of the kinethmoid (Fig. 4C).

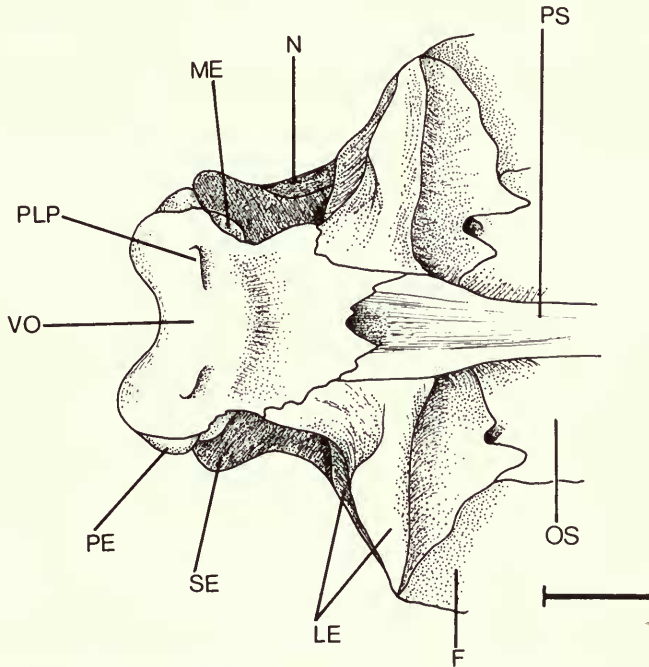


Fig. 3 *Opsariichthys*. Ventral view of ethmo-vomerine region.

The vomer (V, Figs 1–3) is short, its posterior margin extending to a line of the lateral ethmoid walls. Anteriorly it curves ventrad and is transversely convex. The anterior border is concave and bears a wide groove to accommodate the kinethmoid. The ventral surface of the vomer bears, on either side of the midline, two small processes (PLP) onto which the palatine ligament attaches. Laterally the bone forms into a wedge-shaped platform which provides the lower part of the preethmoid fossa. The vomer is overlain anteriorly by the ethmoid and posteriorly by the parasphenoid. There is a cavity between the posterior part of the vomer and the parasphenoid into which insert the ligaments attaching the dorsal borders of the suspensorial elements to the length of the parasphenoid. Postero-laterally the vomer is sutured to the bases of the lateral ethmoids.

### *Zacco*

*Zacco* differs from *Opsariichthys* in that the *mesethmoid* is narrower and deeper with a ventro-lateral nasal cavity; the dorsal surface of the *supraethmoid* is strongly curved rostrad; the olfactory foramen scarcely indents the posterior border of the mesethmoid. The depth and curvature of the ethmoid block is particularly noticeable in *Zacco platypus* (Fig. 5). The *lateral ethmoids*

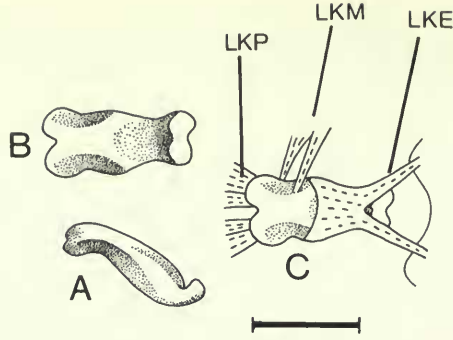


Fig. 4 *Opsariichthys*. Kinethmoid in A, lateral, and B, ventral view. C. Ligamentous connections, ventral view.

are thicker basally and laterally truncated; medially they are indented to form a shallow anterior myodome. The *vomer* is thinner than that of *Opsariichthys*, contributes less to the preethmoid fossa, extends further forward and bears a deeper anterior notch. The *preethmoids* are smaller; the *kinethmoid* is longer and more tubular with a gutter-like groove along its anterior face, its dorsal surface is expanded into two rounded heads which curve forward and are attached to the premaxillaries by ligaments (Fig. 8A).

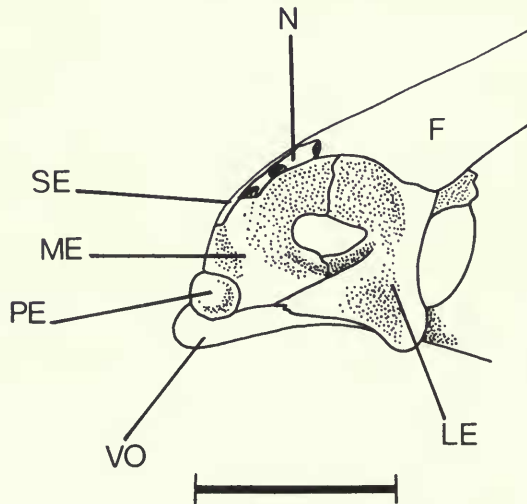


Fig. 5 *Zacco platypus*. Lateral view of ethmo-vomerine region.

### *Luciosoma*

*Luciosoma* differs from *Opsariichthys* in the following features: the *supraethmoid* is more extensive its dorsal surface having a bowl-shaped depression for accommodating the kinethmoid (Fig. 6); the kinethmoid is S-shaped but more compressed; the *preethmoids* are exposed ventrally, not being completely covered by the vomer; the walls of the *lateral ethmoids* are curved anteriorly and thickened basally, they contain the major part of the olfactory nerve foramen which is produced anteriorly as a bony tube. The orbital part of each lateral ethmoid is inflated. The *vomer* is deeply concave and not swollen as in *Opsariichthys*.

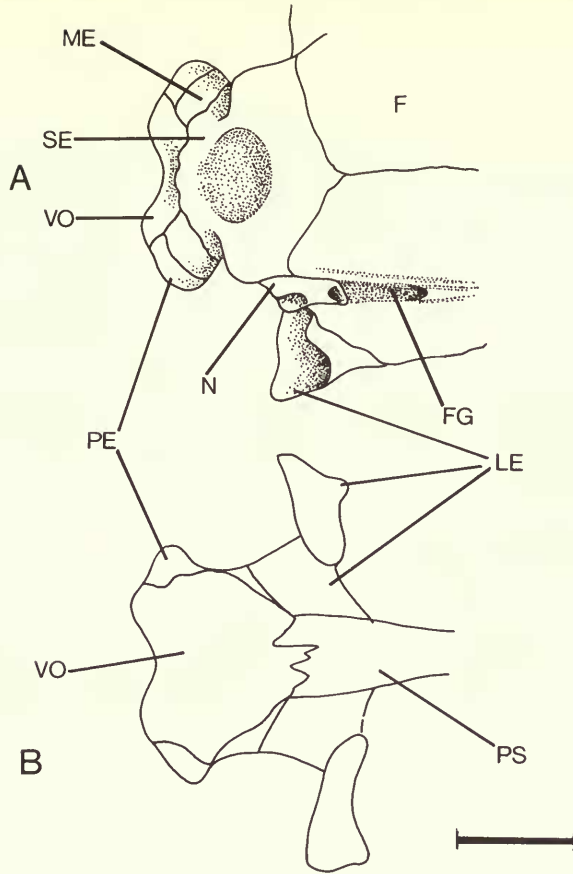


Fig. 6 *Luciosoma bleekeri*. Ethmo-vomerine region in A, dorsal and B, ventral views.

### *Barilius*

*Barilius* displays considerable variation in the morphology of the ethmo-vomerine region and, as in this and other characters to be discussed, at least three major groups of species can be distinguished. For the purposes of the descriptive anatomical section these are designated as *Groups A, B and C*. Formal taxonomic treatment of these groups is given in pp. 189–193. Differences are as follows:

*Group A*. The *mesethmoid* narrow and deep; dorsal surface of *supraethmoid* strongly curved rostrad; *kinethmoid* rod-like with a groove along the anterior surface; *lateral ethmoids* laterally truncated, not extending beyond the frontal margin; *preethmoids* reduced; *vomer* short and deeply notched anteriorly.

Examples of this group of species are *Barilius barila* and *B. ornatus* (see p. 189).

*Group B* (Fig. 7). The *mesethmoid* is wide and shallow, the dorsal surface of the *supraethmoid* is flat or gently sloped rostrad; the *kinethmoid* bears greatly expanded dorsal heads which give the bone a triangular appearance (Fig. 8B). These heads articulate closely with the premaxillaries, connection being effected through a broad, ligamentous sheet. Whereas in the two Asian species assigned to this group the ventral aspect of the *kinethmoid* is curved backwards as in *Opsariichthys* in the Africa species it is rounded or curved forward. The *vomer* is short but widely flared anteriorly, medially it is deep and rises steeply beneath the ethmoid.

Examples of species in this group are *Barilius bola*, *B. loati* and *B. salmolucius* (see p. 193).

*Group C*. The *mesethmoid* is wide and deep, the dorsal surface of the *supraethmoid* slopes rostrad; the *kinethmoid* is rod-like and the *vomer* greatly thickened anteriorly.

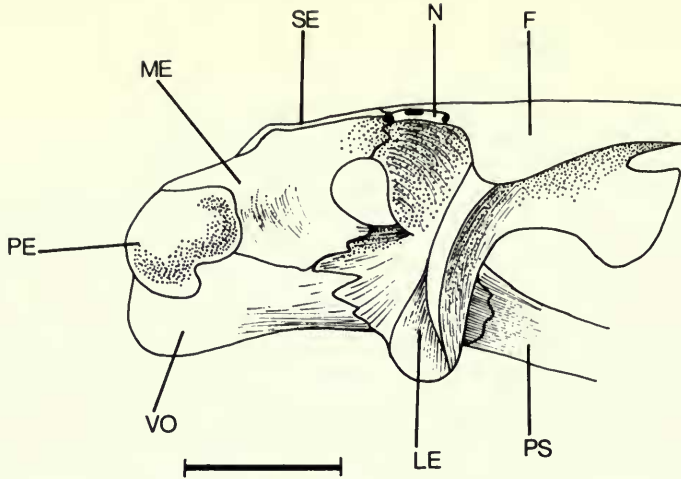


Fig. 7 *Barilius bola*. Lateral view of ethmo-vomerine region.

Examples of species in this group are *Barilius microcephalus*, *B. zambesensis* and *B. ubangensis* (see p. 191).

### *Engraulicypris*

*Engraulicypris* differs markedly from the genera described above. The ethmoid block (*supraethmoid*+*mesethmoid*) is elongate and shallow (Figs 9A–E), its anterior border deeply indented in the shape of a horseshoe. Each arm is broadly bevelled ventro-laterally so as to accommodate the underlying vomer. The anterior face of each arm is broad and sloped backwards at  $45^\circ$  to the vertical, on its medial tip there is a prolongation. The *supraethmoid* has a slightly convex lateral margin and a shallow medial depression, its posterior border forming an irregular suture with the frontals. Each large *preethmoid* (Fig. 9C) lies antero-laterally to its respective ethmoid arm, ventrally it is supported by the vomer. Each *lateral ethmoid* (Fig. 9E) scarcely extends from below its respective frontal. The olfactory foramen is contained almost entirely within the bone's medial face.

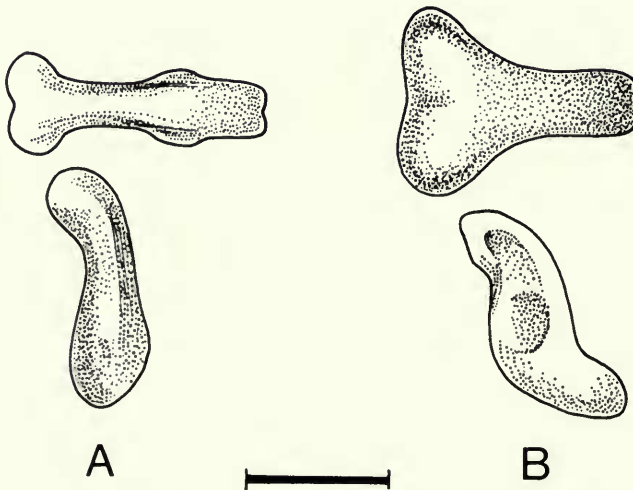


Fig. 8 Kinethmoid of A, *Zacco macrophthalmus*, B, *Barilius bola*, in dorsal and lateral views.



The *kinethmoid* is long and somewhat rod-shaped, its ventral tip articulating with the anterior vomerine notch. Its distal tip is slightly bifurcated and a ligament runs from each bifurcation to the tip of the maxillary. From either side of the kinethmoid shaft a ligament attaches to the dorsal rim of the maxillary (see p. 162).

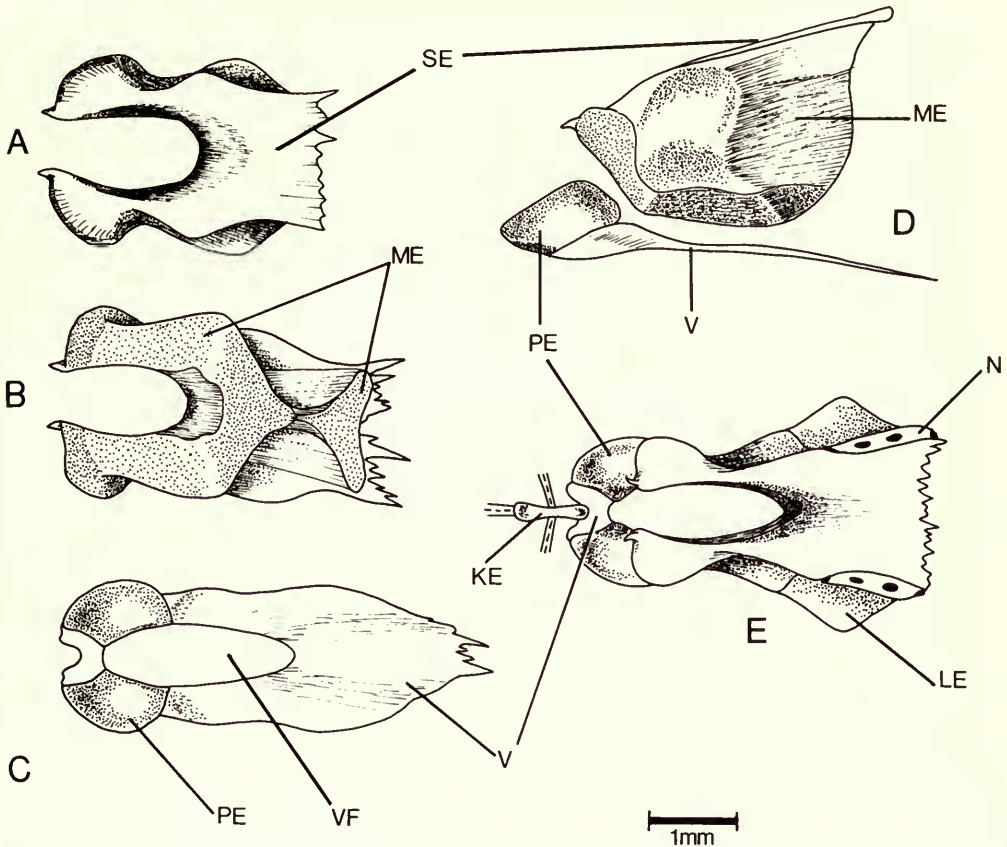


Fig. 9 *Engraulicypris sardella*. Ethmo-vomerine region. A, dorsal and B, ventral views of the ethmoid block. C, dorsal view of vomer. D, exploded lateral view of ethmo-vomerine block. E, dorsal view of entire ethmo-vomerine region showing articulation of the kinethmoid.

The *vomer* (Figs 9C & D) is short and broad, its posterior tip lying below the posterior border of the lateral ethmoids. The anterior half of the vomer is perforated by an ellipsoidal foramen (VF, Fig. 9C), the boundary of which coincides with the rim of the overlying ethmoid. The lateral border of the vomer is slightly raised to form a support for the preethmoid and its anterior rim is deeply notched.

#### Orbital region

#### *Opsariichthys*

The *orbitosphenoids* (Fig. 10) are deep, anteriorly expanded bones. Ventro-medially they are joined to form a thick interorbital septum which contacts the parasphenoid. The *pterosphenoids* (Figs 10 & 12) provide the walls of the optic foramen and the roof to the anterior part of the posterior myodome. Anteriorly each pterosphenoid is bordered by the orbitosphenoid, dorsally it is overlain by the frontal and posteriorly by the sphenotic and part of the prootic. The junction

with the prootic is along a narrow medially directed portion of that bone which forms the dorso-medial wall of the trigeminofacialis foramen. Ventrally the pterosphenoid is produced into a narrow stem which contacts the medial face of the ascending lateral wing of the parasphenoid. The orbital face of the pterosphenoid bears a groove for the passage of the supraorbital nerve trunk. Ventrally the groove enters the *pars jugularis* of the trigemino-facialis chamber of the prootic. The posterolateral face of the pterosphenoid bears a deep concave fossa from which runs a tendinous sheet to underlie the *levator arcus palatini* muscle (PTSF, Figs 10 & 12). Part of the anterior hyomandibular fossa extends onto the dorsal surface of the pterosphenoid.

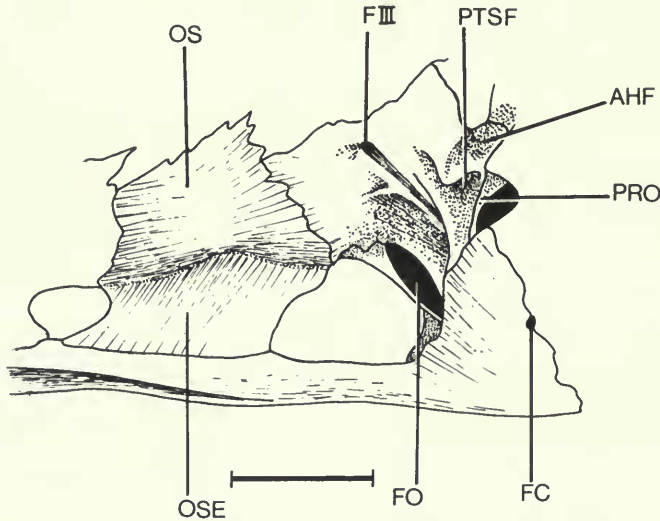


Fig. 10 *Opsariichthys*. Lateral view of orbital region.

The *parasphenoid* (Figs 11 & 12) is horizontally aligned, thin and grooved anteriorly where it overlies the vomer. On either side, posteriorly are ascending wings each of which contacts the pterosphenoid wing along a narrow front. The posterior dorsal edge of the wing is sutured to the prootic. This suture is interrupted by the carotid foramen (hypophysial foramen of Ramaswami, 1955). Below the prootic the parasphenoid widens to form a platform against which articulate the infrapharyngobranchials, the edges of this apophysis are formed by the prootics (parasphenoid platform of Howes, 1978). A prominent ridge runs along the ventral midline of the parasphenoid but becomes lessened posteriorly. The posterior ventral part of the bone is rounded and lies below the basioccipital.

### *Zacco*

The *orbitosphenoid* differs from that of *Opsariichthys* in that it is much shallower and has a deeper interorbital septum. The *pterosphenoid* (Fig. 16) is much like that in *Opsariichthys*, bearing in its orbital face a deep furrow for the supraorbital nerve trunk. A major difference, however, is that the pterosphenoid does not articulate with any part of the parasphenoid but is sutured only to the medial projection of the prootic and, furthermore, there is no fossa in its posterolateral face.

The *parasphenoid* differs from that in *Opsariichthys* in being curved upward instead of horizontally aligned. The carotid foramen is greatly expanded in *Zacco* to form a large fenestra between the parasphenoid wing and the prootic (Fig. 16). The fenestra is partially covered by a fascia from which extends part of the *adductor arcus palatini* muscle. There is a moderately developed dorsal medial crest along the length of the parasphenoid but this never extends upwards to contribute to the interorbital septum stemming from the orbitosphenoids. As in

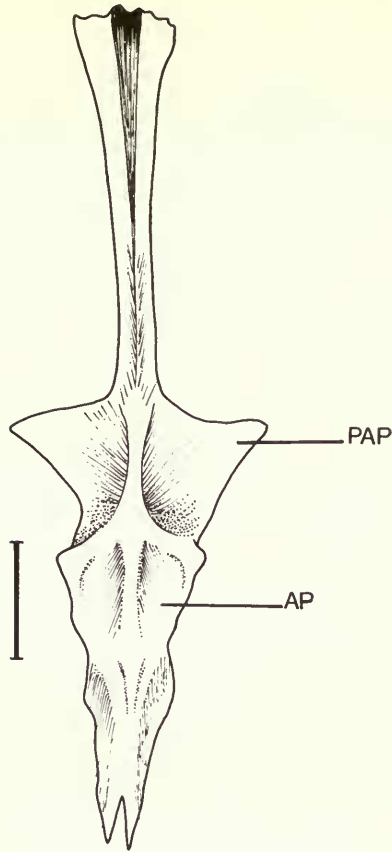


Fig. 11 *Opsariichthys*. Ventral view of parasphenoid.

*Opsariichthys* the parasphenoid bears a ventral groove for half its length. The apophyseal platform below the prootic is narrow and receives no contribution from the prootics.

#### *Luciosoma*

The *orbitosphenoid* is shallow and contacts the parasphenoid *via* a narrow interorbital septum. The *pterosphenoid* (Fig. 18) closely resembles that of *Opsariichthys* but whereas in that genus the bone forms the border of the anterior trigemino-facialis opening, in *Luciosoma* it is sutured without interruption both to the prootic and to the parasphenoid ascending process. There is a strong lateral ridge along the descending limb which makes contact with the parasphenoid and a shallow partially covered lateral fossa. Part of the anterior hyomandibular fossa extends onto the parasphenoid.

The *parasphenoid* ascending process contacts both the *pterosphenoid* and prootic. The carotid foramen is small, and the apophyseal platform is extensive with small lateral contributions from the prootics, features shared with *Opsariichthys*.

#### *Barilius*

*Group A*. There is some variation in the depth of the *orbitosphenoid* septum. The *pterosphenoid* contacts the *parasphenoid* ascending process across a very narrow front. In some species (e.g. *B. bendelisis*) contact between the two bones is almost prevented by the intrusion of a thin wedge

from the prootic. There is no lateral pterosphenoid fossa, and the carotid foramen is sometimes extensive, as in *Zacco*. The posterior margin of the parasphenoid is deeply indented and does not extend to meet the posterior border of the basioccipital. Thus, there is a ventral opening leading into the posterior myodome (see pp. 146–147).

*Group B.* The *orbitosphenoid* septum is narrow as in *Opsariichthys*. In *Barilius bola* a shallow ridge runs along the lateral face of the orbitosphenoid, broadening posteriorly into a wide shelf continuous with that on the pterosphenoid. The *pterosphenoid* (Fig. 19) contacts the anterior edge of the prootic without interruption; its ventral edge is sutured to the ascending process of the parasphenoid. There is some variation in the extent of contact between these bones, being greatest in *B. bola* and *B. guttatus*. The anterior hyomandibular fossa extends onto the pterosphenoid. Although a fossa is present on the lateral face of the pterosphenoid, it is very shallow. The *parasphenoid* ascending processes are short, but with long dorsal borders contacting the pterosphenoids. There is a depression in the lateral ascending process for the insertion of the *adductor arcus palatini* muscle. The carotid foramen is reduced. The apophyseal platform is well developed and receives lateral contributions from the prootics.

*Group C.* The *orbitosphenoid* has a lateral shelf which is confluent with a similar feature on the pterosphenoid. The *pterosphenoid* (Fig. 17B) contacts the prootic medially as well as laterally and its connection with the parasphenoid is also medial across a very narrow spur of that bone. There is a cavernous fossa on the lateral face of the pterosphenoid (PTSF, Fig. 19A), it is of the basin-type like that in *Opsariichthys*, but is covered laterally so as to become a deep, conical chamber. The *parasphenoid* is wide anteriorly. Posteriorly its ascending process forms a wide connection with the prootic. The carotid foramen is reduced. The prootics contribute only marginally to an apophyseal platform. The parasphenoid does not provide a floor to the myodome.

### *Engraulicypris*

The *orbitosphenoid* is produced into a long, shallow interorbital septum. The *pterosphenoid* (Fig. 22A) bears a deep lateral fossa (PTF) and it contacts the ascending process of the parasphenoid across a narrow front. The *parasphenoid* ascending process is high and broad with a lateral depression. Its otic portion is flat, with the posterior border deeply indented and not entirely flooring the basioccipital.

### *Otic region*

### *Opsariichthys*

The *prootic* (Figs 10 & 12) is the largest bone in the braincase. The lateral face bears a wide commissure covering the trigemino-facialis chamber. Anteriorly, contact is made with the pterosphenoid along a narrow surface just above the anterior opening of the chamber. Ventro-anteriorly the prootic is sutured to the ascending process of the parasphenoid. Ventrally, the prootic is flattened and contributes to the apophyseal platform formed on the lateral border of the parasphenoid. The posterior border of the prootic is contacted by the basioccipital and epioccipital. The postero-dorsal face of the prootic is depressed and forms part of the medial wall of the subtemporal fossa. Dorsally, the prootic is bordered by the autosphenotic and the autopteric. The anterior and posterior hyomandibular fossae are confined to these two latter bones and do not invade the prootic. The medial face of the prootic bears a shelf extending from below the trigemino-facialis chamber to meet its partner from the opposite side in the midline and so forming the roof of the myodome (Figs 12 & 15). A large depression in the medial face of the prootic forms the *cavum utriculus* (Figs 12B–C).

The major part of the dilatator fossa lies in the *sphenotic* (Fig. 13) which is overlapped along its medial margin by the pterotic and the frontal. Anteriorly the bone extends laterally as a thin concave wall, the ventral surface of which forms part of the anterior hyomandibular fossa. Between the dorsal borders of the sphenotic and pterotic is a lateral temporal foramen. The

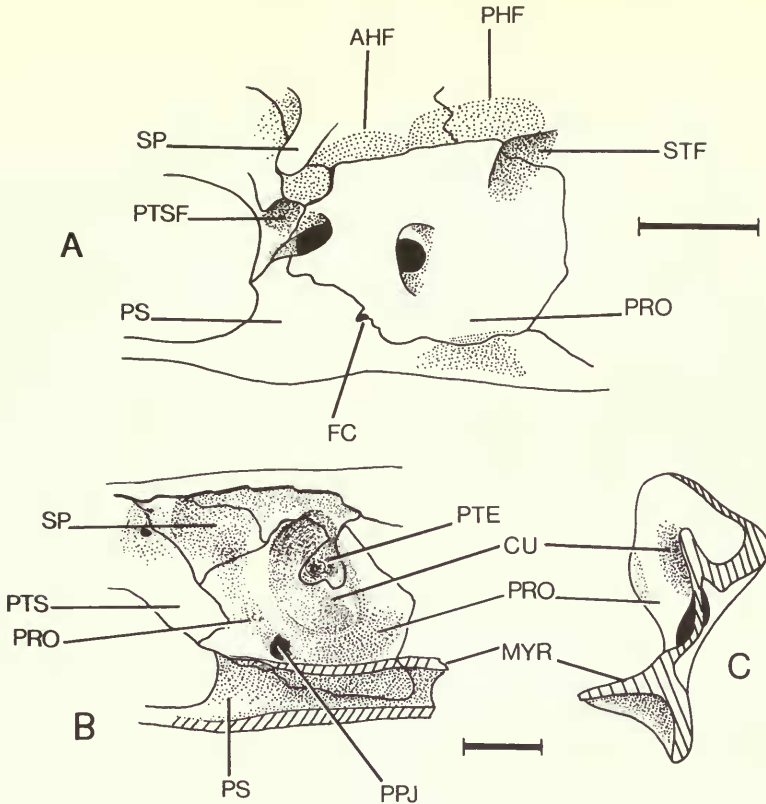


Fig. 12 *Opsariichthys*, otic region in A, lateral and B, medial views. C, cross-section through anterior part of the prootic.

lateral process of the sphenotic is sloped antero-ventrally, its dorsal surface is broad which narrows ventrally into a lamellar wall.

The *pterotic* (Figs 12–14) is bordered dorso-medially by the parietal and epioccipital, and dorso-anteriorly by the frontal and sphenotic. The exposed cranial surface of the pterotic is narrow. Ventrally it is sutured to the prootic and extends posteriorly as a thick limb terminating in a ventrally directed spine. The ventral border of the pterotic houses the greater portion of both hyomandibular fossae. The pterotic contributes to the lateral wall and roof of the subtemporal fossa and it also provides, posteriorly, the lateral wall of the posttemporal fossa. Medially this wall is perforated and opens into the subtemporal fossa; thus the subtemporal fossa is connected to the posttemporal fossa via an intrapterotic tunnel (PSFF, Fig. 13B). Epaxial muscle fibres run through this tunnel to insert along the lateral wall of the subtemporal fossa.

The *exoccipital* (EXO, Figs 13–15) is bounded dorsally by the epioccipital with which it forms the medial wall of the subtemporal fossa; anteriorly it is bordered by the prootic, and ventrally by the basioccipital. Ventrally, the exoccipital is slightly inflated to form part of the saccular recess, and laterally it is pierced by the foramen for the vagus nerve. Dorso-posteriorly, that part of the bone containing the semi-circular canal turns outward to contact the pterotic and the intercalar. The posterior portion of the epioccipital surrounds the lateral occipital foramen, its dorsal surface being bounded by the supraoccipital. Medially, a horizontal sheet of bone extends from each exoccipital to contact one another in the midline and so form the roof of the cavum sinus imparis.

The *lateral occipital fenestra* (LOC, Fig. 14) is covered by connective tissue which thickens around the border of the foramen. There appears to be no insertion of muscle fibres onto this tissue and it lies as a 'window' covered by epaxial musculature.

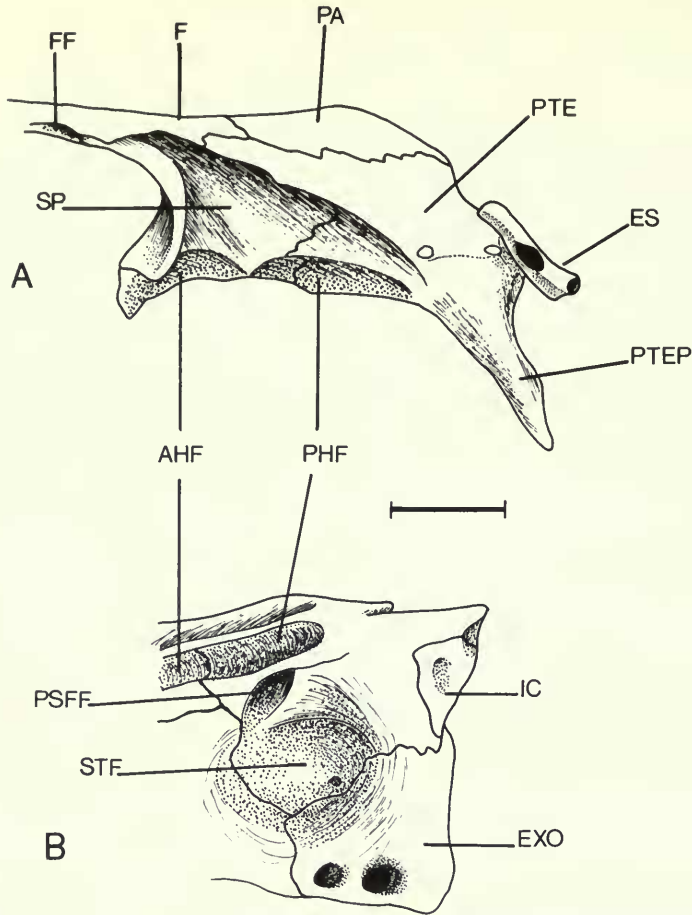


Fig. 13 *Opsariichthys*, pterotic region in A, lateral and B, ventral views.

The *epioccipital* (EPO, Fig. 14) is bordered medially by the supraoccipital, posteriorly by the exoccipital, anteriorly by the parietal and laterally by the pterotic. Its lateral face forms the upper medial wall and roof of the posttemporal fossa (PTF, Fig. 14). The dorsal surface of the epioccipital also contributes to the roof of the subtemporal fossa.

The *intercalar* (IC, Figs 13B & 14) is large and overlaps the suture between the exoccipital and the pterotic.

The *basioccipital* (BO, Fig. 15) is bordered dorsally by the exoccipital, anteriorly by the prootic and ventro-medially by the parasphenoid. Medially, each basioccipital contacts its partner to form the floor of the cavum sinus imparis and the roof of the posterior myodome (see below). The walls of the cavum sinus imparis are formed by dorsal extensions of each basioccipital on either side of the midline, the extension contacting the roof formed by the exoccipital (Fig. 15). Ventro-posteriorly there is a pharyngeal process which bears a high dorsal ridge; its ventral surface is expanded into a triangular masticatory plate (BOP, Fig. 15) which terminates in a high blade-like wing. The aortic foramen (AF) lies dorsal to the plate.

The *posterior myodome* (MYO, Fig. 15) extends far into the basioccipital. The basioccipital walls of the myodome converge to contact each other and seal the myodome posteriorly. In a specimen of 38.5 mm SL, however, the basioccipitals do not contact one another and the myodome is open posteriorly.

The *supraoccipital* (SO, Fig. 14) bears a medial ridge which runs backwards as a low lamellar

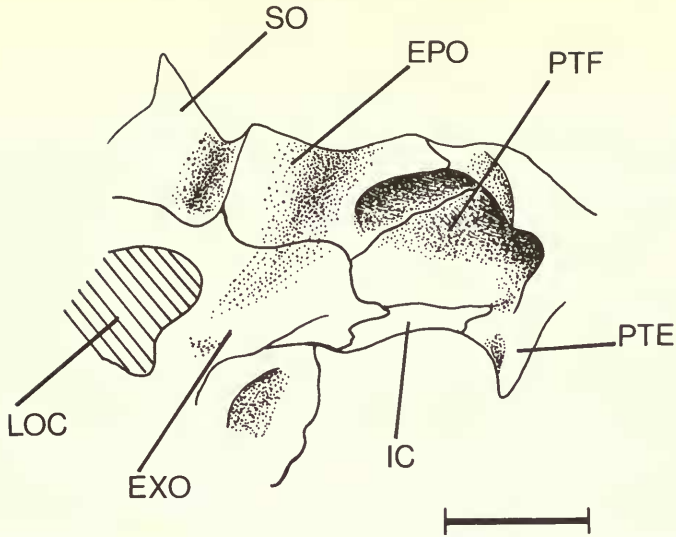


Fig. 14 *Opsariichthys*, pterotic region, right side, posterior oblique view.

process. Together with the epioccipitals, the supraoccipital forms a narrow post-parietal platform (see Howes, 1978).

#### *Zacco*

The *prootic* is of a similar shape to that in *Opsariichthys*, and likewise forms the border of the anterior foramen to the trigemino-facialis chamber. However, unlike *Opsariichthys* the lateral commissure is narrow, and the carotid foramen is greatly enlarged (Fig. 16). The *sphenotic* (Figs 16 & 17A) bears a thin lateral process which is curved ventro-posteriorly; its anterior face is deeply indented and provides a site of origin for part of the *levator arcus palatini* muscle. Only part of the sphenotic contributes to the dilatator fossa, the frontal forming the anterior part. The anterior hyomandibular fossa extends along the ventral surface of the sphenotic.

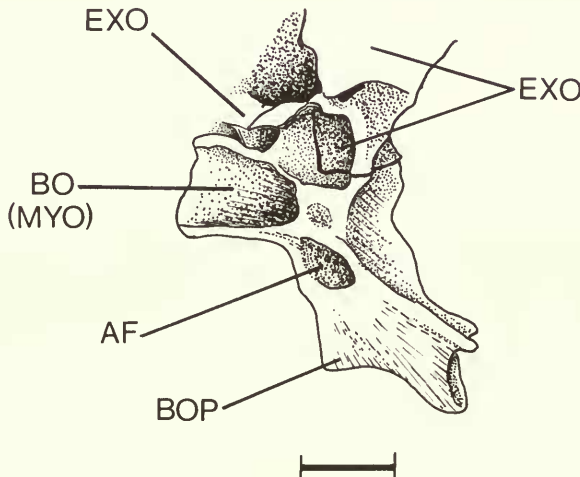


Fig. 15 *Opsariichthys*, basioccipital region cut through to show posterior myodome in anterior oblique view.

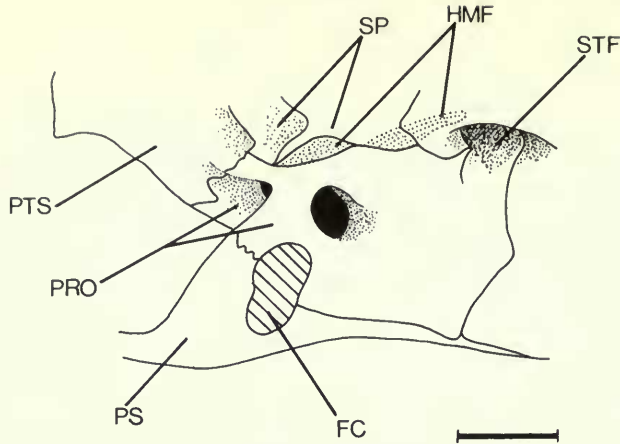


Fig. 16 *Zacco macrophthalmus* otic region in lateral view.

The posterior face of the *pteroic* forms the rear wall of the subtemporal fossa and the floor of the posttemporal fossa. There is no connection between the posttemporal and subtemporal fossae. The ventral surface of the pterotic houses the posterior hyomandibular fossa. The posterior process is of variable length and diameter, being thick and truncated in *Z. platypus* but slender and elongate in *Z. macrophthalmus* (PTE, Fig. 17A). The *basioccipitals* house part of the posterior myodome which is completely floored by the parasphenoid.

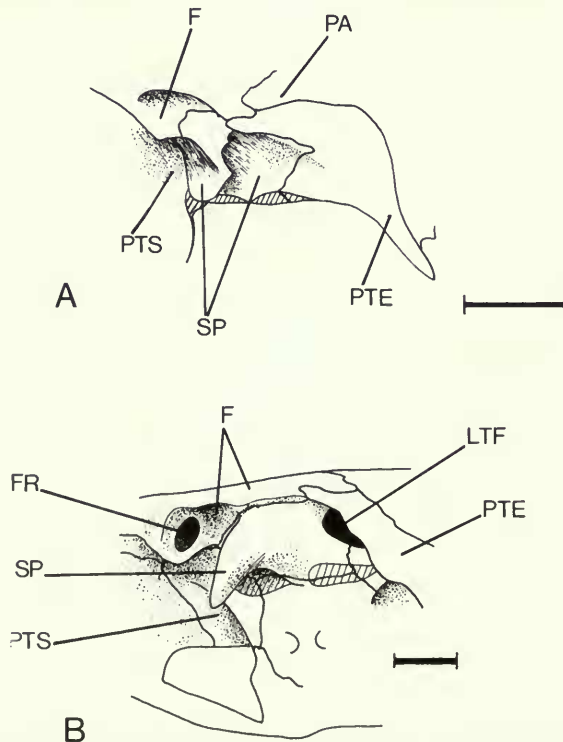


Fig. 17 A. *Zacco macrophthalmus* pterotic region, lateral view. B. *Barilius microcephalus* otic region, lateral view.



*Luciosoma*

The *prootic* is long and relatively shallow when compared with that in *Opsariichthys* and *Zacco* (Fig. 18). Contrary to the condition in those two genera, the anterior trigemino-facialis foramen is situated within the lateral face of the prootic, some way from its anterior border. The lateral commissure is wide. The *sphenotic* (Fig. 18) is long with a thick lateral process. The ventral surface of the bone bears the long anterior, and part of the posterior, hyomandibular fossa. The dorsal border of the sphenotic is sutured with the frontal and pterotic but neither of these bones forms a roof to the dilatator fossa.

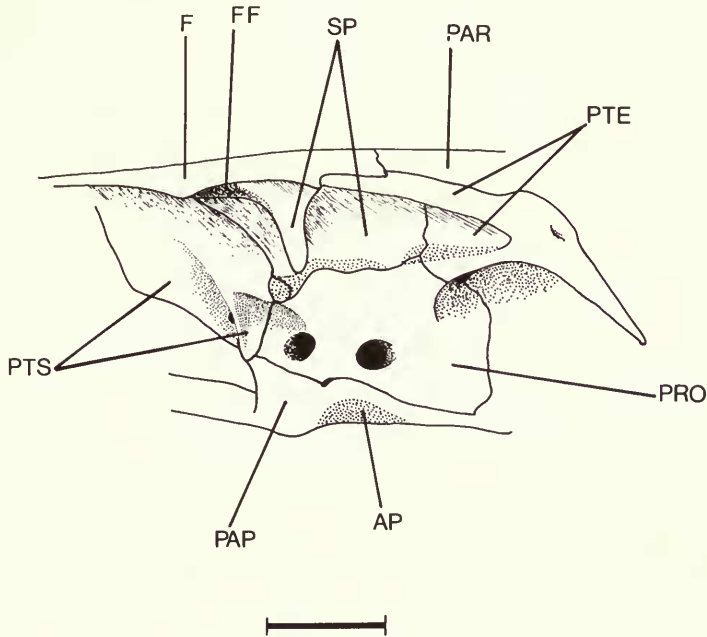


Fig. 18 *Luciosoma bleekeri* otic region, lateral view.

The *pterotic* (Fig. 18) is an elongate bone bearing the greater part of the posterior hyomandibular fossa on its ventral surface. The posterior process is long and spine-like but not so obliquely angled as in *Opsariichthys*. The pterotic forms the outer and posterior walls of the subtemporal fossa and part of the lateral wall of the posttemporal fossa which opens into it by way of an intramural channel. A *posterior myodome* is enclosed posteriorly by the basioccipitals and is floored ventrally by the parasphenoid. The *lateral occipital fenestra* is almost rectangular, a feature shared with some *Rasbora* species. There is no post-parietal platform and the *supra-occipital crest* is greatly reduced.

*Barilius*

*Group A.* The *prootic* resembles that of *Opsariichthys* and *Zacco* in that the anterior trigemino-facialis foramen is situated on the border of the bone. The *sphenotic* forms the major part of the dilatator fossa, its lateral process varies interspecifically from a thin lamella, as in *Opsariichthys*, to a stout spine. The posttemporal fossa contained in the pterotic is connected with the subtemporal fossa through a small foramen.

In some species of this group the posterior myodome is open ventrally so as to provide a passage for part of the eye musculature (see below, p. 147).

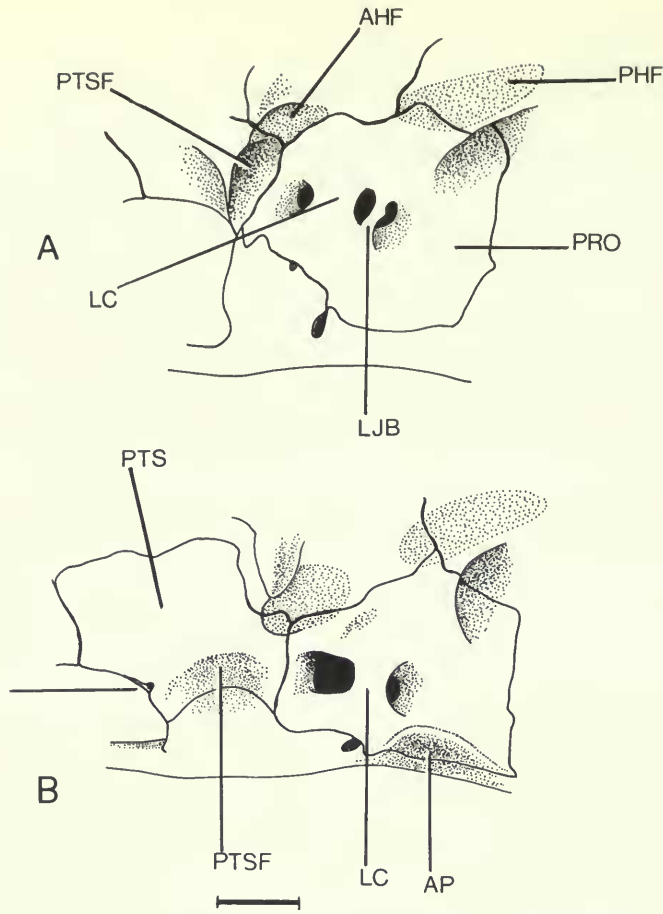


Fig. 19 Otic regions of A, *Barilius microcephalus* and B, *Barilius bola*, lateral views.

*Group B* (Fig 19B). The *prootic* bears the anterior trigemino-facialis foramen in its lateral face, and the lateral commissure is narrow. The carotid foramen is small. The lateral process of the *sphenotic* is a stout limb projecting either at right-angles or directed caudad. The anterior hyomandibular fossa is small and confined to the anterior ventral surface of the bone. There is no dilatator fossa, the lateral face of the sphenotic being almost perpendicular. There is a lateral temporal foramen shared between the sphenotic and pterotic. The *pterotic* does not provide a solid rear wall to the subtemporal fossa but is perforated by the greatly enlarged posttemporal foramen (see Howes, 1978). The posttemporal 'fossa' does not exist as an intramural channel as it does in *Opsariichthys*, *Luciosoma* and *Barilius Group A* species. The large subtemporal vault is roofed by the epioccipital and parietal and partly by the pterotic which also forms the lateral wall and posterior ventral bridge (Fig. 20).

The *posterior myodome* is open ventrally in the African species but closed in the two Asian representatives, *B. bola* and *B. guttatus* of this group. The form of the opening is similar to that described below in species of *Barilius Group C* but is not as extensive. A trend towards the closure of the myodome is apparent in various species of this group, the myodome being largely open in *B. loati* but the opening much reduced in *B. salmolucius*. This morphocline is correlated, as are other characters, with an elongation of the cranium (see p. 181).

*Group C* (Fig. 19A). The *prootic* is large and the anterior trigemino-facialis foramen is in its lateral face, the lateral commissure is long. The *sphenotic* is short but deep and bears an extensive

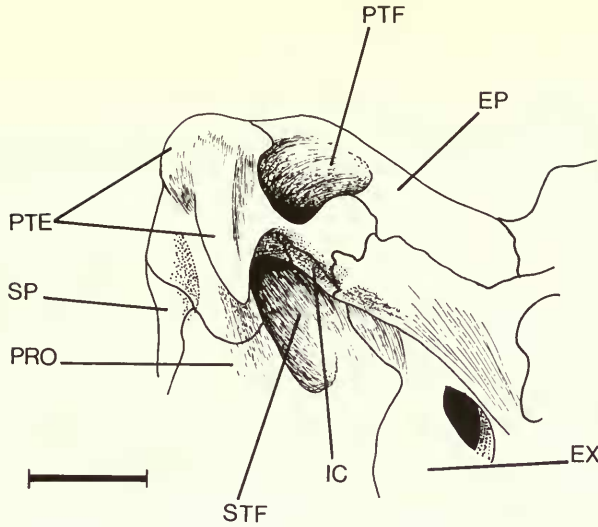


Fig. 20 *Barilius bola*. Ventral oblique view of posttemporal and subtemporal fossae.

lateral process. In *Barilius microcephalus* there is a large lateral temporal foramen, a feature shared with species of *Barilius Group B* and *Opsariichthys* (LTF, Fig. 17B & Howes, 1978 : 35). The ventral surface of the sphenotic contains part of the anterior hyomandibular fossa. The *basioccipital* is unfloored so that the *posterior myodome* is open ventrally (Fig. 21). The *recti inferioris* eye muscles extend from the medial edges of the basioccipital process to enter the myodome; the *recti exterioris* originate from the prootic walls of the myodome. This feature is discussed further below, p. 153.

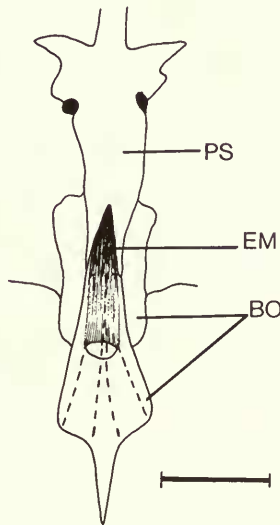


Fig. 21 *Barilius microcephalus* otic region seen ventrally. Dashed lines indicate path of the eye muscles through the myodome.

### *Engraulicypris*

The *prootic* (Fig. 22A) is of similar shape to that in *Luciosoma*. The anterior trigemino-facialis foramen is situated in the lateral face of the bone, the lateral commissure is narrow and there is a deep jugular groove crossed by a narrow spur. The *sphenotic* (Figs 22 & 23) bears a broad,

ventrally directed lateral process. Its dorsal surface forms the major portion of the dilatator fossa and ventrally bears the anterior hyomandibular fossa.

The *pteroic* (Figs 22–24) has a broad cranial surface and a short, stout, posterior process. Its medial face forms the lateral wall of the subtemporal fossa which is perforated by a small foramen leading into the posttemporal fossa (Figs 22 & 24); no muscle element passes through into the subtemporal fossa. The *basioccipital* is unfloored so that the posterior myodome is open ventrally (Figs 22 & 23). The *recti inferioris* eye muscles extend from a notch in the ventro-lateral border of the bone to enter the myodome. The basioccipital process is very short with a ventral channel and the masticatory plate is weakly developed.

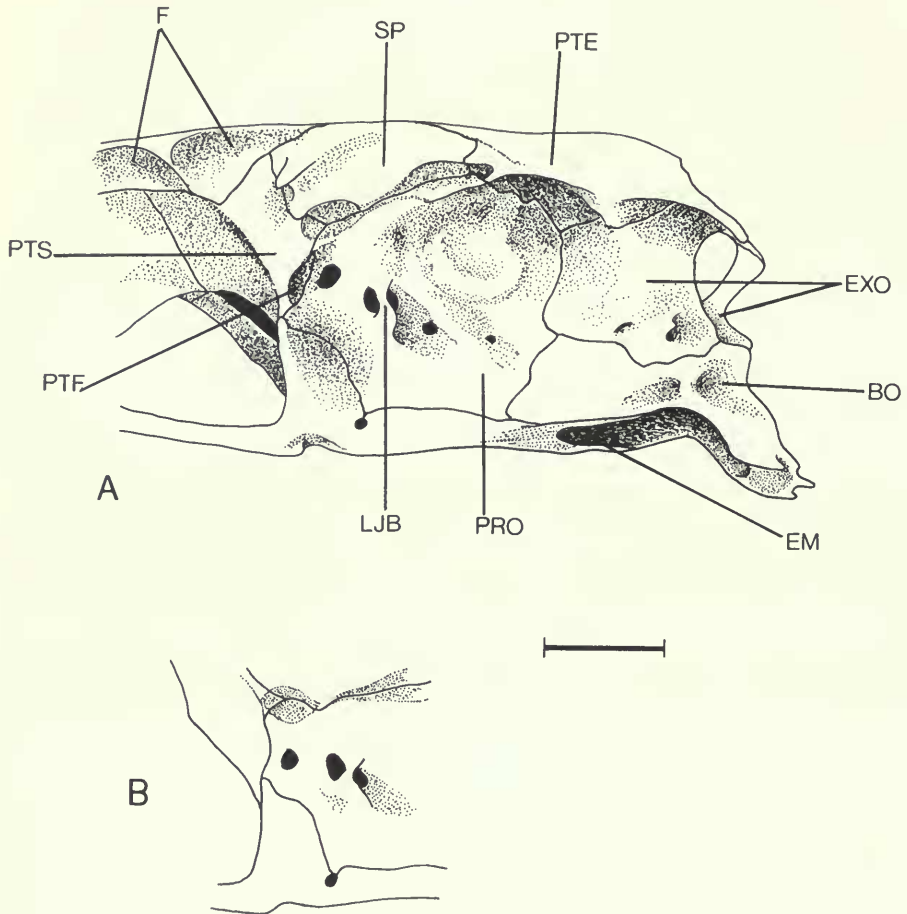


Fig. 22 A. *Engraulicypris sardella* neurocranium, ventro-lateral view. B. *Barilius* (= *Leptocypris*) *niloticus* otic region, lateral view.

#### Comments on the neurocranium

The broad, shallowly notched ethmoid block which is characteristic of *Opsariichthys* is a feature shared with *Luciosoma* and *Barilius* species of Groups B and C. This broad type of ethmoid appears to represent a plesiomorph condition amongst the Cyprinidae. In the various groups investigated so far, it is the most plesiomorph members which possess a wide, shallowly notched supra-ethmoid-mesethmoid and a vomer that protrudes little beyond the anterior ethmoid border (see Howes, 1978). With elongation of the cranium and jaws, there is seen a correlated narrowing of the ethmoid and a posterior elongation of the anterior notch. Such a morphocline can be found

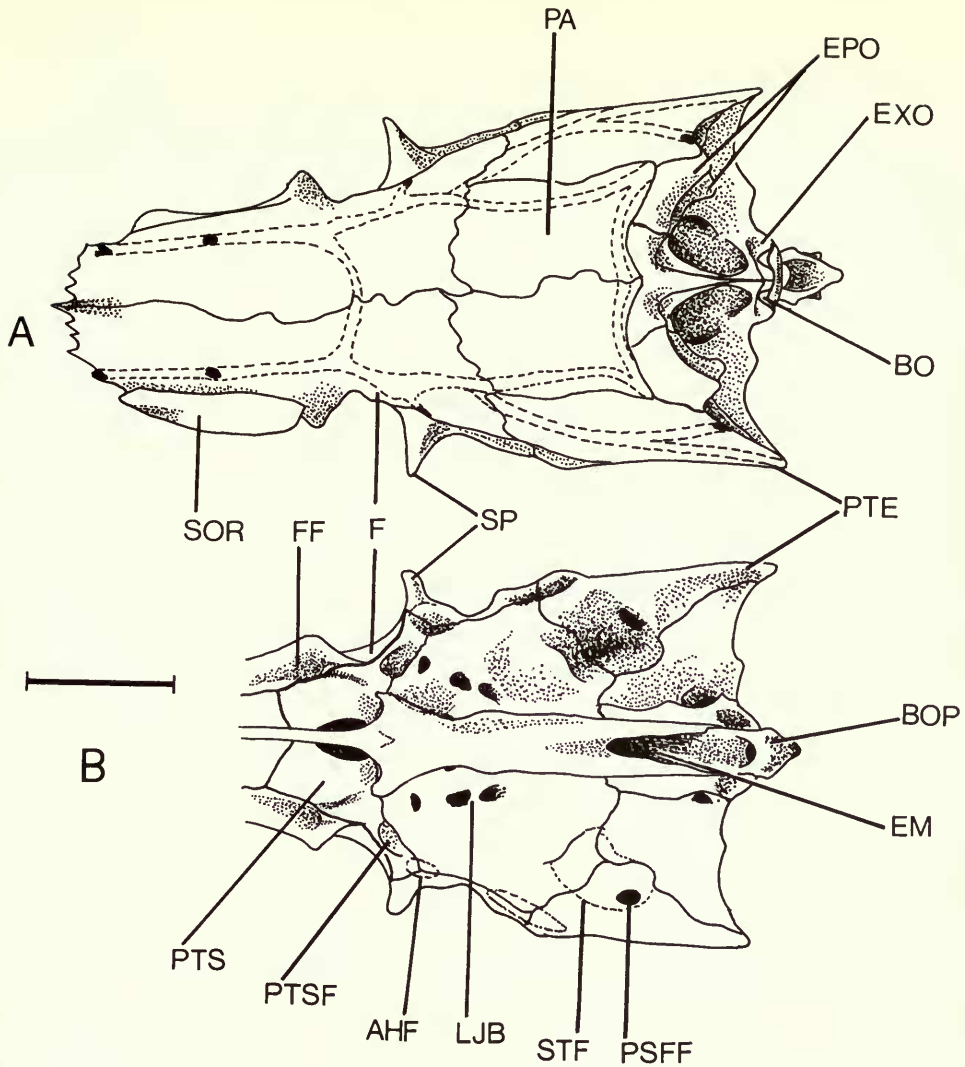


Fig. 23 A. *Engraulicypris sardella* cranium in A, dorsal and B, ventral views. The left side is unshaded for clarity and the limits of the various fossae are indicated by dotted lines.

in the cultrines (*Culter-Erythroculter*), aspinines (*Aspius-Luciobrama*) and hemicultrines (*Xenocypris-Ochetobius*). (In barbines and labeines, the most derived members of the respective groups possess a medial elongation of the ethmoid block. This is presumably an adaptation involved with the inferior position of the mouth.)

In the taxa reviewed in this paper, the dorsally excavated supraethmoid of *Luciosoma* is considered apomorphic. A similar ethmoid morphology is found in some *Rasbora* species (see p. 183). The thickened vomer of *Opsariichthys* and *Barilius Groups B and C* is also considered a synapomorphy (see Howes, 1978).

The ethmoid region of *Engraulicypris sardella* is highly derived, its modification making for a highly protrusile jaw mechanism (see p. 164). In this respect it shares no feature with any of the genera described above.

The preethmoids of *Opsariichthys*, *Zacco*, all *Barilius* and *Luciosoma* are large and articulate with the palatine. This is presumably the plesiomorph condition for in those taxa which show

cranial elongation the preethmoids are reduced in size and in some hemicultrines (e.g. *Ochetobius*) the palatine no longer articulates with the preethmoid but has moved posteriorly so as to contact the edge of the mesethmoid.

There is no anterior myodome in any of the genera discussed here.

A character which appears to have some significance as an indicator of relationship amongst the genera under discussion is the connection between the pterosphenoid, parasphenoid and prootic. In *Opsariichthys*, *Luciosoma*, some species of *Rasbora*, all *Barilius* and *Engraulicypris* there is some connection (either medial or lateral or both) between the pterosphenoid and the ascending wing of the parasphenoid. In an earlier paper (Howes, 1978) I stated that in some species of *Barilius* the pterosphenoid did not contact the parasphenoid. Having now re-examined all the specimens used in that study I find that there is such a connection, albeit a slight one in some cases. An exception is in *Zacco* where the pterosphenoid has no connection with the parasphenoid.

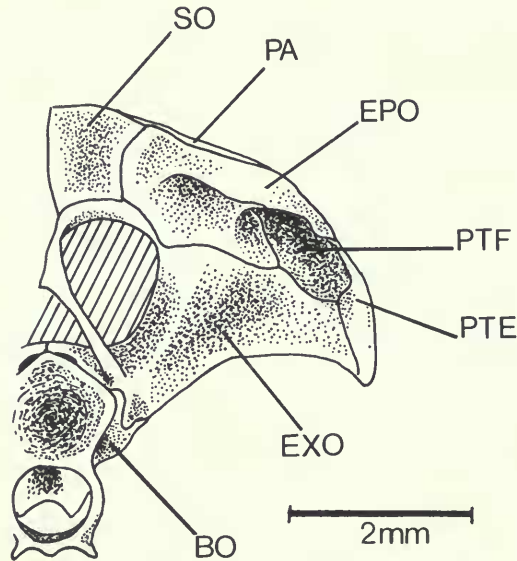


Fig. 24 *Engraulicypris sardella* cranium, posterior view of left side.

An associated character is the position of the anterior foramen of the trigemino-facialis chamber. In all genera apart from *Luciosoma*, *Engraulicypris* and *Barilius* Groups B and C it is formed by the anterior border of the prootic, but in the exceptional taxa the foramen is situated within the lateral face of the prootic.

In order to determine the significance of these features a morphological survey was made of the otic region in the Cyprinidae; the following 'classification' emerges.

Type 1. Pterosphenoid makes no contact with the parasphenoid; the anterior trigemino-facialis foramen is formed by the anterior border of the prootic; lateral commissure variable in length; myodome of variable depth; hyomandibular fossa sometimes invades the pterosphenoid.

Type 2. Pterosphenoid contacts the medial face and a narrow dorsal area of the parasphenoid wing; the anterior trigemino-facialis foramen is formed by the anterior border of the prootic; lateral commissure wide; myodome deep; hyomandibular fossa extends on to the pterosphenoid.

Type 3. Pterosphenoid contacts the dorsal border of the parasphenoid wing; the anterior trigemino-facialis foramen is situated within the lateral face of the prootic; lateral commissure narrow; myodome shallow; hyomandibular fossa does not invade the pterosphenoid.

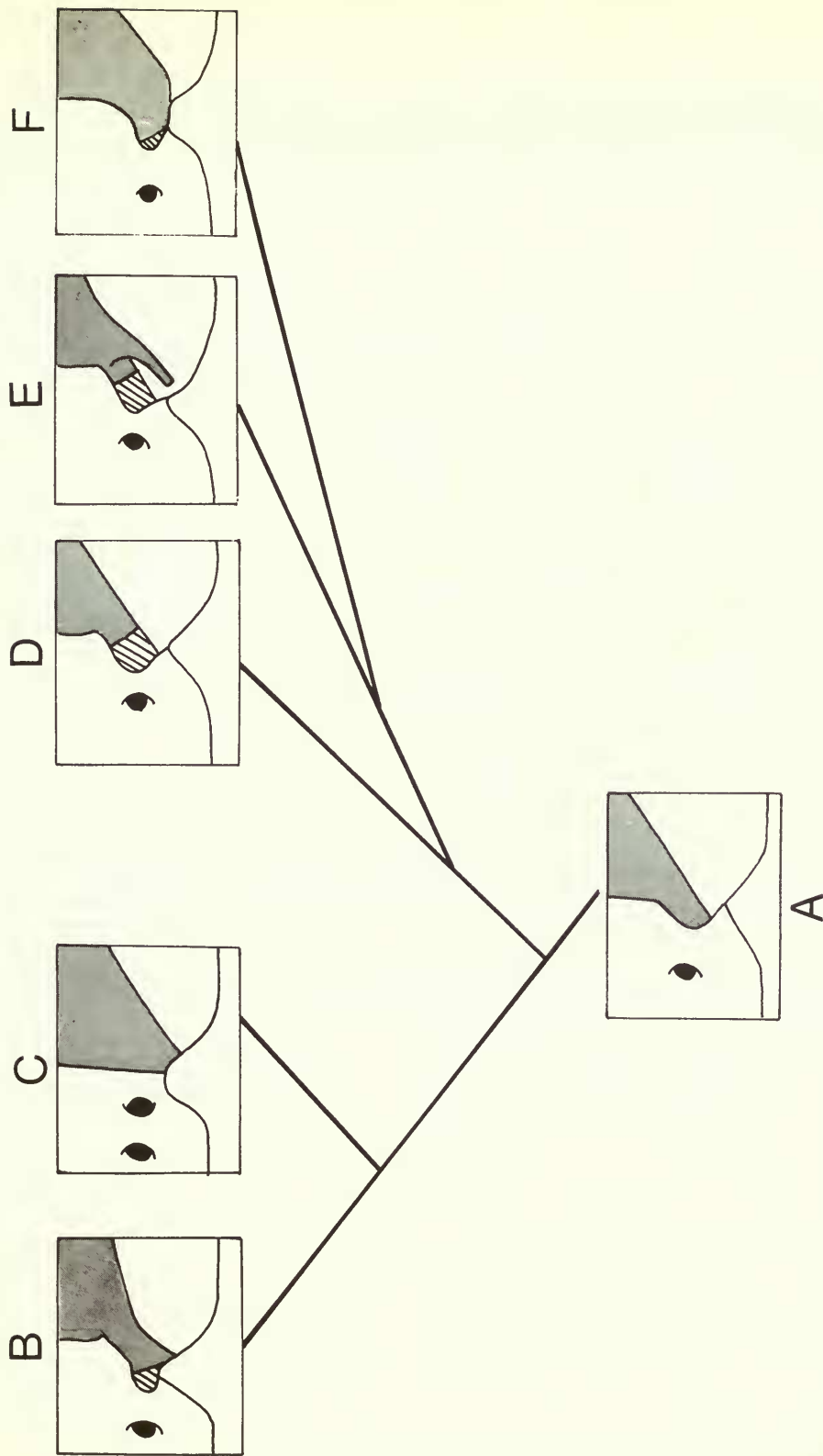


Fig. 25 Schematic diagram of the pre-otic neurocranium illustrating the possible derivation of four major morphotypes. A. Assumed ancestral type. B. Type 2 (*Opsarichthys*). C. Type 3 (*Barilius bola*). D. Type 1 (*Carassius*). E. Type 4 (*Oreoleuciscus*). F. Type 1 (*Rutilus*). G. Type 4 (*Oreoleuciscus*). The medial part of the prootic is cross-hatched, the pterosphenoic darkly shaded.

Type 4. As type 3 but the anterior trigemino-facialis foramen formed by the anterior border of the prootic and the hyomandibular fossa invades the pterosphenoid.

Type 5. Pterosphenoid contacts the parasphenoid *via* a medial parasphenoid process; lateral commissure excessively narrow; myodome reduced; the pterosphenoid does not bear the anterior hyomandibular fossa.

This classification is a basic one and a degree of intermediacy exists between the five types.

Type 1 appears to be the plesiomorph condition on the basis of the following evidence: (a) It is the type of contact found in members of those cyprinid groups so far investigated which are considered plesiomorphic on other grounds. (b) In juvenile specimens of *Opsariichthys* (c. 40 mm SL) the pterosphenoid fails to contact the parasphenoid and the ascending parasphenoid wing projects anteriorly as a small spur. During ontogeny a ventro-lateral process of the pterosphenoid contacts the parasphenoid spur. (c) In the characoids and presumed 'primitive' teleosts (i.e. Elopiformes) there is no contact between the parasphenoid and pterosphenoid.

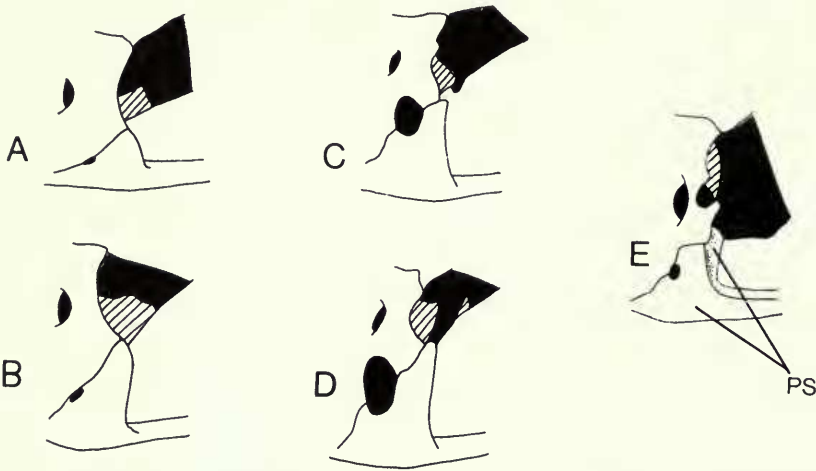


Fig. 26 Semi-diagrammatic drawings of the pre-otic neurocranium of A. *Cyprinus*. B. *Catla*. C. *Rutilus*. D. *Alburnus*. E. *Labeo*. The medial part of the prootic is cross-hatched, the pterosphenoid darkly shaded.

As well as being present in *Zacco* and *Barilius Group A*, Type 1 morphology is characteristic of *Cyprinus*, *Carassius*, *Catla* and *Xenocypris* (Figs 25D; 26A & B).

A derived condition of Type 1 is present in *Leuciscus* and *Rutilus* where a lateral strut of the pterosphenoid extends ventrally but does not make contact with the parasphenoid wing (Fig. 26C). However, in *Alburnus*, *Abramis*, *Squaliobarbus*, *Capoetobrama*, *Oreoleuciscus*, *Barbus intermedius* and some other taxa such a strut extends to join the parasphenoid (Fig. 26D).

Rognes (1973) described in labrids a strut extending from the pterosphenoid to the prootic; this he termed the 'internal jugular bridge'. Rognes (1973) illustrated variable conditions in the development of this strut which did not always contact the prootic. No link with the parasphenoid was described. Greenwood (1976) also described an internal jugular bridge in centropomids and again illustrated the variability of contact – only in one case was there found to be a direct pterosphenoid/parasphenoid contact.

No such variability exists in any of the adult cyprinids examined and the 'incomplete' contact of the pterosphenoid spur and parasphenoid (e.g. *Rutilus*) or complete contact (*Abramis*) are taxon-defining characters.

Type 2 morphology is confined to *Opsariichthys*. In this taxon the medial wall of the prootic does not extend beyond the anterior border of the parasphenoid wing, in contrast to the situation in Type 1 where the prootic extends well forward (cf. Figs 25B & D).



Type 3 morphology is confined to *Barilius* Groups B, C, *Engraulicypris* and *Luciosoma* (Fig. 25C); in no other taxa so far examined is the anterior trigemino-facialis foramen placed within the lateral face of the prootic. This is considered a derived condition and is seen as a 'sequential development' of Type 2.

Type 4 morphology appears to be a derived Type 1 condition in that there has simply been an elongation of the pterosphenoid and a lengthening of the parasphenoid wing. Numerous examples of this condition can be cited (e.g. *Barbus barbuis*; *Schizothorax esocinus*; *Ochetobius elongatus*; *Erythroculter mongolicus*; *Elopichthys bambusa*) all of which are amongst the most derived members of their respective lineages in terms of cranial elongation (see comments on the ethmoid region, p. 149). This morphotype is best exemplified by *Oreoleuciscus* (Fig. 27). In this genus there is an extensive contact between the parasphenoid and pterosphenoid but an elongate fenestra exists between the pterosphenoid and the prootic, posterior to the parasphenoid ascending wing; the anterior trigemino-facialis foramen is also contained on the border of the prootic. (It is interesting to note that the closure of the pterosphenoid-prootic-parasphenoid fenestra would produce a condition approximating to that in *Barilius* Group B; cf. Figs 19B & 27.)

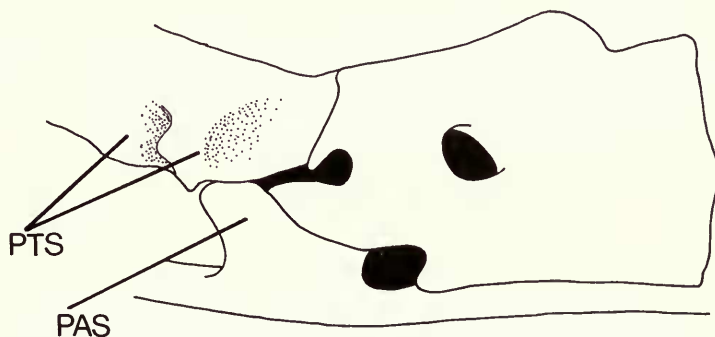


Fig. 27 Orbital-otic region of *Oreoleuciscus pewslowi*, lateral view.

Type 5 morphology has been encountered only in *Labeo*, *Barbichthys* and *Tylognathus* and is considered to be a derived condition (Fig. 26E).

A seemingly derived character shared by *Zacco* and *Barilius* Group A is the enlarged carotid foramen between the prootic and parasphenoid. This feature is also found in *Cyprinus*, *Rutilus* and *Abramis*. The common condition in the Cyprinidae is a small carotid foramen.

Mention should be made here that Vanderwalle (1974) considers the trigemino-facialis chamber of *Gobio* to represent a 'derived' condition because the jugular vein is not enclosed within a separate channel or tunnel. I have not found such an enclosure in any cyprinid examined, although in *Engraulicypris*, *Leptocypris* and some species of *Barilius* Group C there is a deep jugular groove along the lateral face of the prootic. Associated with this feature is a thin bridge of bone (LJB, Figs 19A; 22A & B; 23) crossing the posterior foramen of the pars jugularis and serving to separate the jugular from the trigemino-facialis nerve bundle. In some species of *Barilius* this bridge is incomplete and developed only as a thin process arising from the ventral part of the groove. A similar lateral jugular bridge occurs in alburnines and cultrines. Until the distribution of this feature is more fully documented for the cyprinids, no polarity can be ascribed to it.

The pterotic, when viewed dorsally, in *Opsariichthys*, *Luciosoma*, *Engraulicypris* and *Barilius* Groups B and C is seen to extend well posteriorly, whereas in *Zacco* and *Barilius* Group A, the posterior margin of the bone is truncated (Fig. 28).

A ventrally open posterior myodome is a feature of *Barilius* species in Group A, B and C. The only other cyprinid genera in which I have found an open myodome are *Leptocypris* and *Engraulicypris sardella*. Likewise, in those taxa the morphology of the eye muscles associated with the myodome is similar to that in *Barilius* (see p. 147). A ventro-posteriorly open myodome is present in several groups of characoids, and in these too some of the eye muscles originate from

outside the myodome, the most specialized condition being found in the bryconines, acestro-rhynchines and some characinines (pers. obs.). An open myodome and externally originating eye muscles also occurs in clupeoids, salmonids and some elopids. Patterson (1975) gave an account of the possible phylogenetic history of the posterior myodome, believing the open myodome to be a derived condition. Verraes (1976) showed that in *Salmo* the myodome opens during ontogeny and the eye muscles extend posteriorly through it. Thus, it would seem that the open myodome in cyprinids must be thought of as a derived state and synapomorphic for those genera possessing it. It was noted (p. 142) that in a small specimen of *Opsariichthys* the myodome was open, but closed during later ontogeny. Certainly the morphology of the posterior myodome in *Opsariichthys* differs quite considerably from that of other cyprinids in that the basioccipital is constricted below the lagenar capsule. Thus the posterior portion of the myodome is enclosed within the anterior part of the basioccipital, whereas in other cyprinids it extends to the posterior wall of the basioccipital. The same myodome morphology is apparent in the most derived species of *Barilius Group B* which suggests that the closed myodome is, as in *Opsariichthys*, secondarily derived, although I have been unable to ascertain whether in fact an open myodome occurs during ontogeny in these *Barilius* species.

The connection between the *subtemporal fossa* and *posttemporal fossa* is a feature common to all the genera presently under consideration with the exception of *Zacco*. This character has also been found in *Leptocypris* and in some species of *Rasbora*; its occurrence in these genera is discussed later (p. 180). As no other cyprinid taxon examined has such a connection between the fossae, this character is considered to be a synapomorphy.

#### *Dermal bones of the skull*

##### *Opsariichthys*

The *frontals* (F, Fig. 28) are broad and short with an irregular midline suture. The lateral border of each frontal is markedly concave where it contacts the supraorbital. Medial to its suture with the sphenotic there is a deep ridge from which stems the anterior part of the *levator arcus palatini* (FF, Fig. 13A). The frontal slightly overhangs the sphenotic to form a medial roof to the dilatator fossa. It contacts the pterotic across a narrow area.

Each *parietal* (PA, Figs 13 & 28) is broad and short (contained 4 times in the length of the frontals) with an irregular midline suture. The lateral border contacts the pterotic and the posterior border, the epioccipital and supraoccipital. The posterior border of the parietal is marked by a deep ridge through which runs the laterosensory canal. Each *nasal* (N, Figs 1-3) is small with a single dorsal opening. The *supraorbital* (SOR, Fig. 29) is very wide and does not contact the 5th infraorbital, the bones being separated by the outward curvature of the frontal. The 1st, 2nd, 3rd and 4th *infraorbitals* are large bones (Fig. 29). The 3rd and 4th do not cover the cheek but leave a naked area between their posterior borders and the preoperculum. The 5th infraorbital is reduced and contacts the pterotic.

##### *Zacco*

The *frontals* are narrow anteriorly and their lateral margins are gently concave (Fig. 28B). The *parietals* are broad and short, their posterior margins truncated. The *supraorbitals* are long and narrow. The 1st *infraorbital* is deep, the 2nd and 3rd shallow, 4th deep, and 5th reduced to an ossification around the sensory canal; it does not contact the supraorbital. There is interspecific variability in the size of the infraorbitals which are deeper and longer in *Zacco macrophthalmus*, *Z. temmincki*, *Z. barbatus* and *Z. pachycephalus* than in *Z. platypus*.

##### *Luciosoma*

The *frontals* are broad and long, with their lateral margin gently concave. As in *Opsariichthys* there is a deep frontal fossa (FF, Fig. 18). A particular feature of *Luciosoma* is a deep channel between the anterior opening of the frontal sensory canal and the posterior opening of the nasal

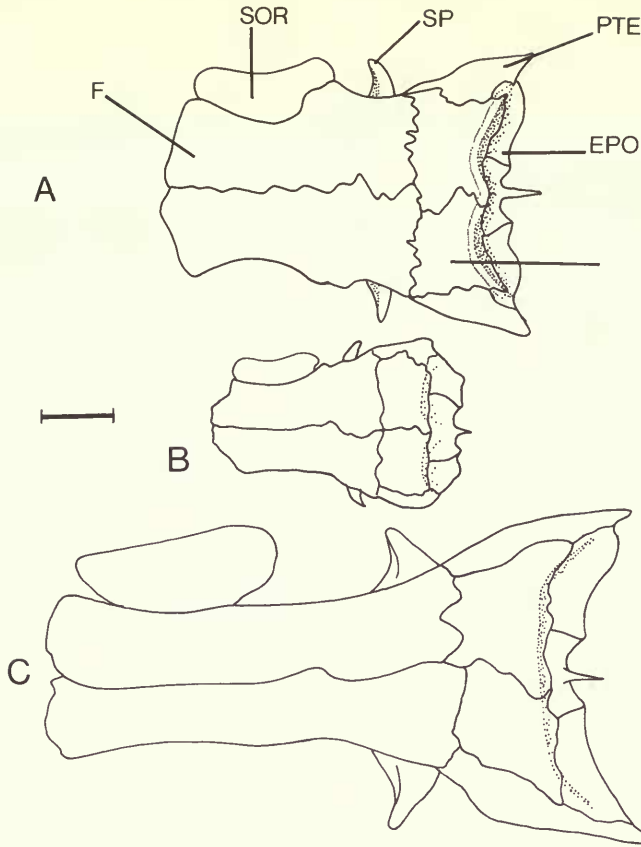


Fig. 28 Cranial roof of A. *Opsariichthys*. B. *Zacco platypus*. C. *Barilius bola*.

canal (FG, Fig. 6A). The *nasal* is short without a central dorsal pore (Fig. 6A). Each wide *supraorbital* contacts the 5th *infraorbital*. The 1st and 2nd *infraorbitals* are shallow, the 3rd expanded to almost cover the cheek, the 4th and 5th long.

### *Barilius*

*Group A.* The *frontals* are narrow as compared with *Opsariichthys*, their lateral margin gently concave. The dilatator fossa deeply indents the postero-lateral margin of each frontal. The *parietals* are long, varying interspecifically from 2.5 to 2.8 times in the length of the frontals (cf. 3.8–4.0 in *Opsariichthys* and in other *Barilius* groups). The *nasals* are elongate each with 2 dorsal pores. The 1st and 2nd *infraorbitals* are shallow, the 3rd, 4th and 5th expanded (Fig. 29B). The 5th *infraorbital* contacts the narrow *supraorbital*.

*Group B.* The *frontals* are elongate and narrow, their lateral margin gently concave where the *supraorbital* joins. The *parietals* are slightly longer than those of *Opsariichthys* (3.8 times in frontal length) and their posterior lateral margins are extended (Fig. 28C). The 1st and 2nd *infraorbitals* are deep, the 2nd being elongate. The 3rd, 4th and 5th *infraorbitals* are expanded so as to cover the entire cheek region and contact the preoperculum (Fig. 29C); the 5th contacts the broad *supraorbital*.

*Group C.* The *frontals* are elongate but broader than those in *Group B*. In *Barilius microcephalus* the ventral frontal fossa is perforated so as to form a lamellar ring (FR, Fig. 17B). Part of the *levator arcus palatini* originates from the ventral surface of the frontal anterior to the ring, the muscle passing through it to join its other section which originates from the deep fossa dorso-posteriorly to the ring. In other species included in the group there is a deep frontal fossa similar

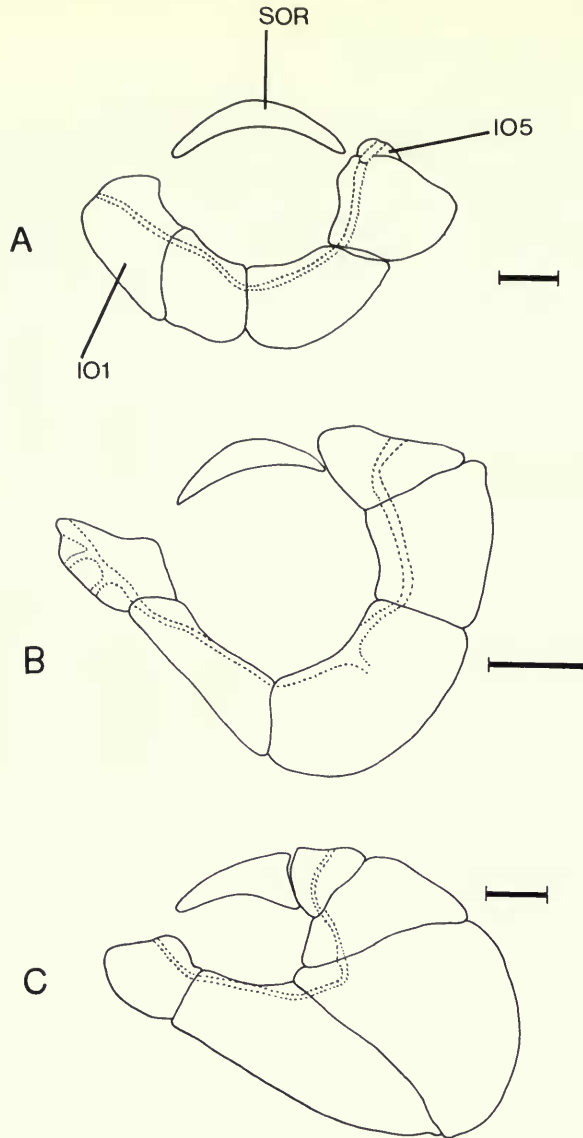


Fig. 29 Circumorbital series of A. *Opsariichthys*. B. *Barilius barila*. C. *Barilius bola*.

to that in *Opsariichthys* (see above). The arrangement of the circumorbital bones is like that in species of *Group A*.

#### *Engraulicypris*

The *frontals* (Fig. 23) are long and narrow and formed anteriorly into a shallow pit. The sensory canal contains a single pore midway along its length. Ventrally, each frontal bears a fossa which serves as a site for the origin of part of the *levator arcus palatini* muscle. The *parietals* are long, being contained twice in the length of the frontals. The *nasals* are elongate and curved so as to lie in the concavity of the ethmoid margin; each nasal has two dorsal pores. The *supraorbital* is long and broad and contacts the 5th infraorbital. The 1st infraorbital (Fig. 30) is extensive and when the jaws are retracted, it completely covers the maxilla and premaxilla. The posterior border is

markedly concave and covers the anterior third of the 2nd infraorbital; the 3rd, 4th and 5th infraorbitals are long.

#### Comments

There is no contact between the supraorbital and the 5th infraorbital in *Opsariichthys* or *Zacco* but such contact is present in *Luciosoma*, *Engraulicypris* and all groups of *Barilius* and in these taxa the infraorbitals are expanded.

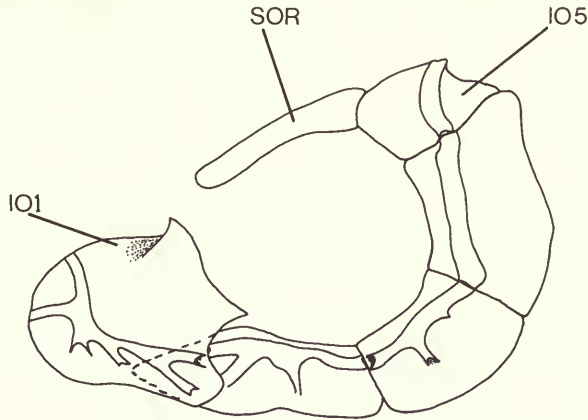


Fig. 30 Circumorbital series of *Engraulicypris sardella*.

In the majority of cyprinids the infraorbitals are reduced, presumably a secondary regression from an expanded ancestral condition (Tretiakov, 1946). In some groups such as the aspinines, where there has been elongation of the cranium, the infraorbitals are reduced to the canal-bearing part of the bone, whereas in the long-headed bariliines the infraorbitals are expanded. This condition appears to be due in part to the lateral expansion of the cranial musculature in bariliines, as evidenced by the produced sphenotic processes (Fig. 28C) and the need for a protective shield (p. 158). In the case of *Barilius Group B* (Fig. 29C), it appears that the expansion of the infraorbitals is a derived condition. This is clearly seen in the excessively elongate 2nd infraorbital and the pronounced orbital narrowing of the 3rd. Indeed, a transformation series of this character state can be witnessed in species of *Group B* and the more extreme forms of this morphocline are represented in various bariliine genera (see Figs 29A–C) where *Opsariichthys* represents the plesiomorph state and *Barilius bola* the derived.

Ramaswami (1955) has already commented on Regan's (1911) statement that *Opsariichthys* has a '... complete series of circumorbitals'. Ramaswami thought Regan's use of the word 'complete' ambiguous. Regan may have been referring to a series without interruption, in other words he believed there to be a contact between the 5th infraorbital and the supraorbital. The separation is only a narrow one and the interposing frontal could be mistaken for part of the supraorbital.

A *frontal fossa* is present in all the genera under discussion with the exception of *Zacco*. In *Opsariichthys* and *Luciosoma* the fossa is shallow and serves to support the *levator arcus palatini* muscle. In *Barilius Group A* the fossa is a deep anterior extension of the dilatator channel; in *Group C*, the fossa is also deep (and in *B. microcephalus* is penetrated by a foramen) but, as in *Opsariichthys* and *Luciosoma* it provides the site of origin for the *levator arcus palatini*. In *Barilius Group B* the frontal fossa has all but disappeared and exists only as a narrow ventral ridge. Apart

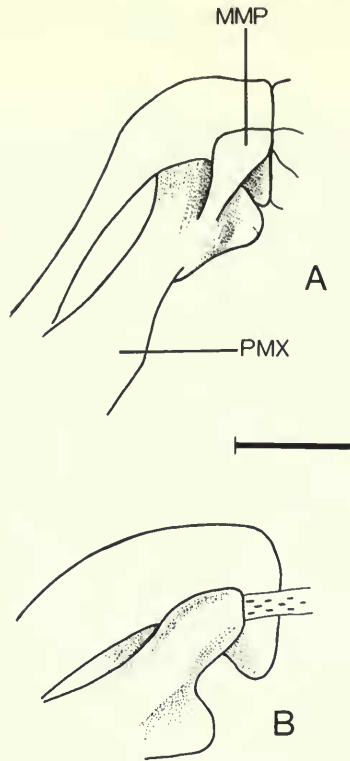


Fig. 31 Anterior of maxilla and premaxilla of A. *Opsariichthys*. B. *Zacco macrophthalmus*. Ventral views.

from *Leptocypris* and *Engraulicypris sardella* and some *Rasbora* species, I have not found any cyprinid with this type of frontal cavity. Many taxa, however, possess a sphenotic fossa, lying anteriorly to the sphenotic lateral process, from which the *levator arcus palatini* originates (e.g. *Zacco*, *Alburnus*).

Forey (1975) commented on a frontal ridge in clupeoids where it also serves as a site of origin for the *levator arcus palatini*. He also pointed out the apparent correlation between a frontal ridge and a hyomandibular process (see p. 165).

### *The jaw bones*

#### *Opsariichthys*

The jaws have been described in some detail previously (Howes, 1978), therefore it is necessary here to note only the more pertinent features: The *premaxilla* is very slender with the anterior ascending process sloped backwards. The *maxilla* bears, antero-medially, an axe-shaped process which underlies the premaxilla and which contacts its partner from the opposite side along a narrow lateral face (Fig. 31A). The anterior tip of each maxilla extends almost to the symphysis of the premaxillaries (Fig. 32A). The *dentary* is deeply notched anteriorly and has a strong symphyseal process. The ventral border bears 7-8 pores of the sensory canal. Posteriorly there is a high coronoid process, see Fig. 36E in Howes (1978).

#### *Zacco*

The *premaxilla* is a thick bone with a short ascending process. The anterior tips of each *maxilla* are widely separated from one another across the midline. Each anterior medial maxillary

process is rounded distally and joined to its partner across the midline *via* a ligament (Fig. 31B). The *dentary* is shallow with a high coronoid process; a symphyseal process is lacking.

In *Zacco pachycephalus* and *Z. barbatus* the jaws are like those in *Opsariichthys* in that (i) the premaxilla is thin and separated by a slight gap from the maxilla, (ii) the medial maxillary processes contact each other directly across the midline and not *via* a ligament and (iii) the anterior maxillary tips extend well forward.

### *Luciosoma*

The *premaxilla* is exceedingly shallow, with a wide and short anterior ascending process which joins its partner to form an almost beak-like jaw. The *maxilla* is also shallow, overlapping the premaxilla for that bone's entire length. The anterior medial maxillary process is wide and contacts its partner along the midline. The outer anterior tip of the maxilla extends almost to the premaxillary symphysis (Fig. 32C). The *dentary* is shallow, with a short symphyseal process. The lateral wall is curved outward as in *Opsariichthys* and the coronoid process is high.

### *Barilius*

*Group A.* The *premaxilla* and *maxilla* are narrow, the former with a rather long ascending process and the latter with its anterior medial process making contact with its partner in the midline. The anterior tips of the maxillaries are widely separated from each other (Fig. 32B). The *dentary* is very shallow with a high coronoid process and there is no symphyseal knob or anterior notch.

*Group B.* The jaws of *Barilius bola* are described in an earlier paper (Howes, 1978) and those of other species assigned to this group correspond in having shallow *premaxillaries* with short, wide, beak-like anterior ascending processes, shallow *maxillaries* each bearing a wide palatine notch and a wide medial anterior process. The anterior tip of each maxilla almost contacts its fellow across the midline (Fig. 32E). The *dentaries* are long and shallow with high coronoid processes and they lack symphyseal knobs and anterior notches.

*Group C.* The jaws are closely similar to those of *Group B* except for deeper and shorter jaw bones and the tips of the premaxillary ascending processes being triangular instead of curved (Fig. 32D).

### *Engraulicypris*

The *premaxilla* (Fig. 33C) has a short anterior ascending process, which is slightly indented in its leading edge, and a broad midlateral ascending process. The *maxilla* (Fig. 33A) bears a high, narrow midlateral ascending process from which extends a ligament to attach to the medial face of the 2nd infraorbital. The anterior tip of the maxilla is bifurcated, the medial process extending ventrally to contact its partner in the midline (Fig. 33B). The posterior part of the maxilla is rounded and expanded ventrally, this expanded portion is grooved so as to articulate with the dorsal posterior margin of the premaxilla. The *dentary* (Fig. 33D) is deep, with a short, broad, upright coronoid process, the posterior border of which is deeply concave. The *anguloarticular* is large with a long convex dorsal margin.

### *Hyopalatine arch*

### *Opsariichthys*

The *hyomandibula* possesses two articular heads separated from each other by a shallow depression. The anterior facet has a long sloped face which abuts against the pterosphenoid wall of the articulatory fossa. The posterior facet has a narrow surface which fits into the channel-like pterotic fossa. The anterior border of the hyomandibula is rounded below the anterior facet and

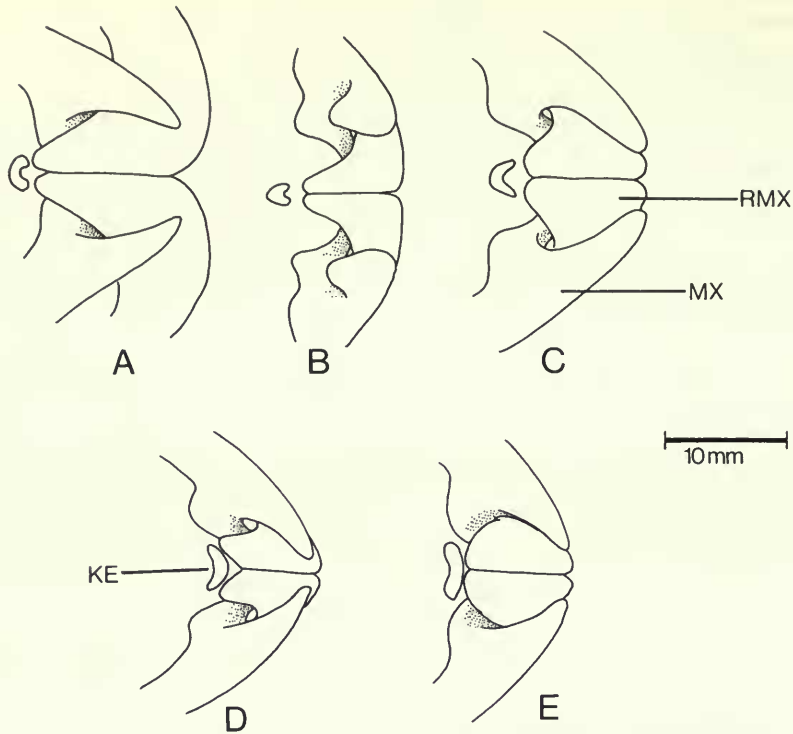


Fig. 32 Anterior of maxilla and premaxilla of A. *Opsariichthys*. B. *Barilius barila*. C. *Luciosoma bleekeri*. D. *Barilius microcephalus*. E. *Barilius bola*. Dorsal views.

then becomes perpendicular to form a broad shaft. The upper lateral face bears a well-developed flange across which passes the *dilatator operculi* muscle and from which part of *adductor mandibulae* A<sub>2</sub> originates. The posterior border of the hyomandibula overlaps the dorsal part of the preoperculum and its medial face is almost flat and produced dorso-posteriorly as a compressed condyle with which the operculum articulates.

The *metapterygoid* has a markedly concave dorsal border, the posterior part of which is formed into a wide triangular process directed somewhat anteriorly. This process is a point of attachment for the *levator arcus palatini* muscle. The ventral border is concave and forms the dorsal margin of a large fenestra. Posteriorly the metapterygoid extends to overlap the lower limb of the hyomandibula.

The *symplectic* is a long curved bone forming part of the ventral border of the fenestra. It is separated by cartilage from both the lower limb of the hyomandibula and the metapterygoid.

The *quadrate* has a long ventral border overlapping the symplectic. The lateral face of this part of the bone projects as a wide shelf and provides a surface for the origin of the *adductor mandibulae* A<sub>1</sub> muscle. The ascending face of the quadrate is axe-shaped, its concave inner border forming the anterior margin of the fenestra, its outer border is curved slightly backwards.

The *entopterygoid* has a slightly convex dorsal border and is directed medially to contact the parasphenoid. It underlies the medial faces of both the metapterygoid and quadrate.

The *ectopterygoid* is a narrow lamellate bone with a convex border. It articulates with a narrow ledge along the border of the metapterygoid.

The *palatine* is triangular in cross-section, its ventral border produced into a lamellate edge. The bone narrows anteriorly to form into an articular head bearing a lateral process and a medial facet which abuts against the prethmoid cartilage. Posteriorly the palatine fits into a right-angled excavation in the border of the entopterygoid; a ligament joins its ventral edge to the ectopterygoid (see Fig. 38A in Howes, 1978).



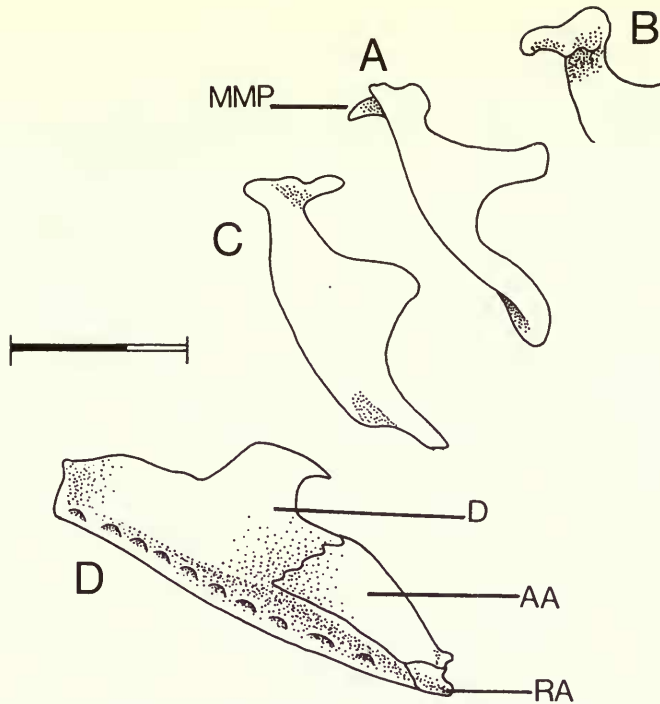


Fig. 33 *Engraulicypris sardella*, upper and lower jaws. A. Maxilla (lateral view). B. Maxillary process (medial view). C. Premaxilla (lateral view). D. Dentary (lateral view).

### *Zacco*

The *hyomandibula* differs from that of *Opsariichthys* in that there is no separation of the anterior and posterior facets; the entire dorsal border being a condylar surface. The anterior dorsal edge slopes forward at a more oblique angle, the upper part of the bone is narrower and has an almost perpendicular anterior margin and the lateral flange is absent.

*Zacco pachycephalus* differs from other species in that the *hyomandibula* bears a well-developed lateral flange (see p. 189).

Other features in which the *hyopalatine arch* of *Zacco* differs from that of *Opsariichthys* are the lack of a *metapterygoid* process (except in *Z. pachycephalus*; see p. 189), a smaller *metapterygoid*–*quadrate* fenestra (the correlate of a wider *quadrate* and a deeper *metapterygoid*) and the absence of a ventral lamellate ridge on the *palatine*.

### *Luciosoma*

The *hyomandibula* closely resembles that of *Opsariichthys* in having a long dorsal border, shallowly separated articular facets and well-developed lateral flange. The *quadrate* lacks the lateral shelf present in *Opsariichthys*. The *metapterygoid* process is absent and the *metapterygoid*–*quadrate* fenestra, although present, is very small. The ventral border of the *entopterygoid* is longer than in *Opsariichthys* and there is a corresponding lengthening of the *ectopterygoid*. The *palatine* bears a rounded ventral ridge.

### *Barilius*

*Group A*. There is some interspecific variation in the morphology of the *hyopalatine arch*, viz.: the *hyomandibula* bears separate condyles, although the degree of separation is variable, as is the

development of the lateral flange. The *metapterygoid* dorsal process is absent in all species but in *B. bendelisis* the dorsal border is markedly concave and shaped into a long posterior process. A *metapterygoid*-*quadrate* fenestra is sometimes lacking.

*Group B.* The anterior and posterior condyles of the *hyomandibula* are widely separated, the anterior extending forward at an angle of  $45^\circ$  to the vertical to articulate in a small sphenotic-*pterosphenoid* fossa; the posterior condyle is high, its narrow dorsal surface articulating with the long *pterotic* fossa. The lateral face of the *hyomandibula* bears a long, laterally extending flange which, in *B. bola*, is curved upwards so as to form a deep cavity. The anterior *hyomandibula* border is concave.

The *metapterygoid* in all species bears a long anteriorly directed dorsal process. This process is in the form of a gutter with the open side being dorsad. It provides both an insertion channel for fibres of the *levator arcus palatini* muscle and as a point of origin for fibres of the *adductor mandibulae*  $A_3$  muscle. This process is developed to the greatest extent in *Barilius bola* and *B. guttatus*, its distal tip almost reaching the same horizontal plane as the top of the anterior *hyomandibular* condyle. The posterior border of the *metapterygoid* extends more than halfway along the lateral surface of the *hyomandibular* stem (see Fig. 38B in Howes, 1978).

The *symplectic* is well developed and deep; the *quadrate* is also deep with a laterally produced ventral border as in *Opsariichthys*. The *ectopterygoid* is very elongate with a strongly concave lower margin. As in *Opsariichthys* the *palatine* bears a strong ventral ridge. A *metapterygoid*-*quadrate* fenestra is absent.

*Group C.* As in *Group B* the *hyomandibular* condyles are widely separated but the anterior condyle is much thicker than in any of those species and in this respect more closely resembles the *Opsariichthys* condition. The lateral flange is weakly developed and the anterior border irregularly concave. The *metapterygoid* bears a small posterior lamellate process similar to that in *Opsariichthys*. The *quadrate* is shallow, its ventro-lateral border well produced; the *symplectic* elongate and the *palatine* with a well-developed, knife-edged ventral ridge. There is no *metapterygoid*-*quadrate* fenestra.

### *Engraulicypris*

The *hyomandibula* has a long upper face, with an almost continuous articulatory dorsal border and a convex anterior margin. The dorsal posterior edge is extended to form a triangular condyle. The *metapterygoid* is directed medially at a sharp angle so as to form an almost flat shelf. The medial part of the bone is produced into a long lamellar process. The *quadrate* is deep, its ventral posterior border produced into a thin spine. The *palatine* bears a slight lateral process which is separated from a medial process by a deep channel. A ligament joins the lateral process to the antero-dorsal part of the maxilla (LPM, Fig. 34). Another ligament (LPE) joins the palatine shaft to the ethmoid, and a further one (LPEK), which passes over the ethmoid arm, attaches the medial palatine process to the kinethmoid shaft.

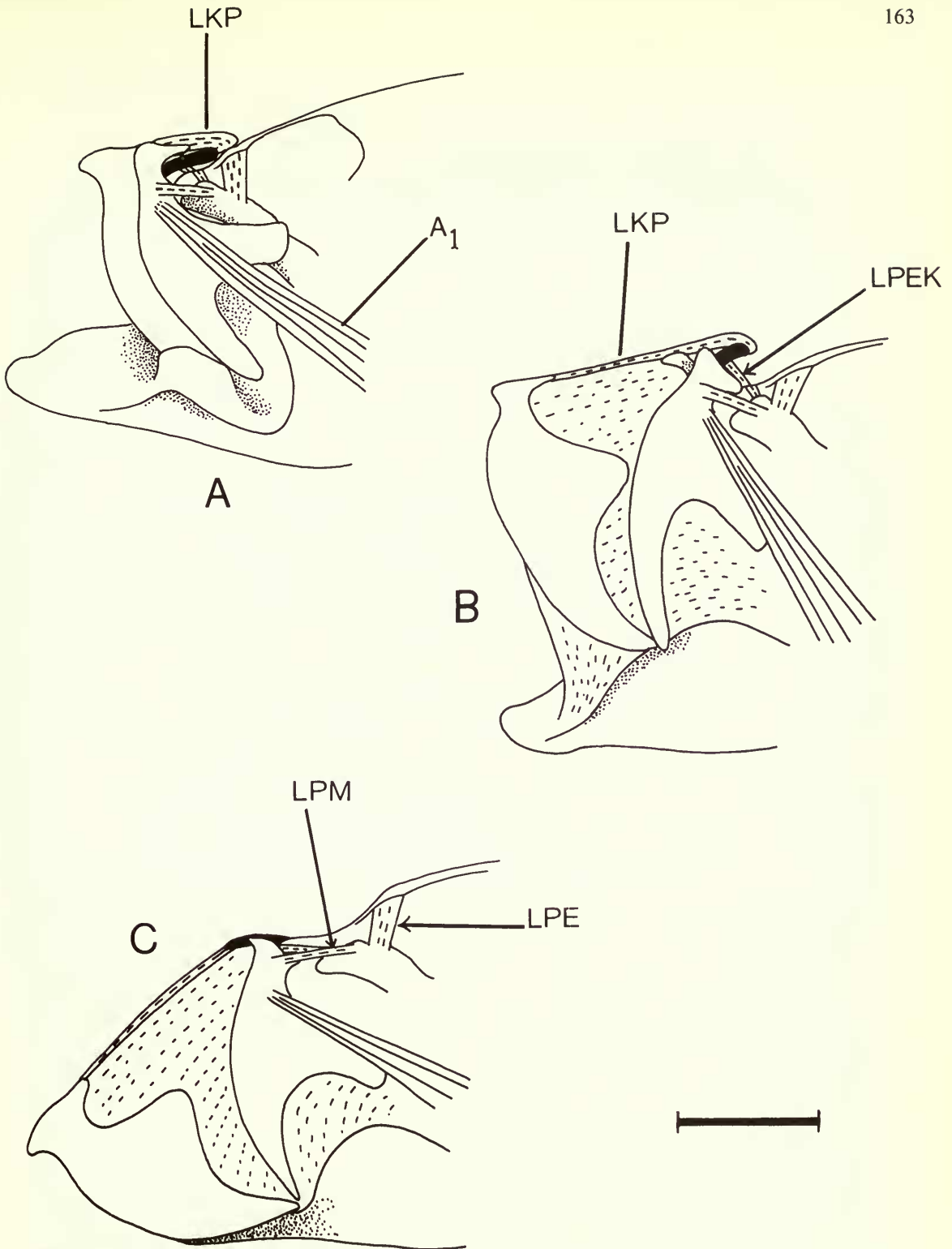
### *Opercular series*

#### *Opsariichthys*

The *operculum* is deep with a short dorsal border, the dorso-anterior process is curved outwards. The articulatory facet for the *hyomandibular* condyle is situated dorso-medially; extending posteriorly from the facet is a thin strut pierced by two foramina. The *preoperculum* bears four latero-sensory canal pores along its nearly vertical upright limb and three along the horizontal part. The *suboperculum* has a well-rounded ventral border and dorsally is partially covered by the *operculum*. The *interoperculum* is wide and is largely covered by the *preoperculum* laterally.

#### *Zacco*

There is little difference between *Zacco* and *Opsariichthys*, except that the anterior dorsal process of the *operculum* is feebly developed.



**Fig. 34** *Engraulicypris sardella*, sequence of jaw protrusion (semi-diagrammatic). A. 1st stage, mouth partially open. B. Intermediate stage, mouth completely open. C. Final stage, upper jaw fully extended

*Luciosoma*

The upright limb of the *preoperculum* is aligned at 45° to the vertical, and its horizontal limb is short. The *operculum* has a well-rounded border and is much shallower than in either *Opsariichthys* or *Zacco*; its anterior dorsal process is feebly developed.

*Barilius*

*Group A.* The opercular series differs little from that of *Opsariichthys* or *Zacco*, but in the species of *Group B* the upright part of the preoperculum is inclined at an angle of 30° to the vertical and the horizontal limb is short. In *Barilius loati*, *steindachneri* and *kingsleyae* the width of the *operculum* is greater and the anterior dorsal process more highly developed and anteriorly extended than in any other species of the group. In *Group C* the opercular border is slightly concave and its lower posterior border produced.

*Engraulicypris*

The *operculum* has a long, straight dorsal border and its posterior margin is only slightly convex.

*Comments on the jaws, hyopalatine and opercular series*

In a previous paper (Howes, 1978) I made some comment on the jaw bones of various cyprinids and considered those of *Opsariichthys* as relatively primitive. However, I now realize that in some respects they are highly specialized and that the separation of the premaxilla and maxilla, and the strongly developed symphyseal knob and notch must be considered as derived features. Only in *Macrochirichthys* is there a similar development of the symphyseal knob, but this is regarded as a parallelism; Howes (1979). The coronoid process of all the genera under consideration is of the plesiomorph form, i.e. relatively high and without any contribution from the angulo-articular bone (Howes, 1978).

There is some variation in the degree of development of the anterior ascending premaxillary processes in the taxa under discussion. In *Opsariichthys*, *Zacco* and *Barilius Group A*, the ascending processes are long, with concave lateral borders and rounded dorsal tips. In *Luciosoma* the processes are shorter with broader tips and in *Barilius Group B* the processes are much reduced with a completely convex lateral border. Although in *Barilius Group C*, the lateral border of the premaxillary process is concave the dorsal tip is triangular, allowing for closer contact with the expanded kinethmoid (Fig. 32). Likewise, a transformation series can be seen in the development of the anterior part of the maxilla where in *Barilius Group A*, the tips of each maxilla are widely separated from each other but become progressively more elongate in *Opsariichthys* and *Luciosoma* until, in *Barilius Groups B* and *C*, they almost contact each other across the midline.

The curved walls of the dentary are shared features of *Opsariichthys* and *Luciosoma*; the anterior medial maxillary processes make direct contact along the midline in all genera except *Zacco* where contact is indirect and *via* a ligament; this is the condition usually encountered in the Cyprinidae and is therefore considered to be the plesiomorph one.

*Engraulicypris sardella* differs from all other genera reviewed here in the marked development of highly protrusile jaws. The high degree of protrusibility is attained by the prolongation of the ethmoid arms in conjunction with ventrally directed maxillary processes which enables the kinethmoid to rotate through more than 180°. The ligament connecting the distal tip of the kinethmoid to the anterior border of the premaxilla is extremely long and when the jaws open and protrude, the tensed ligament extends almost horizontally. When the jaws close and retract, the kinethmoid pivots (in the anterior vomer notch, see p. 137) so that it again lies horizontally between the ethmoid arms. The long ligament curls over and folds into the ethmoid indentation (Figs 34A–C). The ventrally directed medial maxillary process is a feature shared with *Leptocypris* (see p. 181).

The most significant features of the hyopalatine series concern the hyomandibula and the metapterygoid. Only in *Zacco* and *Engraulicypris* does the *hyomandibula* lack the marked separation of its articular condyles. The most extreme separation is found in *Barilius Group B*. It could

be argued that such a separation of the condyles is a correlate of the elongation of the head. Admittedly this is partly so, for in *Barilius Group B* there is some lengthening of the otic region. However, in other cyprinids (such as the aspinines) where there has been considerable elongation of the skull (see Howes, 1978) there is no correspondingly great separation of the hyomandibular condyles. Neither have I found such a feature in piscivorous long-headed characins. The significance of the bipartite hyomandibula in functional terms is probably to be explained by the vertical elongation of the suspensorium rather than through the horizontal elongation of the skull. Whether or not this is so, the feature is certainly a derived one and is synapomorphic for *Opsariichthys*, *Barilius* and *Luciosoma*. In these genera the *hyomandibula* also bears a lateral flange, which again is developed to the most marked degree in *Barilius Group B*. Although a character occurring in other cyprinids (see Howes, 1978 and comments by Forey, 1975) it is here identified as a synapomorphy.

The metapterygoid in *Opsariichthys* and *Barilius Groups B* and *C* bears a dorsal posterior process. An incipient condition of this process is present in *Opsariichthys* and *Barilius Group C*, whilst an increasing grade of development is manifest throughout *Group B*, as is also a deepening of the metapterygoid. I have failed to find such a feature in any other group of cyprinids and therefore regard this as a synapomorph character linking those genera in which it occurs.

*Engraulicypris sardella* differs from the other genera both in the form of the hyomandibula and the metapterygoid. Although there is no marked separation of the hyomandibular condyles, the posterior condyle is produced into a triangular shape which articulates with a fossa on the posterior border of the pterotic. In this taxon, unlike *Zacco*, it is probably a derived feature, the form of the articulation suggesting a wide lateral movement of the hyomandibula. The metapterygoid spine in *Engraulicypris* also differs from that in *Barilius Groups B* and *C* in that it originates from the anterior part of the metapterygoid and serves as a site of attachment for the *adductor arcus palatini* instead of the *levator arcus palatini* as in the other taxa. A deep lateral shelf along the ventral part of the quadrate is also shared by *Opsariichthys* and *Barilius B* and *C*.

The metapterygoid-quadrate fenestra has been discussed at some length in an earlier paper (Howes, 1978). It need only be mentioned that of those genera discussed here it is present in *Opsariichthys*, *Zacco* and *Luciosoma*; its occurrence in other groups of cyprinids (Howes, 1979) suggests that it is a plesiomorph feature.

The elongate *symplectic* found in *Opsariichthys*, *Zacco*, *Barilius Groups A* and *C* and in *Luciosoma* is the 'usual' cyprinid condition and is thus considered to be plesiomorphic. The short, deep *symplectic* in *Barilius B* is a derived feature.

The *opercular series* differs little between the genera; only in *Luciosoma* and *Engraulicypris* is there any marked elongation of the operculum and shortening of the preoperculum, whilst in *Engraulicypris* the interoperculum is finely serrated.

### *Hyoid and branchial arches*

#### *Opsariichthys*

There are few features distinguishing these elements from those of other cyprinids (Ramaswami, 1955; Howes, 1978). Attention is drawn to the narrow waisted ceratohyal, reduced ventral hypohyal and the three broad branchiostegal rays. The basihyals are all short.

Each *ceratobranchial* bears 8-9 gill rakers. The pharyngeal bone bears three rows of curved teeth (dental formula, 2.3.5). The 4th *epibranchial* has a broad, triangular dorso-medial process posteriorly and a short, rod-like process midway along its length (Fig. 35). There are two ossified *infrapharyngobranchials* identified as the 2nd and 3rd. The 3rd is an extensive triangular element spanning the medial surfaces of epibranchials 3 and 4. A cartilaginous element at the outer edge of *infrapharyngobranchial* 3 and articulating with the 4th epibranchial probably represents the 4th *infrapharyngobranchial*.

Chu (1935) studied the pharyngeal bones of *Opsariichthys* and *Zacco* and noted that those of the former genus were narrow and elongate, whilst those of the latter were short and broad. A

similar distinction can be found within the groups of *Barilius*, those of *Group A* resembling *Zacco*, with *Groups B* and *C* and *Luciosoma* resembling *Opsariichthys*.

In *Engraulicypris sardella* the *ceratobranchials* are very long and bear 24–25 long, slender gill-rakers. The pharyngeal bone has 3 rows of compressed teeth (dental formula: 5.3.2) with finely serrated cutting edges and recurved tips.

*Pectoral girdle* (nomenclature follows that of Brousseau, 1976)

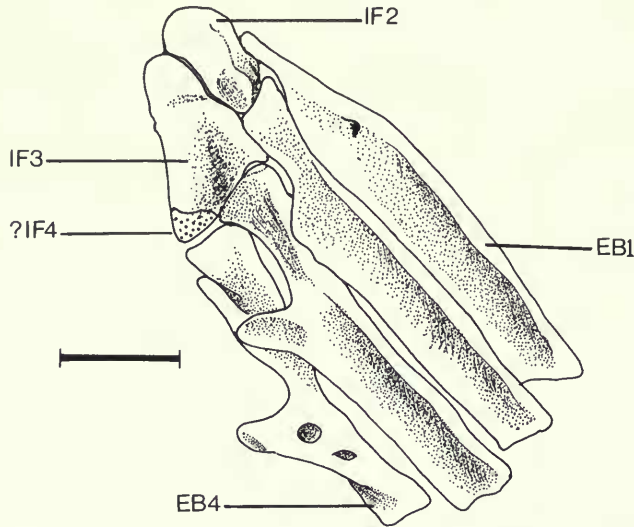


Fig. 35 *Opsariichthys*. Upper branchial arches, dorsal view.

### *Opsariichthys*

The upright part of the *cleithrum* is perpendicular and bears a well-defined ridge along its anterior border (Fig. 36A). This ridge broadens ventrally and fans out to form a broad, horizontal cleithral lamina; the leading edge of the horizontal limb is rounded. There is a well-developed ventro-medial cleithral ridge. The posterior cleithral lamina is broad with a straight border. The anterior fenestra is well developed. The *supracleithrum* is very elongate. Each *coracoid* is small and when viewed laterally is seen to extend only slightly below the ventral margin of the cleithrum. The coracoids diverge, meeting only anteriorly; the *mesocoracoid* shaft is long, rounded and perpendicular. The *postcleithrum* is short and spatulate, curves mesially with its ventral tip on a line level with the ventral border of the coracoid (Fig. 36B). There are four proximal *radials*, the 3rd and 4th being lamellar.

### *Zacco*

The pectoral girdle morphology is basically that of *Opsariichthys* but the sternohyoid ridge on the cleithrum is greatly produced anteriorly resembling that in *Danio* (see Howes, 1979). The *supracleithrum* is short and its anterior edge straight with a slight distal notch. The *postcleithrum* is shorter than in *Opsariichthys* and its ventral tip pointed instead of spatulate.

### *Luciosoma*

The upright part of the *cleithrum* is shorter than in *Opsariichthys* or *Zacco* and the posterior lamina is extended (Fig. 37A). The horizontal limb is broad with a moderately developed ridge.

The *supracleithrum* is short, the *coracoids* shallow, meeting each other along the midline and containing a large anterior fenestra. The most outstanding feature of the pectoral girdle is the form of the postcleithrum. It is a broad lanceolate bone attached to the edge of the posterior cleithral lamina extending laterad to the body scales. Its tip is enclosed in a fleshy sheath and this sheath extends as the pectoral axial lobe (see Fig. 37A & p. 168) to lie between the pectoral fin and the body. There are no tendons attached to the postcleithrum.

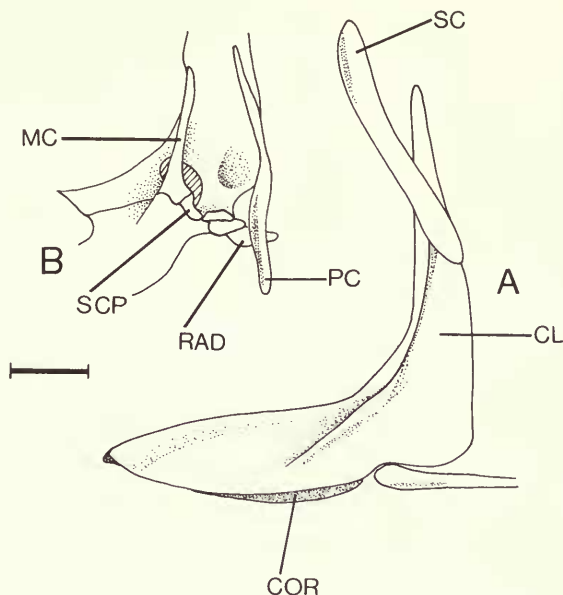


Fig. 36 *Opsariichthys*. Pectoral girdle in A, lateral and B, medial views.

### *Barilius*

Within *Group A* there is some variation in the morphology of the pectoral girdle; the upright part of the *cleithrum* is generally short with a posteriorly extended lamina; the *supracleithrum* is elongate, the *coracoids* variable in depth but never joining along their medial faces.

In *Group B* the upright part of the *cleithrum* is very narrow with a well-developed anterior ridge, and the *supracleithrum* is long and narrow (Fig. 37B). The *coracoids* are very shallow and meet anteriorly along their ventral margins; the *mesocoracoid* shaft is broad and lamellar. The development of the anterior fenestra is variable, being small in *B. loati* and extensive in *B. bola*.

Species of *Group C* possess a broadly lamellate upright cleithral limb with an expanded posterior edge to which is attached a spatulate postcleithrum. The *supracleithrum* has only a slight anterior inclination as compared with other *Barilius* where it is inclined at 45° to the cleithrum. The coracoid is well developed, with a curved ventral margin and a large anterior fenestra. The mesocoracoid shaft is broad and lamellar.

In all *Barilius* species examined the *postcleithra* are small and spike-like, medially directed bones which unlike the postcleithrum in *Luciosoma* do not support an axial flap or scale.

### *Engraulicypris*

The upright part of the *cleithrum* is short, its ventro-posterior edge extended backwards as a long spine. The *coracoids* are shallow and meet each other along the midline. A *postcleithrum* is absent.

### *Comparisons*

The most notable variations in the pectoral girdle are in the vertical and horizontal extensions

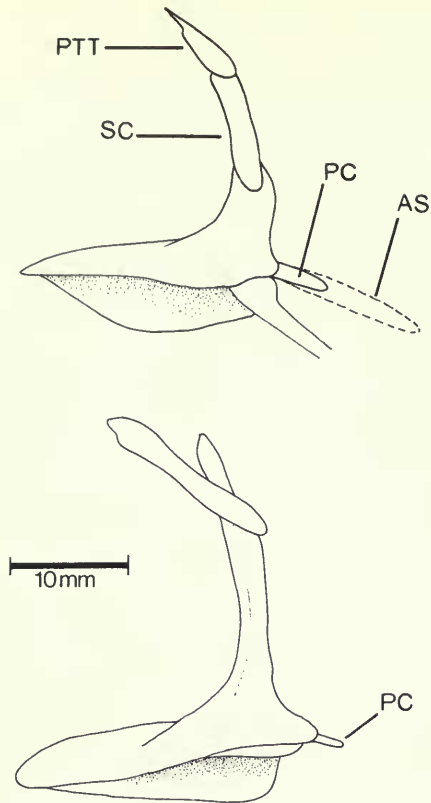


Fig. 37 Pectoral girdles of A, *Luciosoma bleekeri*, B, *Barilius bola*.

of the cleithrum. It has been noted previously (Howes, 1978) that in some long-jawed cyprinids such as *Barilius bola* the vertical limb is long and narrow. In *Luciosoma*, on the other hand, as in the aspinines (Howes, 1978), the upper limb is short and broad and more closely resembles that in *Opsariichthys*. The postcleithrum in *Opsariichthys* and *Zacco* is elongate and medially directed as, indeed, it is in the majority of cyprinids examined – and this is taken to represent the plesiomorph condition. In all *Barilius* species it is reduced to a spike-like or scale-like bone and in *Luciosoma* lies horizontally above the axial aperture and supports the axial lobe. The only other cyprinids in which the postcleithrum supports the axial lobe is a group of *Rasbora* species (represented by *R. argyrotaenia*); however, here the postcleithrum is thin and ventrally directed. In the cheline *Securicula* the postcleithrum is absent and ‘replaced’ by a large scale covering the dorsal border of the axial aperture. In chelines a reduction of the postcleithrum was considered a derived character but some forms of postcleithral elongation, as in the case of *Macrochirichthys*, could also be interpreted as derived (Howes, 1979). In the case of the bariliines I regard reduction of this element as an apomorphy, likewise in *Engraulicypris* where it is absent.

#### Vertebral skeleton

##### *Opsariichthys*

*Weberian apparatus* (Fig. 38). The 1st vertebra bears strong lateral processes which are rounded proximally and compressed distally. The 2nd vertebra has a thick lateral process which is inclined upward. The 2nd and 3rd vertebrae are not fused together and the 3rd bears a wide fossa on its postero-lateral face for the articulation of the tripus. The 3rd vertebra is expanded dorsally into



the 3rd neural plate which extends laterally and curves forward along the top of the 2nd centrum. The anterior border of the 3rd neural plate slopes downward and is joined to the 2nd neural plate. The neural complex is steeply raised, its curved dorsal border being deeply grooved; the anterior border is rounded and extends forward to above the 2nd neural plate. The ossicles differ little from those of other cyprinids (Ramaswami, 1955; Howes, 1978) except that the tripus is much elongated, its posterior tip extending to below the 6th centrum.

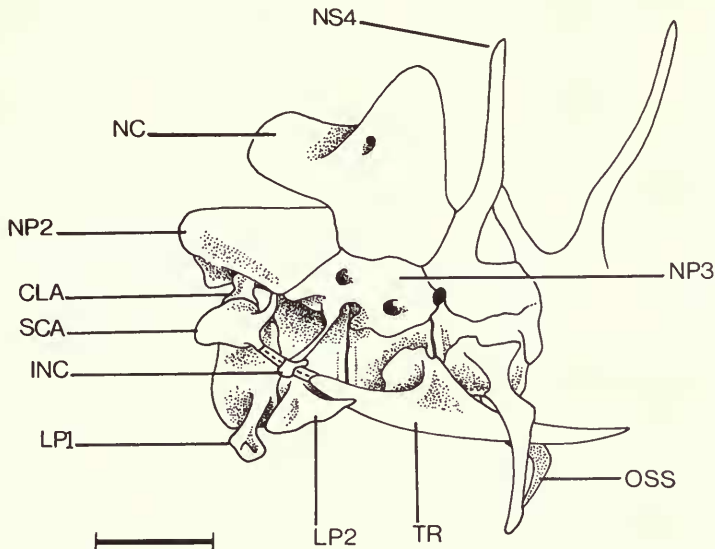


Fig. 38 *Opsariichthys* Weberian apparatus, lateral view.

#### Vertebral column

There are 44 vertebrae (21 abdominal, including the 4 comprising the Weberian apparatus + 22 caudal + the fused pre-ural and 1st ural vertebra – counted as a single element in Table 1) and 6–7 supraneurals, the first being an irregularly shaped lamellate element, the others lanceolate.

*Caudal fin skeleton* (Fig. 39). There are 6 hypurals, none of which are greatly expanded, the 6th being a small element. The fused pre-ural and ural centrum (PU1+U1) bears a blunt neural spine. There is one epural and a pair of slender uroneurals lying above hypural 6. The parhypural bears a well-developed broad hypurapophysis.

#### Comparisons

The intergeneric differences in the morphology of the vertebral column are those involving the anterior vertebrae which form the *Weberian apparatus*.

In *Zacco* the lateral processes of the 1st vertebra are reduced, whilst those of the 2nd are greatly extended. This is similar to the condition in *Opsariichthys*, and likewise the 2nd and 3rd vertebrae are separate.

In *Barilius Group A* the 1st and 2nd vertebrae are of the type encountered in *Opsariichthys* and *Zacco* but the 2nd and 3rd centra are fused. The lateral processes of the 1st vertebra in *Barilius Group B* are short and those of the 2nd are elongate with pointed tips and are directed posteriorly at 45° to the transverse plane. In *Barilius Group C* the processes of the 1st vertebra are curved backwards and partly underlie those of the 2nd vertebra. The lateral processes of the 2nd are long with rounded tips and extend horizontally. The 2nd and 3rd vertebrae of all *Barilius* species examined are fused together.

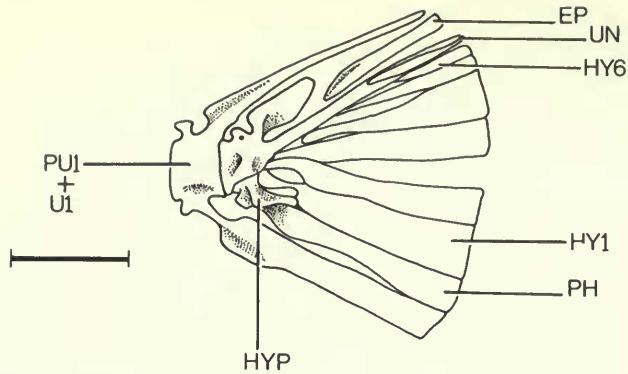


Fig. 39 *Opsariichthys* Caudal fin skeleton.

*Engraulicypris* has short lateral processes on the 1st vertebra and long, posteriorly directed ones on the 2nd (similar to *Opsariichthys*). *Luciosoma*, on the other hand, has long 1st vertebral processes and expansive, wing-like processes on the 2nd vertebra (Fig. 40), a feature shared with some species of *Rasbora* (p. 182).

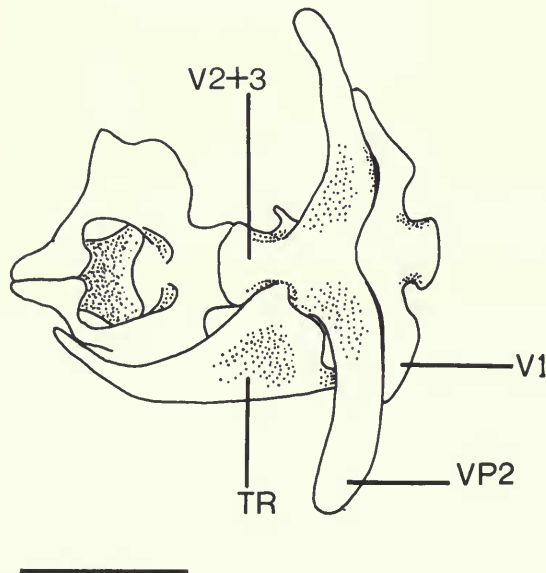


Fig. 40 *Luciosoma bleekeri* Anterior vertebrae, ventral view.

The morphology of the 1st and 2nd vertebrae exemplified by *Opsariichthys* appears to be widespread amongst the cyprinids and is taken to represent the plesiomorph condition. The long, sharply caudally directed 2nd vertebral processes of *Raiamas* and the expanded type of *Luciosoma* are considered apomorphies.

One feature that seems common to all genera studied here is the form of the *ossa suspensoria*. These bones are obliquely angled backwards so that their tips come to lie below the centre or posterior part of the 5th centrum. Also, the lateral extension of the os suspensorium (4th pleural rib of Ramaswami, 1955) is short and directed somewhat anteriorly. Only in *Zacco* are the *ossa suspensoria* long and vertically directed, their tips meeting below the 4th centrum. This latter condition is widespread amongst the cyprinids and is therefore reckoned as being the plesiomorph one.

Previously (Howes, 1978) I had given the caudal fin ray count in cyprinids as I9+9I. This is an error, I have now examined radiographs of many cyprinid genera and am in agreement with Roberts (1973) that the count is I9+8I.

**Table 1** The modal number of vertebrae of various species used in this study

	<i>Opsariichthys uncirostris</i>	44	(4+17+22+1)
	<i>Zacco temmincki</i>	43	(4+18+20+1)
	<i>Zacco pachycephalus</i>	40	(4+17+18+1)
	<i>Zacco platypus</i>	40	(4+17+18+1)
	<i>Zacco macrophthalmus</i>	42	(4+17+20+1)
	<i>Zacco barbatus</i>	42	(4+18+19+1)
	<i>Luciosoma setigerum</i>	43	(4+21+17+1)
	<i>Luciosoma bleekeri</i>	42	(4+21+16+1)
	<i>Luciosoma trinema</i>	39	(4+18+16+1)
	<i>Luciosoma spilopleura</i>	40	(4+18+17+1)
	<i>Rasbora argyrotaenia</i>	34	(4+12+17+1)
	<i>Rasbora elanga</i>	42	(4+17+20+1)
Group A	<i>Barilius barila</i>	40	(4+15+20+1)
	<i>Barilius tilheo</i>	42	(4+16+21+1)
	<i>Barilius ornatus</i>	41	(4+16+20+1)
Group B	<i>Barilius bola</i>	47	(4+20+22+1)
	<i>Barilius guttatus</i>	47	(4+18+24+1)
	<i>Barilius lujae</i>	41	(4+16+20+1)
	<i>Barilius salmolucius</i>	43	(4+16+22+1)
	<i>Barilius macrostoma</i>	44	(4+17+22+1)
	<i>Barilius kingsleyae</i>	41	(4+15+21+1)
	<i>Barilius loati</i>	44	(4+17+22+1)
	<i>Barilius moori</i>	43	(4+15+23+1)
	<i>Barilius microlepis</i>	47	(4+17+25+1)
Group C	<i>Barilius ubangensis</i>	43	(4+16+22+1)
	<i>Barilius microcephalus</i>	45	(4+16+24+1)
	<i>Leptocypris modestus</i>	40	(4+15+20+1)
	<i>Barilius niloticus</i>	37	(4+14+18+1)
	<i>Engraulicypris sardella</i>	44	(4+19+20+1)

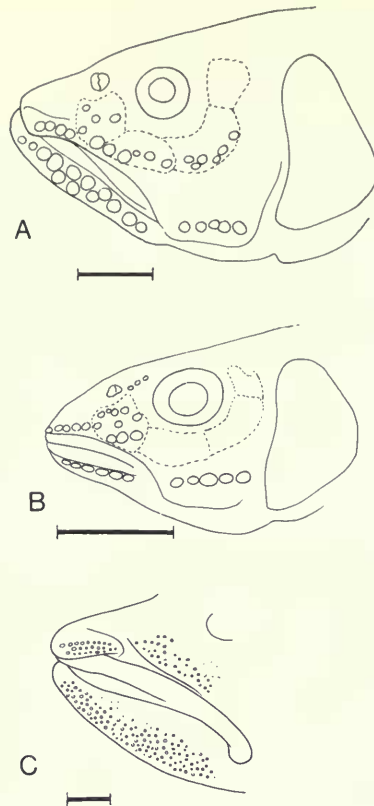
Note: Those species in which there is a high number of vertebrae are either very elongate fish (*B. bola*, *B. guttatus*) or lacustrine species (*B. microlepis*).

## External anatomical features

### Tubercles

#### *Opsariichthys*

Keratinized tubercles are present on the head and sometimes on the scales of the flanks and anal fin rays of all species. They are present in both sexes but are most prominently developed on males with ripe testes. The arrangement of the tubercles on the head is shown in Fig. 41A and is: 1st infraorbital, 2 or 3 on the dorsal border, 2 on the ventral; 2nd infraorbital 5; 3rd infraorbital 5 or 6; 4th absent; 5th absent; preoperculum, 5 or 6 along the lower border; premaxilla (upper lip) 5-8; dentary, 3 rows, 8 dorsal, 12 middle, and 8 ventral; nasal 2-3 situated lateral to the nasal bone; supraorbital 4-5; cheek, 10-12, small and irregularly scattered.



**Fig. 41** Arrangement of tubercles on the heads of A. *Opsariichthys uncistrostris*. B. *Zacco macrophthalmus*. C. Tubercle arrangement on the jaws of *Barilius microlepis*. Scales = 5 mm.

The tubercles are conical but are inclined so that on the anterior part of the lower jaw and the 1st infraorbital the cones point caudad; on the 2nd and 3rd infraorbitals they are perpendicular whereas on the posterior part of the cheek they incline forward. The tubercles are attached to the skin through thickened pads of tissue and when a tubercle is removed there remains a circular pit bearing lamellar radii. In specimens where the tubercles have been shed in life, there remains a shallow, saucer-shaped depression.

#### *Zacco*

The tubercles are of the same conical form as in *Opsariichthys* and are present on the snout, 1st infraorbital, nasal, cheek below the infraorbitals, lower jaw, preoperculum and operculum (Fig. 41B). They are also well developed on the anal fin rays and on the scales both below and above the lateral line. Bănărescu (1968) described the tubercle distribution in the various species of this genus.

#### *Luciosoma*

No tubercles have been found in any species examined. The skin covering the ethmoid region is deeply grooved by two or three S-shaped channels which extend from the nasal opening to the midline (see p. 175).

#### *Barilius*

Tubercles are present in many species of *Barilius* of all three groups. In Groups A and B they are small and in many species appear to be present only on the head. In *Barilius gattensis* the tubercles

of the lower jaw extend onto its medial surface (Fig. 42). In a specimen of *B. ansorgii* (Group B) tubercles are distributed over most of the dorsal and lateral parts of the body. In ripe males of *Barilius microlepis* (Group C) of Lake Malawi, the area covering the tip of the upper jaw, the infraorbitals and the entire lower jaw are covered with minute tubercles giving the jaws a granular appearance (Fig. 41C). In these specimens tubercles are also present on the anal fin rays. In other species of this group (*B. ubangensis* and *B. zambesensis*) the tubercles are well developed and in their pattern resemble those of *Opsariichthys*.

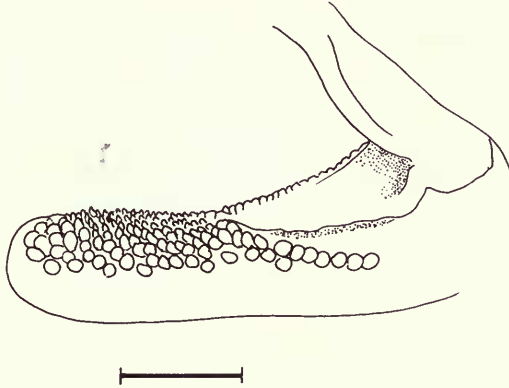


Fig. 42 *Barilius gatensis*. Tubercle arrangement on the left lower jaw.

#### *Engraulicypris*

No tubercles have been found in *Engraulicypris sardella*.

#### *Pectoral and pelvic lobes*

#### *Opsariichthys*

An axial pectoral lobe is present in the form of a minute fleshy appendage. There is also a fleshy triangular lobe lying medial to each pelvic fin.

#### *Zacco*

There is some intraspecific variability in the form of the pectoral and pelvic lobes. In *Z. platypus* the pectoral lobe is very small and the pelvic lobe is in the form of a scale with a fleshy border. In *Z. temmincki* the pectoral lobe is well developed and the pelvic scale has a fleshy border. In *Z. macrophthalmus* the pectoral lobe is barely developed and the pelvic one is an elongate scale without a fleshy margin. In *Z. pachycephalus* the pectoral lobe is bipartite and the pelvic lobe a thick fleshy wedge (see p. 189).

#### *Luciosoma*

The pectoral axial lobe is an elongate, ventrally curved structure originating from the postcleithrum (see p. 167). An elongate pelvic scale is also present.

#### *Barilius*

The pectoral and pelvic lobes are developed as fleshy structures only in Group C. This is particularly so in *B. ubangensis* and *B. microlepis*. In the latter species the pectoral lobe in males is

expanded and in a specimen of 430 mm SL the lobe is a complexly divided structure (Fig. 43); in females it is reduced and scale-like.

In *Barilius Group A* a pectoral scale with a wide fleshy border is developed, and in *Group B* the scale is elongate without such a border.

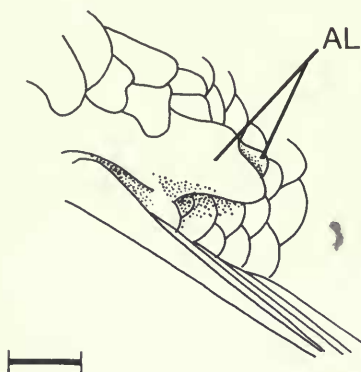


Fig. 43 *Barilius microlepis*. Axial pectoral fin lobe of a specimen 430 mm SL.

### *Engraulicypris*

Pectoral lobes are absent, but an elongate pelvic scale is present.

#### *Anal fin*

In *Opsariichthys* and *Zacco* the 3rd, 4th and 5th anal fin rays in both sexes are extended, particularly so in males. The tips of the rays are expanded and separate into 9–10 branches. The posterior ventral surface of the caudal peduncle in both genera is somewhat fleshy and particularly in *Zacco* becomes ventrally extended into a keel. This keel forms an uninterrupted margin to the ventral aspect of the body when the long anal fin is folded and presumably aids in streamlining (Figs 44A & B).

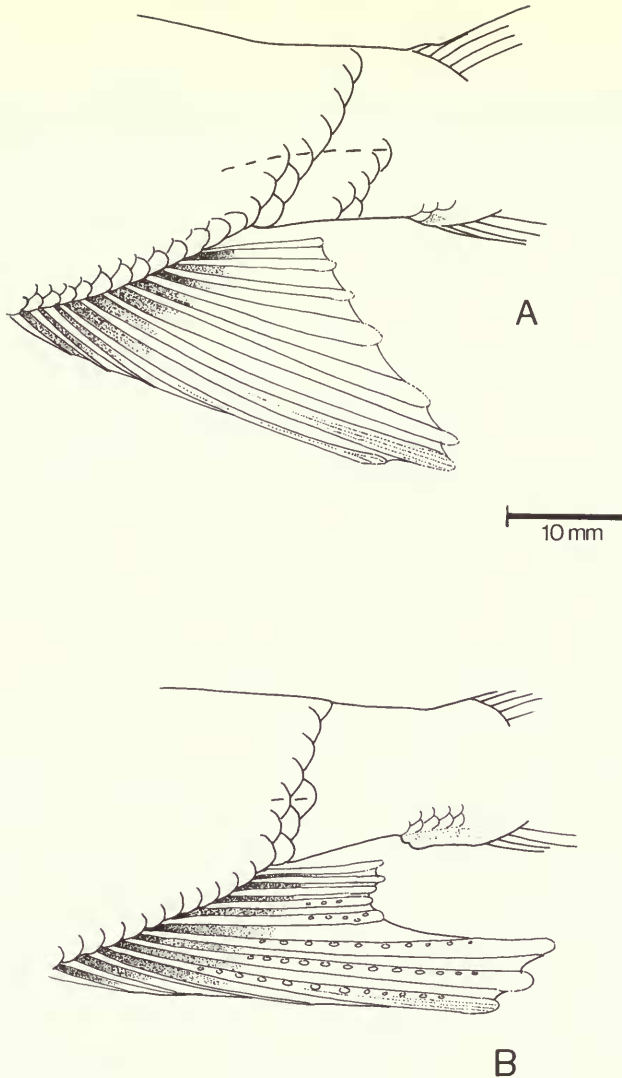
The anal fin is not extended in males of *Luciosoma* species, although in some individuals a filament is developed from the first ray.

In *Barilius Group C* there is an extension of the first four to six rays in males. This is particularly evident in *B. ubangensis* which also displays a colour pattern of the dorsal fin remarkably similar to that of *Zacco*. The anal fin is not extended in other groups of *Barilius*.

#### *Comments on tubercles, axial lobes and fins*

The tubercles, axial lobes and anal fin are considered together because their development appears to be correlated. A series of well-developed tubercles on the head, body and anal fins is associated with marked secondary sexual dimorphism exhibited by the attenuation of the anal fin in the males, by fleshy pectoral axial and pelvic lobes and distinctively marked dorsal and anal fins in both sexes. Such a combination of features is shared by *Opsariichthys*, *Zacco* and *Barilius Group C*.

It seems likely that these characters are associated in a reproductive context. It has been assumed that tubercles play some part in reproductive behaviour, possibly functioning as stimulatory tactile organs (see Wiley & Collette, 1970). In this regard Nakamura (1969) states that in *Zacco* the male makes use of the tubercles to drive away intruders and rival males from its territory. It must be said that it is not clear from the English translation of this passage whether Nakamura has actually observed this behaviour or conjectures it. Okada (1960) notes that in *Zacco* the male '... moves quickly against rocks' cleaning areas for the deposition of the eggs. He goes on to say '... In this connection, it is interesting to note that the pearl organs of Japanese Cyprinoid fishes develop mostly about the tip of the snout and on the side of the face'. Presumably the connection implied, but not stated, is that the tubercles in some way either aid in cleaning the



**Fig. 44** Anal fins of A, *Opsariichthys uncirostris bidens* (BMNH 1901.3.6 : 6) and B, *Zacco platypus* (BMNH 1969.4.15 : 29–31).

rock surfaces or act as a buffer. But then Okada proposes that ‘. . . The tubercles probably serve as contact organs, holding the mating pairs entangled by increasing the roughness of the surfaces of the body of the male which come into contact with the body of the female’. I cannot see how the second statement is linked with the first, and there are no published first-hand observations to justify it.

In contrast to the idea that tubercles act as contact organs, Reid (unpublished thesis and pers. comm.) has hypothesized that at least in *Labeo* their presence is more likely to serve some hydrodynamic function but one nevertheless correlated with reproductive activity in as much as these fishes move upstream to spawn, thus encountering a particular kind of water turbulence. This is likely to be the case in *Opsariichthys*, *Zacco* and some *Barilius*. The orientation of the tubercles on the head of *Opsariichthys* and *Zacco* (see above, p. 172) suggest a hydro-mechanical function. A similar function may be attributed to the transverse grooves on the snout of *Luciosoma*

(p. 172) which possibly serve to counteract turbulence in that region by improving streamlining (Reid, pers. comm.).

A fleshy axial pectoral fin lobe is not confined only to the genera considered here, but is also present in the American cyprinid, *Platygobio*, some cultrines, alburnines and some species of *Rasbora*. In *Platygobio* it is a small structure not attached to the cleithrum. In the *Rasbora* species it is large, usually elongate and attached to the postcleithrum as in *Luciosoma*. In the cultrines and alburnines the lobe can be small or elongate, ventrally curved and is attached to the cleithral lamina. No data are available on the possible use of this organ. It is possibly associated with reproductive behaviour and could act as (i) a visual stimulant when the male extends his pectoral fins, and/or (ii) a tactile organ if the female curves her body around that of the male and/or (iii) as an area in which pheromone-producing cells are concentrated.

Another character, possibly correlated with the development of the anal fin and axial lobes, is the presence of 'pectoral pads' in some species of *Barilius*. These pads were first mentioned by Hora (1921) in *Barilius bendelisis* and *B. barila*. He described them in *B. bendelisis* as: '... The chest is flattened and the scales in this region are poorly developed. There are characteristic muscular pads in front of the bases of the pectorals'. Dr Tyson Roberts reports (pers. comm.) that these pads are only evident in large, ripe males of this species, and that the epidermal surface of the pad is ridged transversely. A similar, but smaller, swollen area is found in some specimens of *Barilius zambesensis* and *B. ubangensis*. It seems likely that these pads may be used to steady the fish in fast flowing water. Perhaps significant in this respect is the comment on *Barilius bendelisis* made by Hora & Mukerji (1936): '... The pectoral fins are fan-like and horizontal and are never folded even when the fish moves from place to place. Some of the rays are especially strengthened and it seems likely that they are used either for digging in sand or for holding on to rocks in somewhat rapid waters.'

In view of the unknown distribution of this character amongst the cyprinids I am unable to ascribe to it any polarity, but I would suggest that it represents a derived character for a group of Indian *Barilius*. If the development of axial lobes is to be regarded as an apomorph condition (Howes, 1979), then *Opsariichthys*, *Zacco*, *Luciosoma*, *Barilius Group C* and some species of *Rasbora* would be linked by this character. Indeed, the development of the axial lobes and anal fin, together with the distinctive colour pattern, appear to be the only characters *Zacco* shares with the other bariliine and opsariichthine genera.

According to Nakamura (1969) it appears that the extended anal fin is used to mix the eggs and milt, which would suggest that this is a derived morphological character evolved in concert with a specialized reproductive behavioural pattern. There is no evidence at present to suggest that the marked sexual dimorphism apparent in the development of the anal fin is a plesiomorph character. Thus, if this character or character combination is viewed as synapomorphic, then *Zacco* must be united with other opsariichthine and bariliine genera, an action which would disregard other, perhaps more significant, osteological characters. Present indications are that *Zacco* is not closely related to the bariliine group (see p. 180) and so I consider this set of derived characters to be the result of convergent evolution in reproductive strategy.

### *Barbels*

#### *Opsariichthys*

Barbels are present in one species, *O. barbatus*. This species was formerly assigned to the genus *Zacco*; reasons for placing it in *Opsariichthys* are discussed on p. 189. Only a single pair of minute posterior maxillary barbels is present.

#### *Luciosoma*

Two pairs of maxillary barbels are developed in all but one species. The rostral barbels are long and lie along the dorso-lateral border of the premaxilla and under the ventral edges of the 1st and



2nd infraorbitals. Each barbel stems from a thick pad of tissue which is connected by ligamentous strands to the edge of the 1st infraorbital. The tissue is embedded in the lateral groove of the maxilla and is intimately connected with the ligamentous bands which join the maxilla to the palatine. The insertion point of the *adductor mandibulae* A<sub>1</sub> muscle lies beneath the tissue pad but there is no direct connection and no muscle fibres run into the barbel. The barbel is innervated by a branch of the maxillary ramus of the trigemino-facialis nerve. The posterior maxillary barbel also stems from a thick fibrous pad, and is innervated by a branch of the nerve supplying the anterior barbel. The proximal head of the barbel is swollen and surrounded by bands of elastic-like tissue which extend along the outer border of the maxilla.

### *Barilius*

In species of *Group A* barbels are present in one or two pairs, or are entirely absent. In *Group B* they are found in only one species, *B. guttatus*. In this species there is a minute barbel on the ventral border of the maxilla just below the anterior border of the 1st infraorbital and near the distal tip of the maxilla. Barbels are absent in species of *Group C*.

### *Engraulicypris*

Barbels are absent.

### *Comments*

It is perhaps significant that amongst the bariliines (see p. 180), reduction and absence of barbels is correlated with increased piscivorous specialization (cf. *Opsariichthys uncirostris* and *O. barbatus*; long-jawed *Barilius Group B & C* with short-jawed omnivorous *Barilius Group A*). Thus, the inference is that loss or reduction of barbels is a derived condition. Although barbels are widespread throughout the Cyprinoidei (again suggesting the plesiomorph condition) they are not a characteristic feature of the Cyprinidae. Contrary to Roberts' (1973) statement that 'Cyprinidae have one or two pairs of simple maxillary barbels', most of the species comprising the large assemblages of cultrine, cheline, alburnine, hemicultrine, aspinine and leuciscine groups do not have barbels. It could be argued that barbels are a derived feature. If this is so, then of those taxa presently under discussion, all the Indian and South-East Asian bariliines possessing barbels would have to be more closely related to barbine, or other carp groups, than to the African and Amur bariliines without barbels. From other anatomical evidence, this is clearly not the case. Where barbels are present in non-barbine or carp groups they appear, superficially, to be of a different morphological type. Gilbert & Bailey (1972) discussed the use of barbels in classifying some American cyprinids and concluded that this character was of little value as '... their diversity in position and structure points to repeated independent development and loss'. These authors discovered in American cyprinids at least six structural types, noting them as '... perhaps indicative of as many independent evolutionary lines'. The whole question of barbel morphology and homology in the cyprinids, and indeed in the ostariophysans, is obviously one to be investigated.

Roberts (1973) states that in cyprinids the movement of barbels is passive. This is not always so, for from personal observations on aquarium specimens of *Luciosoma* and *Leptobarbus* I can report that there is a definite movement of the posterior barbels which is independent of any jaw movement.

### **The brain**

The possibility of using the gross morphology of the brain as a phylogenetic character was suggested by observations made by Dr R. Vari on various characoids and on *Opsariichthys* (pers. comm.).

The outstanding feature of the brain in *Opsariichthys* is the size and shape of the telencephalic lobes which are elongate, sausage-like structures separated from the mesencephalon by long

posterior trabeculae. The usual situation in cyprinids, and it seems the majority of teleosts, is for the telencephalic lobes to be globular or ovate and closely apposed to the mesencephalon.

The olfactory bulb in *Opsariichthys*, and other cyprinids, is situated in the lateral ethmoid and thereby far removed from the telencephalon, the olfactory tracts being extended. Such extension of the olfactory tracts is also known in some characoids, in the siluroids, mormyroids and gadoids (Evans, 1940). It is known that in some cyprinids (e.g. *Carassius*) there is an ontogenetic change in the olfactory bulbs and tracts (Schnitzlein, 1964); in young specimens the olfactory bulbs are adjacent to the telencephalic lobes but with growth the olfactory tracts extend forward. As there is an actual lengthening of the tracts it appears that there is a disproportionate growth of parts of the cranium.

In small specimens of *Opsariichthys* the telencephalic hemispheres are large, occupy most of the orbitosphenoidal cavity and are well separated from the mesencephalon (Fig. 45A). The olfactory tracts are short and the bulbs located in the lateral ethmoids. In large specimens the telencephalic lobes, whilst still well separated from the mesencephalon, are more closely apposed and lie in the pterosphenoïd; the olfactory tracts are long.

Thus, the difference between *Opsariichthys* and *Carassius* lies in the fact that although in *Opsariichthys* the olfactory lobes lie close to the telencephalon in early stages of development, it is the retreat of the telencephalon which gives rise to extension of the olfactory tracts whereas in *Carassius* (? and all other cyprinids) the telencephalon remains adjacent to the mesencephalon throughout growth. In a specimen of *Opsariichthys uncirostris amurensis* 82 mm SL the left telencephalic lobe is elongate and lies in advance of the right lobe, being connected to the mesencephalon by a long trabecula. In this and all other specimens examined the cerebellum is small.

#### *Zacco and Barilius*

The morphology of the brain in *Zacco* and *Barilius* Groups A & B is little different from that described in *Carassius* and *Cyprinus* by Evans (1940) and Schnitzlein (1964), i.e. the telencephalic lobes are rounded to ovate and separated from the mesencephalon by a deep recess (Fig. 45B). This condition appears to be invariable in the species examined. The olfactory tracts are long, slender and divergent anteriorly; the cerebellum is small.

In *Barilius* Group C there is a similarity to *Opsariichthys*. In *Barilius zambesensis* (Fig. 45D) and *B. ubangensis* the telencephalic lobes are elongate and separated from the mesencephalon by short posterior trabeculae. The same situation is found in *B. microcephalus* but in this species the olfactory tracts are thickened and the cerebellum large (Fig. 45C). In all species of this group the olfactory tracts lie close together and do not diverge anteriorly, the olfactory bulbs lie close together within the lateral ethmoids.

*Engraulicypris* is like *Barilius microcephalus* in the shape and size of the telencephalic lobes and the cerebellum (Fig. 45E). It should be noted here that the reference made by Evans (1940) to the particular brain morphotype of *Engraulicypris* refers only to the species *argenteus* assigned herein to *Rastrineobola* (see p. 195).

In *Leptocypris* the telencephalic lobes are also elongate but separated from the mesencephalon by a fissure; the olfactory bulbs are very large and the tracts short and thick. The cerebellum is larger than in any of the other genera examined.

The telencephalon of *Luciosoma* is small in comparison with the other genera, and the overall brain morphology resembles that of *Zacco*.

#### *Comments*

In functional terms the development of the telencephalon in *Opsariichthys* is unexplained. It is possible that the particular development of this part of the brain is in some way associated with integrating patterns of breeding behaviour of increased complexity (see Segaar, 1961; Nieuwenhuys, 1962). The usefulness of forebrain morphology as a phylogenetic character cannot be assessed, although from the apparently conservative morphological structure of the brain in other cyprinids, the condition in *Opsariichthys* possibly may be derived. The elongate telencephalic lobes, widely separated from the mesencephalon, is a feature shared with *Barilius* Group C species.

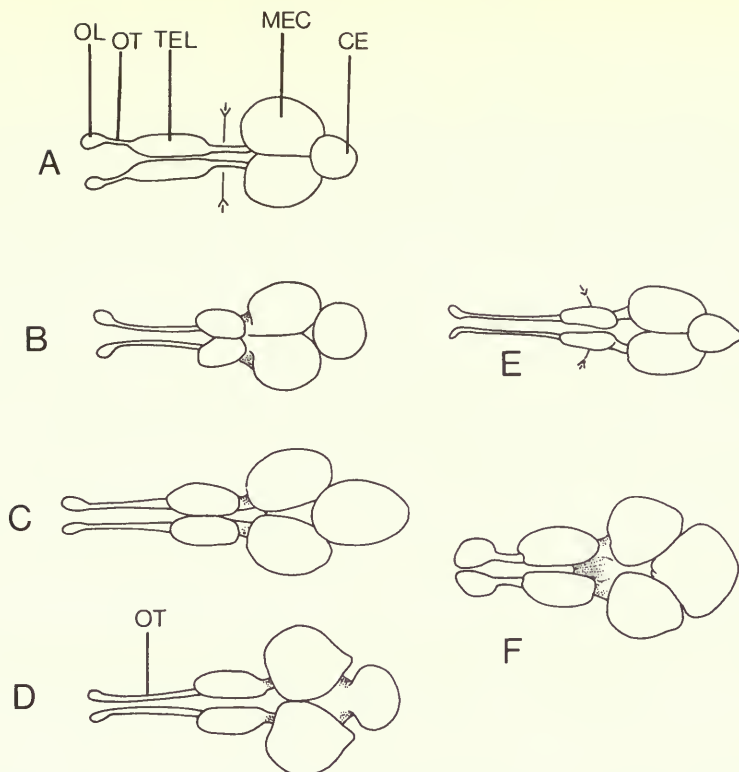


Fig. 45 Diagrams of the brain (dorsal views) in A. *Opsariichthys*. B. *Zacco platypus*. C. *Barilius microcephalus*. D. *Barilius zambesensis*. E. *Engraulicypris sardella*. F. *Luciosoma setigerum*. The arrowed lines indicate the suture between the orbito- and pterosphenoïd.

### Summary of character states

From the foregoing descriptions and analysis, the following characters are considered to be apomorph.

Narrow, deeply notched *supraethmoid*; shallow *mesethmoid*; small *preethmoid*; tubular olfactory foramen in *lateral ethmoid*; medially or distally expanded *kinethmoid*; ventrally thickened *vomer*; *pterosphenoid* contacting *parasphenoid*; *pterosphenoid* lateral fossa; enlarged *carotid foramen*; ventrally open *posterior myodome*; presence of a *jugular channel*; enlarged *sphenotic process*; reduced *dilatator fossa*; posteriorly extended *pterotic*; *posttemporal fossa* entering subtemporal fossa; narrow *frontal* with concave border; elongate *nasal* with more than 2 dorsal pores; elongate *parietal*; elongate *supraorbital*; narrow *infraorbitals*; anterior *maxillary* tips extended; anterior *maxillary* medial process ventrally directed; *dentary* notched anteriorly; *hyomandibular* condyles separated; *hyomandibular* lateral flange; *metapterygoid* process; small *symplectic*; *operculum* with elongate dorsal border; *cleithrum* with short upper part and expanded posterior lamina; *postcleithrum* reduced; *coracoids* in medial contact; 2nd and 3rd *centra* fused; *axial fin-lobes*; *reduction of barbels*; elongate *telencephalon*.

### Relationships of the bariliine genera

Authors who have considered the systematic position and/or anatomy of *Opsariichthys* have assumed it to bear a close relationship to *Zacco* (see, for example, Regan, 1911; Takahasi, 1925; Ramaswami, 1955, Greenwood *et al.*, 1966; Bănărescu, 1968). This supposed relationship has

been based upon the close similarity in external morphology of the two taxa which, in fact, resemble one another mainly in plesiomorph characters. None of the apomorphies identified here show *Opsariichthys* and *Zacco* to be sister taxa.

Characters identified as apomorphic in *Opsariichthys* also occur in *Barilius*, *Leptocypris*, *Engraulicypris*, *Luciosoma* and in some species of *Rasbora*. The synapomorphies which serve to identify these taxa as the **BARILIINE GROUP\*** are:

1. Subtemporal fossa connected with the posttemporal fossa (in its most derived state the posttemporal 'fossa' is formed into a foramen, p. 146).
2. Posterior myodome open ventrally, with an external origin for part of the eye musculature (p. 153).
3. Anterior trigemino-facialis foramen situated entirely within the lateral face of the prootic (p. 153).
4. Frontal fossa (p. 155).
5. Lateral pterosphenoid fossa (p. 140).
6. Hyomandibula with widely separated condyles and lateral flange (p. 164).
7. Metapterygoid with dorsal posterior process (p. 165).
8. Pectoral and pelvic axial lobes or modified scales (p. 176).

Before the relationships of the bariliine genera can be understood, it is first necessary to discuss the classification of the genera *Barilius*, *Leptocypris*, *Engraulicypris* and *Rasbora* (in part).

#### Classification of *Barilius*

As previously recognized, *Barilius* has included both Indian and African species and although subgroups have been recognized (Günther, 1968; Day, 1877, 1889, see below) the 'monophyly' of the taxon has remained unquestioned. On the basis of characters here identified as apomorphic, *Barilius* is seen as polyphyletic. The following classification is not entirely satisfactory as not all the Indian species, and virtually none of those from Thailand and Burma, have been examined. Hopefully, however, the interim scheme presented will permit a more precise systematic evaluation of the various groups until such time as a complete taxonomic revision is attempted.

In the descriptive section of this paper three major groups (*A*, *B* and *C*) of *Barilius* are recognized. However, within *Group A* two subgroups can be identified, *viz.*:

1. *Barilius*. Termed in the descriptive section *Group A* and represented by the type species of the genus *Barilius barila* (Hamilton, 1822). It includes only those species inhabiting the Indian sub-continent, Thailand and possibly Burma. The genus is characterized by the apomorph features of a deep, rostrally curved ethmoid region, long nasals, long parietals, reduced lateral ethmoids and a deep frontal fossa.

Day (1877) recognized three groups of Indian *Barilius* characterized by the absence or presence and number of barbels (see p. 189). I recognize two groups, (i) exemplified by *Barilius barila* in which the jaws are long, the hyomandibular condyles well separated, scales with many radii, body shallow, barbels in two pairs, tubercles small and poorly developed; (ii) exemplified by *Barilius gatensis* in which the jaws are short, hyomandibular condyles barely separated, scales with few radii, body deep, a single pair of barbels, or barbels lacking, and tubercles large and well developed. As yet I have examined too few species to be certain if these groups represent part of a morphocline. The species contained in *Barilius* are listed on p. 189.

2. *Opsaridium*. Termed in the descriptive section *Group C* and represented by the type species of the genus *Opsaridium zambesense* (Peters, 1852). It includes only African species. The genus is characterized by the apomorph features of: an expanded kinethmoid; reduced premaxillary

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\* The use of the name bariliine for this assemblage follows Regan (1922) who first recognized the subfamily Bariliinae (see p. 185).

ascending process; anteriorly extended maxillary tips; deep frontal fossa; pterosphenoid cavity; extensive lateral temporal foramen; broad mesocoracoid and well-developed pectoral axial lobes.

The secondary sexual dimorphic characters of an extended anal fin in males, well-developed axial lobes and distinctively marked dorsal fin (see p. 191) serve to distinguish this genus from other related taxa. The species contained in *Opsaridium* are listed on p. 191.

3. *Raiamas*. Termed in the descriptive section as *Group B* and represented by the type species of the genus *Raiamas bola* (Hamilton, 1822). It includes both African, Indian, Burmese and Malaysian species. The genus is characterized by the apomorph features of: a greatly expanded kinethmoid; long shallow jaws; reduced premaxillary ascending process; extensive pterosphenoid-parasphenoid contact; small dilatator fossa; apophyseal platform formed partly from the prootics; extensive posttemporal foramen; long post-parietal platform; broad mesocoracoid; posteriorly extended cleithrum; elongate pectoral axial scale and extensive development of *adductor mandibulae* A2 muscle which laterally covers the *dilatator operculi* and *levator arcus palatini* muscles. Within this genus a transformation series represented by *R. loati*-*R. salmolucius*-*R. bola* is apparent in cranial elongation.

Previously (Howes, 1978) *Raiamas bola* was used as an example of barililine anatomy when making comparisons with other cyprinids. It is now obvious that this species is not 'typical' of *Barilius* but represents a highly derived morphotype. Nevertheless, the conclusions reached in that study concerning the possible phylogenetic history of certain characters in *R. bola* remain valid within the hypothesis of relationships advanced here.

The inclusion of two Asian species in an otherwise entirely African genus requires some explanation. Four characters are present in *Raiamas bola* and *R. guttatus* which are lacking in their African congeners. These are: a closed posterior myodome; a much broader and S-shaped kinethmoid; extensive contact of the pterosphenoid and parasphenoid and, in *R. guttatus*, two pairs of small barbels. Possession of these characters in no way excludes *bola* and *guttatus* from inclusion in *Raiamas*. These two species are the most extreme members of their lineage in terms of cranial and jaw elongation, and are approached only by the African species *R. salmolucius* and *R. longirostris* (see p. 193). As mentioned above, a transformation series involving the lengthening of the pterosphenoid-parasphenoid suture, broadening of the kinethmoid and the secondary closure of the posterior myodome can be detected amongst the African species of *Raiamas* and the highly derived state of these characters in *R. bola* and *R. guttatus* is simply a continuation of this transformation sequence. It could, of course, be argued that the two Asian *Raiamas* species are simply the result of parallel evolution from an ancestral group of Indian barilines. Such an hypothesis can be tested by identifying synapomorphies between *Raiamas* and *Barilius* and perhaps by showing a similar transformation sequence amongst the Indian barilines. So far, I have found no such characters. The species contained in *Raiamas* are listed on p. 193.

The only species of *Barilius* occurring in the Middle East, *B. mesopotamicus* Berg, 1932, is, in fact, not a member of any of the genera listed above but should, on the basis of synapomorph characters, be included in the *Leucaspis* generic complex (see p. 190).

### Classification of *Leptocypris*

*Leptocypris* has previously been recognized as monotypic; *Leptocypris brevirostris* Blgr, 1919 and *L. clupeioides* Pell., 1922 were synonymized with the type species *L. modestus* Blgr, 1900 by Poll & Gosse, 1963 and Gosse, 1966, respectively. The genus is characterized by its shallow lower jaw, the dentaries being joined at the symphysis by a ligament; inferior position of the mouth; pointed snout; deep, narrow and strongly curved ethmoid region; truncated lateral ethmoid; long, ventrally directed medial maxillary process; elongate parietal; elongate nasal opening; absence of, or reduced *intermandibularis* muscle; absence of, or reduced number of gill-rakers (3-6), and much elongated pectoral and pelvic axial scales.

*Leptocypris* possesses none of those apomorph characters which would suggest a close relationship with *Opsaridium* or *Raiamas* (i.e. extensive posttemporal fossa, broad kinethmoid and gutter-like metapterygoid process), but it does share some of those characters listed above with

*Engraulicypris* (see below). Additionally, it shares the features of an elongate supraorbital, and 1st infraorbital covering the anterior part of the 2nd infraorbital.

Two other species, formerly included in *Barilius*, *B. niloticus* (Joannis, 1835) and *B. weynsii* Blgr, 1899, share with *Leptocypris modestus* the apomorph characters listed above as characterizing the genus and are thus transferred here to *Leptocypris*. The characters distinguishing the three species are tabulated on p. 190.

### Classification of *Engraulicypris*

As previously recognized, *Engraulicypris* has included several species of small-sized African cyprinids. However, the type species of the genus, *E. sardella* (Günther, 1868), possesses many apomorph characters, none of which are shared with any of the species presently included in *Engraulicypris*. For this reason the genus is restricted to the type species.

*Engraulicypris* is included in the bariliine group because it has characters 1, 2, 3, 4, 5 of those listed on p. 180 as typifying the group. The characteristic features of *Engraulicypris* are the extensively modified ethmoid region, the highly protrusile upper jaw and the long, numerous gill-rakers (total number 43–45).

The relationships of *Engraulicypris* with other members of the bariliine group are somewhat difficult to determine owing to the highly derived nature of many of its cranial features (autapomorphies). Other features, involving the pectoral girdle and vertebral column, are plesiomorphic and so offer no clues to relationship. On the basis of its possessing a well-developed pterospheoid fossa and the trigemino-facialis foramen being situated in the lateral face of the prootic, *Engraulicypris* is included in a subgroup of the bariliine assemblage (see below, p. 184). *Engraulicypris* shares with *Leptocypris* elongate parietals; truncated lateral ethmoids; downwardly directed medial maxillary processes; an extensive 1st infraorbital bone overlapping the anterior part of the 2nd infraorbital; elongate supraorbital; ligamentous connection of the dentaries and an elongate pelvic axial scale. In both *Engraulicypris* and *Leptocypris* the subtemporal fossa is narrowly conical with only a small foramen leading into the posttemporal fossa. The small opening is suggestive of a 'precursory' condition leading to the intramural channel and extensive foramen found in other bariliine genera.

*Engraulicypris* and *Leptocypris* are here regarded as sister genera forming a branch of the bariliine assemblage (see below). Which of the two can be considered the more divergently specialized is debatable. Certainly *Leptocypris* is trophically more generalized. Matthes (1963) made the point that *Leptocypris* was probably derived from *Barilius*-like ancestors and although more generalized than *Barilius* did not necessarily represent a primitive form. Matthes' concept of *Barilius* differs from that presented here and the '*Barilius*' species he was comparing with *Leptocypris* are now considered as members of the relatively derived groups *Opsaridium* and *Raiamas*. I would agree with Matthes that *Leptocypris* is not 'primitive' (plesiomorph) and further point out that there is a morphocline in this genus toward a carnivorous type represented by *L. weynsii*. The suggestion made by Goren *et al.* (1973) that *Engraulicypris* is derived from *Barilius* cannot be accepted as these authors too were considering polyphyletic assemblages.

### Classification of *Rasbora* (in part)

Throughout the descriptive section mention has been made of supposedly derived characters shared between *Luciosoma* and some species of *Rasbora*. These characters are: supraethmoid with a broad bowl-shaped depression; an expanded kinethmoid; a deeply concave vomer; a tubular olfactory foramen in the lateral ethmoid; an inflated orbital portion of the lateral ethmoid; a well-developed symphysial knob on the dentary followed by a deep notch; an elongate lateral occipital fenestra; a long operculum; elongate ceratobranchials, and a pectoral axial lobe attached to the postcleithrum. As well as these features, the *Rasbora* species possess characters 1, 4 and 5 of those identifying all bariliine genera. Within this '*Rasbora*' complex, two closely related groups can be identified. One group is referred to a new genus, *Parluciosoma* (see below), and the other to *Megarasbora* Gunther, 1868.

**PARLUCIOSOMA** gen. nov.**Rasbora** (in part) Hamilton, 1822TYPE SPECIES: *Leuciscus argyrotaenia* Bleeker, 1850.

In his revision of *Rasbora*, Brittan (1954) recognized an assemblage of species which he named 'The *argyrotaenia* complex'. He distinguished this from other species complexes within the genus by their medium to large size and by '... conservative structure and color-pattern'. Brittan (1954) did not explain the precise nature of their 'conservatism' and whilst it is true that nearly all members of the group display a distinctive colour pattern comprising a black lateral stripe and dark edges to the caudal fin (in preserved specimens), this character is of little value in formulating relationships. More significant in this regard are the osteological characters which this group of '*Rasbora*' shares with *Luciosoma*: ethmoid region broad, the supraethmoid with a bowl-shaped depression, the kinethmoid compressed and expanded distally; the dentary with a well-developed symphyseal process; the maxilla with an extended anterior tip narrowly separated from its fellow medially; the premaxilla with a short anterior ascending process; the frontal with a ventral fossa (and in one species, *P. dusonensis*, a lateral groove as in *Luciosoma*; see p. 155); a bony tube surrounding the olfactory foramen in the lateral ethmoid; elongate lateral occipital fenestra; the operculum broad and somewhat attenuated, and a well-developed pectoral axial lobe attached to the postcleithrum. Barbels are lacking.

*Parluciosoma* differs from *Luciosoma* in having a shallower supraethmoid depression, a narrow contact between the parasphenoid and pterosphenoid, shorter lateral processes of the 2nd vertebra and a long, medially directed postcleithrum. The jaws also tend to be shorter and deeper with a stronger symphyseal notch on the dentary. The species contained in *Parluciosoma* are listed on p. 194, and the relationships of *Rasbora* (*sensu stricto*) are discussed on p. 185.

**MEGARASBORA** Günther, 1868TYPE SPECIES: *Cyprinus elanga* Hamilton-Buchanan, 1822.

*Megarasbora* was used by Günther (1868) in a subgeneric sense to include *Rasbora elanga*. Brittan (1954) noted that *R. elanga* 'is discontinuous with the remainder of the species in the genus'. He drew attention to the short pair of rostral barbels and the 'peculiar' striae and ridges of the scales as well as to the high number of lateral line scales (40–44) compared with other *Rasbora* species. However, when compared with *Luciosoma* these characters are in concordance.

*Megarasbora* is characterized by a broad ethmoid region, the supraethmoid with a semi-circular depression; the kinethmoid lamellar; the premaxilla with a long, slender medial anterior process; the sphenotic with a broad lateral process which contains a fossa in its anterior face; the dilatator fossa confined to the sphenotic; the dentary with a deeply concave notch posterior to the symphyseal process; the lateral process of the 2nd vertebra containing a ventral fossa; the postcleithrum short and supporting a poorly developed axial lobe; pharyngeal teeth with strongly recurved tips (dental formula: 4.3.2); total number of gill-rakers on 1st gill arch, 8–9.

*Megarasbora* differs from *Luciosoma* and *Parluciosoma* in the nature of the characters enumerated above and in possessing a pair of short maxillary barbels, more obliquely aligned jaws and almost complete lack of body and fin markings. The genus is monotypic; see p. 195 for distribution.

**Interrelationships and classification of the bariliine genera**

The synapomorph characters identified in the foregoing anatomical descriptions (listed on p. 180) serve to relate *Barilius*, *Leptocypris*, *Engraulicypris*, *Opsariichthys*, *Opsaridium*, *Raiamas*, *Megarasbora*, *Parluciosoma* and *Luciosoma* as a monophyletic unit termed the *bariliine group* (see p. 180). The taxa comprising this group can be classified into two assemblages related as sister groups:

1. The bariliine assemblage (*Barilius*, *Leptocypris*, *Engraulicypris*, *Opsariichthys*, *Opsaridium* and *Raiamas*) defined by those characters listed on p. 180.

2. The luciosomine assemblage (*Luciosoma*, *Parluciosoma* and *Megarasbora*) which lacks a ventrally open posterior myodome. In addition to the derived characters shared with the bariliines (nos 1, 3, 4, 5 and 8 of those listed on p. 180), the luciosomines possess the autapomorphic features of: supraethmoid with bowl-shaped depression; compressed and medially expanded kinethmoid; lateral ethmoid inflated posteriorly and containing a tubular olfactory foramen; elongate lateral occipital fenestra and a pectoral axial fin lobe attached to the postcleithrum.

Within these two assemblages various sub-groups or lineages can be recognized as follows:

### Bariliine assemblage

*Barilius* represents the lineage which forms the sister group to the other members of the assemblage. This taxon possesses all the characters listed on p. 180 as defining the group apart from 3 and 7. *Barilius* is distinguished from other included taxa by the apomorph characters of: a deep, strongly curved and narrow ethmoid region; elongate nasals; elongate parietals and truncated lateral ethmoids.

*Leptocypris*, *Engraulicypris*, *Opsariichthys*, *Opsaridium* and *Raiamas* represent the apomorph sister group to *Barilius*. These genera are linked by the synapomorphies: pterosphenoid fossa and anterior trigemino-facialis foramen situated in the lateral face of the prootic.

*Leptocypris* and *Engraulicypris* together form the sister group to the other three genera and possess the synapomorphies: ventrally directed medial maxillary process; elongate supraorbital; 1st infraorbital partially overlapping the 2nd infraorbital and elongate pelvic scale.

*Opsaridium*, *Opsariichthys* and *Raiamas* possess the synapomorphies: anteriorly extended maxilla; bulbous vomer; presence of quadrate flange and lateral temporal foramen.

*Opsaridium* and *Raiamas* form the apomorph sister group to *Opsariichthys* linked by the synapomorphies: dorsally expanded kinethmoid; broad mesocoracoid and extensive posttemporal foramen.

### Luciosomine assemblage

*Parluciosoma* and *Luciosoma* form the apomorph sister group to *Megarasbora*. Apomorphies characterizing and linking these genera have already been discussed (p. 183).

The relationships of the genera forming the bariliine group are shown as a cladogram in Fig. 46.

When dealing previously with monophyletic groups of cyprinids (Howes, 1978, 1979) I refrained from assigning them to formal taxonomic categories and presented them as 'informal groups'. This same policy is followed here and for the same reasons, i.e. lack of congruency at higher level classification. The nature of the cladistic classification tends to inflate hierarchical levels. Thus, when the interrelationships of the bariliine group with those of other monophyletic assemblages are more completely understood it is likely that some of these groups, including the bariliines, will have to be assigned subfamily status.

## Interrelationships of the bariliine group

The search for the sister group of the bariliines has so far proved inconclusive. The reason is that the majority of cyprinid subfamilies, and even genera, currently recognised are non-monophyletic in the cladistic sense and it has not been possible to postulate relationships on the basis of synapomorphic characters. In previous studies I identified some monophyletic lineages (Howes, 1978, 1979) and in dealing with one of these groups, the chelines, I stated that there was no evidence to suggest close relationship with the bariliines (Howes, 1979). Since then, however, this hypothesis has been weakened by the identification of presumed synapomorphies associated with the jaws and otic region of the cranium (work in preparation). Regan (1911) suggested a relationship between *Barilius*, *Danio* and *Opsariichthys* considering that these genera were related to *Aspius* and *Leuciscus*, and stated '... *Hypophthalmichthys* is nearly related to the *Barilius*



group'. Later, Regan (1922) considered the geographical distribution of the Cyprinidae and recognized the Bariliinae as the most primitive members of the family. In this work Regan noted that there were a few Palearctic genera in the Bariliinae, but he did not name them. Furthermore, he was quite explicit with regard to their relationships '... the Leuciscine Cyprinidae is derived from the more primitive and more southern Bariliinae'.

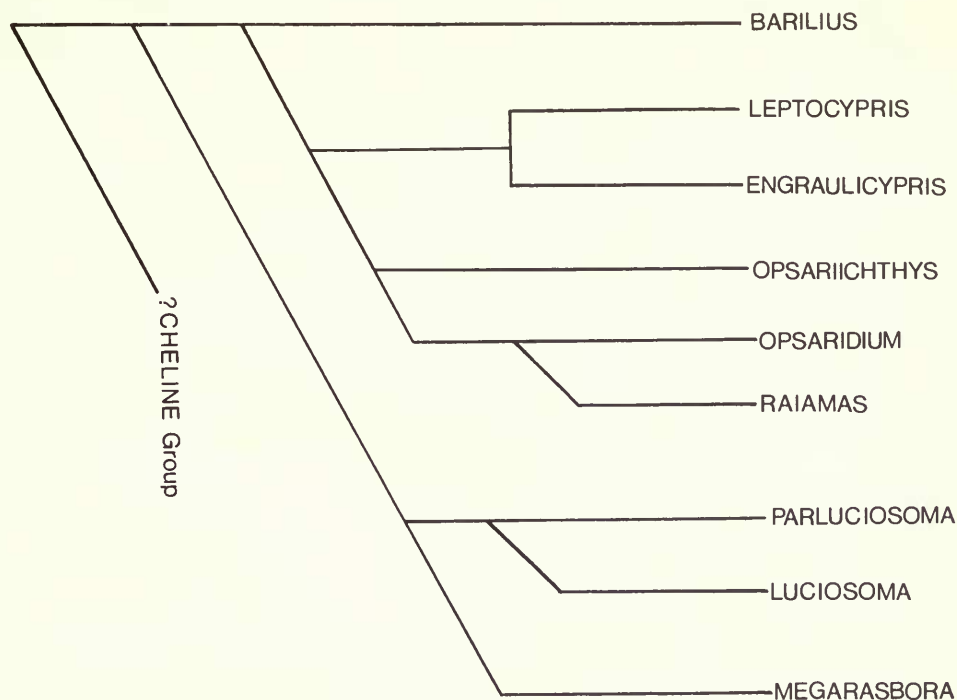


Fig. 46 Cladogram illustrating the relationships of the bariliine genera.

The evidence presented here falsifies Regan's claim for a close association between the leuciscines and bariliines. Neither have any synapomorphies been identified which relate *Hypophthalmichthys* with any bariliine taxon. As remarked previously (Howes, 1978) the Leuciscinae are a polyphyletic assemblage including at least three major groups. Current studies indicate that these three groups can be related at various levels to the aspinines, cultrines and hemicultrines (including the Xenocyprininae) *sensu* Howes (1978, 1979). In turn, this higher-level group appears as the likely sister group to that comprising the bariliines, chelines, rasborines and danioines. The interrelationships of the various monophyletic subgroups have yet to be deduced.

Matthes (1963) considered that the '... "*Barbus* and *Barilius*" types share many characteristics which are indicative of close phylogenetical affinities'. I have found no synapomorph characters indicating close relationship of the bariliines with any barbine or labeine group.

Gosline (1978) considered *Opsariichthys* and *Zacco* to be 'specialized' genera allied with the 'cultrin series of Leuciscinae, but with indications of affinity with the *Tribolodon*-American section of the subfamily'. Gosline gives no clue as to what these 'indications of affinity' might be. The tacit implication of this statement is that the American and Asian 'Leuciscinae' are a monophyletic assemblage. My opinion, based on current investigations of the anatomy of *Tribolodon*, is that this genus is indeed related to a group of the American cyprinids (including *Ptychocheilus*), but that the sister group to this assemblage is, in all probability, the aspinine group *sensu* Howes (1978). There is certainly no indication in terms of shared derived characters of any close relationship between any member of the bariliine group and the *Tribolodon*-American assemblage.

Finally, mention must be made of *Zacco* which in the absence of synapomorphic osteological characters is excluded from the bariliine group. It must be admitted that as yet I have been unable to relate *Zacco* with another monophyletic group. Indications are, however, that derived characters associated with the ethmoid and otic regions of the cranium are shared with members of the alburnine assemblage of 'Leuciscinae'.

### Biogeography of the bariliines

The bariliine group is represented in Africa, India, Burma, the Amur basin, Korea, Japan (Honshu Island only) and the south-east Asian archipelago. Both plesiomorph and derived taxa occur sympatrically in Africa and India. The present distribution and almost complete allopatry of the derived members of the bariliine (*Opsariichthys* and Indian *Raiamas*) and luciosomine (*Luciosoma*) assemblages indicates vicariance events occurring after the break-up of Gondwanaland.

The geographical distribution of the bariliines in Africa is as follows:

*Opsaridium* occurs in the Zambesi drainage and Lake Malawi, extends south to the Limpopo river and north through Zaire to the Ja (Dja) river, as far west as the Cubango river, and east to the Rufiji. *Opsaridium* is the only bariliine genus found in the Zambesi basin and the east-African drainage systems (see Banister & Clarke, in press, for detailed distribution).

*Leptocypris* and *Raiamas* both have similar distribution patterns, ranging through the Nilo-Sudanian and Zairean provinces. *Raiamas* extends far to the west in Sierra Leone while its most southerly distribution is to Lake Tanganyika.

*Engraulicypris* is confined to Lake Malawi.

The partially sympatric distribution of the bariliine genera in Africa suggest a series of vicariance events, with the most derived genus, *Raiamas*, being the most widely distributed. *Engraulicypris* is the only bariliine adapted to a planktonophagous niche, this niche in other Rift lakes being occupied by derivatives of a Euro-Asian assemblage of cyprinids (see p. 196).

The pattern of bariliine distribution in India shows that the relatively plesiomorph species *Barilius bendelisis* and *B. vagra* are widely distributed and indeed are the only *Barilius* species found in the Indus plain (Mirza, 1974) and Sri Lanka (Silas, 1953). *Raiamas* extends eastward, beyond the range of *Barilius* into Shan and the Malay Peninsula.

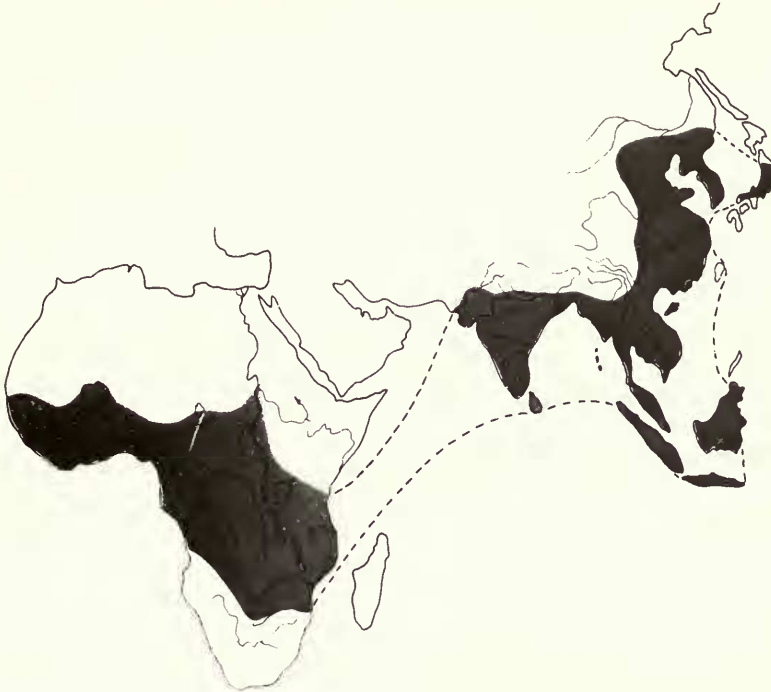
Plesiomorph luciosomines (*Parluciosoma* and *Megarasobra*) are also present in India with the more derived species of *Luciosoma* and *Parluciosoma* extending through the Malay Peninsula and along the Sunda Island chain.

*Opsariichthys* occurs through southern China, the Amur basin, Korea and Honshu Island of Japan. What may prove to be the more plesiomorph species of *Opsariichthys* inhabit Taiwan and Hainan (see p. 189).

The affinity of the Indian with the Malaysian ichthyofauna has been emphasized by Hora (1944) and Menon (1953, 1955). In Menon's view, Indian ostariophysi had their 'origins' in southern China and dispersed along the Himalayas and the Burma-Malayan arc. More recently Briggs (1979) has made a similar assertion that the cyprinoids had their origins in the Oriental Region, more particularly in South-East Asia. These hypotheses suffer from not having as their base-line a well-founded theory of phylogenetic relationship. Furthermore, it seems that these ideas depend upon the ancestral lineages of the present-day ostariophysan groups having been confined to 'evolutionary centres' from which they dispersed (Briggs, 1979). The difficulties inherent in constructing 'dispersal' hypotheses on the basis of palaeogeography are realized when considering the varying views concerning the Gondwanic position of the South-East Asian block and its likely connections with India. Burton's (1970) and Ridd's (1971) proposals are for juxtaposition of the Malay Peninsula with India, whereas Stauffer (1973) considers the Malayan blocks as once having African connections.

The system of interrelationships hypothesized here for the bariliines suggests a Gondwanic (i.e. pre-drift India+Africa) distribution (Fig. 47). Banister & Clarke (1977), in accounting for a Gondwanic distribution of another ostariophysan group, the Clariidae, were puzzled by the narrower geographical gap separating the Indian and African *Barilius* compared with that

separating the *Clarias* of the two continents. These authors had been misled by the misidentification of a middle-Eastern cyprinid as a *Barilius* (see p. 190). Now it is seen that the distribution of the bariliines approximates closely to that of the Clariidae and to that of two other cyprinid groups, the barbines and labeines. However, before too many assertions can be made concerning the distributional history of the cyprinids, the monophyletic integrity of these two groups must be tested, as indeed must that of the entire Cyprinoidei.



**Fig. 47** Map showing distribution of bariliine genera (dark grey) and dispersal track (broken line). Blanket coverage is given to Sumatra, Java and Borneo although the actual distribution of bariliines on these islands is still to be ascertained.

### Conclusions

1. *Opsariichthys* is not a 'primitive' cyprinid – the opinion of previous authors – but a relatively derived member of its group.
2. *Opsariichthys* is a member of a monophyletic unit termed the *bariliine group* comprising two sister assemblages whose constituent genera are: *Luciosoma*, *Parluciosoma* and *Megarasbora*; and *Barilius*, *Leptocypris*, *Engraulicypris*, *Opsariichthys*, *Opsaridium* and *Raiamas*.
3. *Barilius* as previously conceived was a composite genus, it is here restricted to include only those species inhabiting the Indian subcontinent and parts of South-East Asia. Most of the species formerly included in *Barilius* are assigned to *Opsaridium*, *Raiamas* and *Leptocypris*, others are found to possess apomorph characters which relate them to other cyprinid genera.
4. *Engraulicypris* as formerly recognized is a composite genus. It is here restricted to include only the type species, *E. sardella*. This is a derived member of a lineage within the bariliine assemblage whose sister taxon is identified as *Leptocypris*. The other species formerly included in *Engraulicypris* are assigned to various non-bariliine genera (see Appendix 2).
5. *Rasbora* is a composite genus and includes a monophyletic assemblage typified by *R. argyrotaenia* here described as a new genus, *Parluciosoma*. This taxon is the sister group to *Luciosoma* and together they form the sister lineage to *Megarasbora*.

6. Transition series of characters correlated with cranial elongation are identified in both the bariliine and luciosomine clades.
7. The interrelationships of the bariliine group are unresolved although preliminary (unpublished) evidence suggests that they are the sister group to the chelines (*sensu* Howes, 1979).

### Acknowledgements

I am most grateful to all my colleagues in the Fish Section of the British Museum (Natural History) for their assistance during this work. In particular Drs Humphry Greenwood and Keith Banister have aided by means of their stimulating and fruitful discussions and their criticisms of the manuscript. In this regard I must thank Dr Gordon Reid who also permitted me to use some of his unpublished findings concerning the use of cyprinid tubercles.

My sincere thanks are due to Dr Tyson Roberts for providing me with information on Indian and African bariliines and to Drs Max Poll and C. Lavett-Smith for allowing me to borrow the type specimens then under their care of, respectively, *Engraulicypris katangae* and *E. congicus*.

Finally, special thanks to Gina Sandford for typing the manuscript and to Jeff Jacobs for obtaining for me a live (which subsequently became a dead) specimen of *Luciosoma trinema*.

### Appendix 1

#### Annotated list of bariliine genera and species

The following notes concerning the taxonomy of the bariliine taxa are in no way intended as a formal revision but serve to indicate the assignment of species to the genera as now defined. In the course of this study it has been necessary to examine type specimens of many of the species included in the group and some discrepancies in earlier descriptions have been corrected in the light of these examinations.

#### *OPSARIICHTHYS* Bleeker, 1863

TYPE SPECIES: *Leuciscus uncistrostris* Temminck & Schlegel, 1844.

DISTRIBUTION: Northern, central and southern China, Southern tributaries of the Amur, Korea, Japan (Honshu), Hainan and Taiwan.

Bănărescu (1968) appears to be the only author to have revised the genus. This revision was in effect a note on the so-called subspecies of *Opsariichthys*. Bănărescu (1968) made no attempt to define the genus and failed to recognize that two species placed in the genus *Zacco* in fact belong with *Opsariichthys*. These are the species *pachycephalus* Günther, 1868 and *barbatus* Regan, 1908 (see below). I have the following remarks to make concerning the three species now assigned to the genus:

#### *Opsariichthys uncistrostris* (Temminck & Schlegel, 1844)

Bănărescu (1968) follows Nichols (1943), Berg (1949) and Wu (1964) in recognizing other nominal species of the genus as being subspecies of *O. uncistrostris*. The separation of the subspecies appears to have been made only on the basis of the number of lateral line scales, a character in which there is complete overlap throughout the range of the species. Other characters such as the varying morphology of the jaw, cranial osteology and buccal epidermis have been completely disregarded by previous authors.

*Opsariichthys pachycephalus* Günther, 1868

This species has been placed in *Zacco* by various authors but is, in my opinion, a member of *Opsariichthys*. It shares with other species of the genus the notched lower jaw; a metapterygoid process; separated hyomandibular condyles; a hyomandibular flange; pterosphenoid-parasphenoid connection; subtemporal fossa connected with posttemporal fossa; deep infraorbitals; maxilla narrowly separated from the premaxilla. It does not share with *Zacco* the deep, narrow ethmoid block, enlarged carotid foramen nor the produced anterior cleithral lamina.

*Opsariichthys pachycephalus* differs from other species in its low number of vertebrae (40 cf. 44 in *uncirostris* and 42 in *barbatus*) there being fewer caudal vertebrae (17–18) than in all other bariliine taxa except *Luciosoma* and *Parluciosoma* (16–17).

Bănărescu (1968) notes that specimens recorded from Taiwan as *Zacco temmincki* or *Zacco platypus* are most probably misidentified and should be referred to *Opsariichthys pachycephalus*.

*Opsariichthys barbatus* Regan, 1908

This species is recorded only from Lake Candidus on Taiwan and was placed by Jordan & Richardson (1909) in a separate genus *Candida* on the basis of possessing a pair of posterior maxillary barbels. Bănărescu (1968) included the species in *Zacco*, considering the presence of barbels insufficient evidence to warrant generic status. However, Bănărescu had overlooked the form of the lower jaw which is quite different from that of *Zacco*. I disagree with Bănărescu's (1968) assignment of the species *barbatus* to *Zacco* and believe that it should be placed in *Opsariichthys*. Having only the type specimens available I have been unable to check that all the osteological characters necessary for inclusion in this genus are present. However, from radiographs it is clear that the cranium and pectoral girdle have an overall opsariichthine-morphology (the ethmoid block is broad and shallow and a metapterygoid process is present).

The lower jaw of *O. barbatus* is shorter than that in any other *Opsariichthys* species and is completely overlapped by the upper jaw when the mouth is closed (Fig. 48). The jaw is also inclined at a more oblique angle so that its articulation with the quadrate comes to lie on a line passing through the centre of the orbit whereas in other *Opsariichthys* it is below the posterior third of the orbit. The lateral line scales number 54–56, is comparable only to that in *O. pachycephalus* (53) and *O. uncirostris uncirostris* (50–59).

Jaw morphology and low vertebral numbers suggest that *Opsariichthys pachycephalus* and *O. barbatus* are relatively plesiomorph species as compared with *O. uncirostris*. However, the interrelationships of the three species can only be resolved when osteological material of *O. pachycephalus* and *O. barbatus* is available and synapomorphies are identified. Meanwhile, I would hypothesize that the two Taiwan species form the plesiomorph sister group to the *Opsariichthys uncirostris* species complex of China, Japan and the Amur basin.

**BARILIUS** Hamilton, 1822

TYPE SPECIES: *Cyprinus barila* Hamilton, 1822.

The genus as now restricted includes only those species occurring in India, Sri Lanka, Burma and Thailand.

Hamilton (1822) first used *Barilius* as a 'Division' of *Cyprinus* under which he included *B. barila*, noting that it lacked barbels. Heckel (1842) apparently overlooked or disregarded Hamilton's use of *Barilius* and proposed *Pachystomus* in which he included species with 4 barbels and those without barbels.

Bleeker (1849) introduced *Bendelisis* as a subgenus of *Barilius* to include species with 2 barbels. Later, in the *Atlas* (1863) he designated the species *bendelisis* as the type of the subgenus, stating 'cirri 2'. However, Bleeker was in error as *B. bendelisis* (Hamilton) has 4 barbels.

Day (1877) used *Pachystomus*, *Bendelisis* and *Barilius* as divisions of *Barilius*. Species with 4 barbels he included in *Pachystomus*, species with 2 barbels in *Bendelisis* and those without

barbels in *Barilius*. Day (1877) included only a single species in *Bendelisis*, namely *barila*. But, Day too was in error as *B. barila* also has 4 barbels. (Day's mistake was pointed out by Hora, 1921.) At the same time, Day (1877) noticed Bleeker's previous oversight with respect to the number of barbels in *B. bendelisis* (see above) and placed the species in *Pachystomus*. Finally, Jordan (1919) designated *barila* as the type species of *Barilius* by logotypy.

Thus, it would appear that *Pachystomus* and *Bendelisis* are synonyms of *Barilius*.

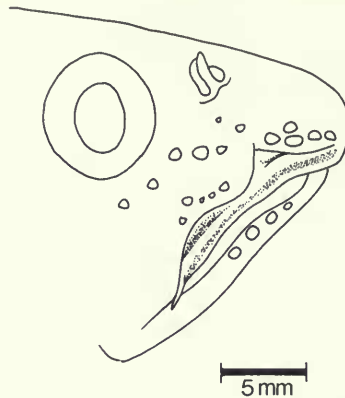


Fig. 48 *Opsariichthys barbatus*, lateral view of the head to show form of the lower jaw.

As noted above, p. 180, two groups of *Barilius* can be recognized, but it is possible that these 'groups' form part of a morphocline. Included species: group (i): *B. barila* (Hamilton, 1822), *B. bendelisis* (Buchanan, 1807), *B. radiolatus* Günther, 1864, *B. vagra* (Hamilton, 1822), *B. shacra* (Hamilton, 1822); group (ii): *B. bakeri* (Günther, 1868), *B. barna* (Hamilton, 1922), *B. canarensis* (Jerdon, 1849), *B. evezardi* Day, 1872, *B. gatensis* (Val., 1844), *B. modestus* (McCl., 1842), *B. ornatus* Sauvage, 1883, *B. tiltheo* (Hamilton, 1822).

The following species are ones which I have not examined and am unable to allocate with certainty to *Barilius*: *B. bernatziki* Koumans, 1937, *B. dogasinghi* Hora, 1921, *B. huahinensis* Fowler, 1934, *B. infrafasciatus* Fowler, 1934, *B. karatensis* Smith, 1931, *B. pulchellus* Smith, 1931, *B. ponticulus* (Smith, 1945), *B. nanensis* Smith, 1945.

Two other species formerly placed in *Barilius* are found not to belong to this genus; they are: *Barilius auropurpleus* Annandale, 1918 from Inle Lake, Burma, possesses characters which relate it to the cheline group.

*Barilius mesopotamicus* Berg, 1933 possesses apomorph characters shared with some species presently assigned to *Leucaspius*.

#### LEPTOCYPRIS Boulenger, 1900

TYPE SPECIES: *L. modestus* Boulenger, 1900.

DISTRIBUTION: Africa; Nile, Niger and Zaire.

Two other species are included in the genus, *L. niloticus* (Joannis, 1835) and *L. weynsii* (Blgr., 1899). The characters distinguishing the three species are as follows:

	<i>L. niloticus</i>	<i>L. modestus</i>	<i>L. weynsii</i>
Gill-rakers on 1st ceratobranchial	3	0	2-3
Lateral line scales	36-40	40-42	44-45
Anal fin rays, branched	11-12	8-9	14-15
Maxillary valve	non-papillate	papillate	non-papillate
Pelvic scale, % of pelvic fin length	25	75	75
Extent of maxilla	to centre of eye	anterior	centre

*Barilius guineensis* Daget, 1962 appears from the description and figure also to belong to *Leptocypris*. Characteristic are the inferior position of the mouth and rather prominent snout. Daget (1962) notes the close similarity between *B. guineensis* and *B. weynsii*.

**ENGRAULICYPRIS** Boulenger, 1911

TYPE AND ONLY SPECIES: *Barilius sardella* Günther, 1868.

DISTRIBUTION: Lake Malawi and upper Shire river.

**OP SARIDIUM** Peters, 1852

*Pelotrophus* Günther, 1864.

*Barilius* (non Hamilton), Boulenger, 1899 (part).

TYPE SPECIES: *Leuciscus zambesensis* Peters, 1852.

DISTRIBUTION: Africa; Zambesi, Zaire, Quanza and Lower Guinea provinces (Roberts, 1975).

*Opsaridium* is the plesiomorph sister taxon to *Raiamas* and is characterized by an extended anal fin in the males, larger and granular tubercles, large and well-patterned dorsal fin (13–15 branched rays) and fleshy or lobate pectoral axial scales. Osteological characters are listed on p. 180.

Included species: *O. zambesense* (Peters, 1852), *O. christyi* (Blgr, 1920), *O. loveridgi* (Norman, 1922), *O. microcephalus* (Gnthr, 1864), *O. microlepis* (Gnthr, 1864), *O. ubangense* (Pellegrin, 1901).

***Opsaridium zambesense* (Peters) and *O. ubangense* (Pell.)**

On the basis of their external morphology and osteology these two species appear to be closely related. Indeed, in Boulenger's (1911) key there is a complete overlap of diagnostic characters. Jubb (1967) placed *Barilius neavii* Blgr, 1907 and *B. peringueyi* Gilchrist, 1913 into the synonymy of *B. zambesensis*, stating that these 'species' represented various growth stages.

I have examined all the specimens in the BM(NH) collections identified as *B. zambesensis* and *B. ubangensis* and have the following comments to make: In *Opsaridium zambesense* (as represented by the types and the types of *Barilius neavii*) the maxilla extends as far as the suture of the 2nd and 3rd infraorbitals, the operculum is long and rather attenuated, the dorsal fin is patterned by dark bands of pigment extending between the rays, except the 6th to 8th rays where the pigment is confined to the distal margin of the fin membrane. (This pattern is admirably illustrated in Poll, 1967, fig. 89.) The pectoral axial scale is small with a fleshy lower margin, the dark bars along the flanks are almost always split anteriorly and number 6–12, lateral line scales number 41–43. The pectoral axial lobe is small; the dark bars along the flanks are almost always split anteriorly and number 6–12, lateral line scales number 41–43.

Specimens from the Cubango river, Angola (BMNH 1965.3.15 : 34–39) previously determined as *B. zambesensis* differ from the above description on having somewhat longer jaws, longer operculum and a clear submarginal band on the dorsal fin.

In *Opsaridium ubangense* (specimens from Ubanghi, Luala and Luluaburg), the maxilla extends to just beyond the anterior border of the eye, the operculum is short, the dorsal fin is similarly patterned to that in *O. zambesense* except that the dorsal anterior margin is without pigment and the tips of the membrane between the last two rays is very dark. The pectoral axial scale is fleshy and short, the dark bars along the flanks are split and number 12–13, lateral line scales number 39–42.

Specimens identified as *O. ubangense* from the Kribi and Ja (Dja) rivers (Cameroon) differ from 'typical' *O. ubangense* in that the 3rd and 4th infraorbitals are broad, almost covering the cheek, the pectoral axial lobes are longer and the dorsal fin lacks the intensely dark posterior distal markings.

Specimens from the Upper Mwanza and Upper Shire rivers are also identified as belonging to the *O. ubangense* group.

At present the limits of the various taxa included within the *zambesense-ubangense* complex cannot be defined and the problem may only be resolved when further, larger samples from a wider geographical area become available.

### *Opsaridium loveridgi* (Norman, 1922)

Described from a single specimen from the Rufiji river, the fish has a well-developed pectoral axial lobe and colour pattern characteristic of the genus *Opsaridium*. Norman (1922) noted that the species was '... Near *B. ubangensis* and *B. peringueyi*'. Certainly *O. loveridgi* belongs to the *O. ubangense-zambesense* group but appears to be a distinct species.

### *Opsaridium microcephalus* (Günth, 1864) and *O. microlepis* (Günth, 1864)

These two species both occur in Lake Malawi. Günther (1864) referred them to the genus *Pelotrophus* on account of their extended anal fins.

*Opsaridium microcephalus* differs from other *Opsaridium* species in possessing a ventral frontal foramen and an extensive lateral temporal foramen (p. 147, Fig. 17). It shares with *O. microlepis* a high vertebral number (47–48) and a high number of dorsal fin rays (15–17).

The relationships of the Lake Malawi species have not yet been explored in great depth but indications are that the closest riverine relative is *O. ubangense*.

Three species formerly included in *Barilius* are recorded from Lake Tanganyika; *moori*, *salmolucius* and *tanganicae* (Poll, 1953; Worthington & Ricardo, 1936). The first two species are now included in *Raiamas* (see below) but *tanganicae* has an *Opsaridium*-like morphology. *Barilius tanganicae* Blgr, 1900 is known only from the holotype, and despite subsequent collecting no specimens have been recorded again. Poll (1953) makes no mention of the species; Worthington & Ricardo (1936) note only the type. The holotype conforms in almost every respect to the description of *Barilius microlepis* given by Boulenger (1911). Although Boulenger (1911) states for *tanganicae* '... 16 or 17 blackish vertical bars on each side of the body' and for *microlepis* '... no markings', there are in fact similar markings present in *microlepis* (see Poll, 1953).

The holotype of *B. tanganicae* was collected by J. E. S. Moore and bears the BMNH register number 1906.9.6 : 26. The locality given in the accessions register is 'N end of L. Tanganyika'. Regrettably there is no collection number or label which can help to identify the locality. In view of the fact that Moore's locality labels have proved to be unreliable in the past (see Trewavas, 1946 : 244) I suspect that *tanganicae* is a specimen of *microlepis* and that it was collected from Lake Nyasa (L. Malawi). Thus, until there is evidence to the contrary I place *Barilius tanganicae* into the synonymy of *Opsaridium microlepis*. This means that the only bariline species known from Lake Tanganyika are of the genus *Raiamas*.

Species which I have not examined but which appear from the literature to belong to *Opsaridium* are: *Barilius maculicauda* Pellegrin, 1926. Described from 3 specimens collected at Tshikapa, Congo. The description and Pellegrin's observation that the species resembles *O. zambesense* indicate its inclusion in *Opsaridium*.

*Barilius leleupi* Matthes, 1965. The prolongation of the anal fin, body markings, shape of the mouth and distribution of the tubercles indicate that this species belongs to *Opsaridium*. Matthes (1965) discussed the likely affinity of *B. leleupi* with *O. zambesense* and *B. boweni* Fowler, 1930; the latter species he considered might be synonymous with *O. zambesense*.

*Barilius engrauloides* Nichols, 1923. Described from a single specimen collected from the Ubangui river. In his description Nichols states '... It seems to be more or less intermediate between species of that genus (*Barilius*) and of *Engraulicypris*'. The figure accompanying the description is crudely drawn and of no help in determining the generic allocation of this species.



*RAIAMAS* Jordan, 1919

*Barilius* (non Hamilton), Boulenger, 1899 (part).

*Bola* Günther, 1868.

*Sagittabarilius* Fowler, 1936.

TYPE SPECIES: *Cyprinus bola* Hamilton, 1822.

DISTRIBUTION: Africa, Nilotic, Guinean and Zairean ichthyofaunal provinces (see Roberts, 1975 for definition of these provinces); northern India; Burma and the Malay Peninsula.

Günther (1868) first recognized a generic separation for *Barilius bola* and used the generic name *Bola*. However, this name was preoccupied and the name *Raiamas* was proposed as a replacement by Jordan (1919).

Hora & Mukerji (1936) accepted Jordan's substitute name but later, Hora (1937) discussed the nomenclatural history of *Barilius bola* and decided that *Raiamas* had been proposed in error because the name *Opsarius* McClelland, 1839 was available. Hora's (1937) contention was that Day (1869) had restricted the use of *Opsarius* McClelland to *Barilius bola*. Day had, however, simply placed *B. bola* in the genus *Opsarius* without designating it as the type of that genus, and later (1889) he included *Opsarius* in the synonymy of *Barilius*. McClelland (1839) had not designated a type species for the genus *Opsarius*, an action subsequently taken by Jordan (1919) who selected the species *maculatus* on the grounds of logotypy. *Opsarius maculatus* is a synonym of *Barilius tiltheo* (Hamilton, 1822).

Smith (1945) used Jordan's name *Raiamas* for *bola* although his reasons for justifying its generic allocation, i.e. on the basis of its pharyngeal dentition, are not those used here. Smith (1945) stated that the two rows of pharyngeal teeth in *R. bola* distinguish it from all other *Barilius*, which have three rows. In all specimens of *R. bola* I have examined there are three rows, a feature also noted and illustrated by Hora (1937).

Included African species: *R. ansorgii* (Blgr, 1910), *R. batesii* (Blgr, 1914), *R. buchholzi* (Peters, 1876), see comments below, *R. kingsleyae* (Blgr, 1899), see comments below, *R. loati* (Blgr, 1909), see comments below, *R. nigeriensis* (Daget, 1951), *R. salmolucius* (Nichols & Griscom, 1917), *R. silax* (Schultz, 1942), *R. senegalensis* (Steind., 1870), *R. steindachneri* (Pell., 1908), *R. longirostris* (Blgr, 1902), see comments below, *R. macrostoma* (Blgr, 1913), *R. moorii* (Blgr, 1900), *R. weeksi* (Blgr, 1899), *R. shariensis* (Fowler, 1949).

*Raiamas buchholzi* (Peters)

Of this species, Boulenger (1911) stated that it was separable from *Barilius kingsleyae* only on the number of lateral line scales (46 cf. 49-51 according to Boulenger) and '... may ultimately have to be regarded as not separable from it'. Although I have not had the opportunity to see the type specimen of *R. buchholzi* it is clear from Peters' (1876) illustration that it should be included in *Raiamas*. In *R. kingsleyae* the number of lateral line scales ranges from 46 to 49 (51 only if counting onto the caudal fin). I find no other differences between *R. kingsleyae* and Peters' description of *R. buchholzi* apart from the apparent lack of body markings in the latter (faint vertical bars are present in *R. kingsleyae* but are lacking in some specimens, no doubt due to the effects of preservation). I therefore propose that *Raiamas kingsleyae* be regarded as a junior synonym of *Raiamas buchholzi*.

*Raiamas longirostris* (Blgr)

Known only from the holotype collected at Ubanghi, this species was placed by Fowler (1936) in the subgenus *Sagittabarilius* along with *R. salmolucius*. The principal features Fowler used to characterize *Sagittabarilius* were the slender body, long maxilla and wide infraorbitals - characters shared by all *Raiamas* species.

Dr K. E. Banister has examined the holotype in Tervuren Museum and reports that the characteristic elongate snout is not an artefact and in this regard *R. longirostris* closely resembles *R. bola* (see below).

#### *Raiamas loati* (Blgr) group

The complex of species represented by *R. loati* in the east, *R. salmolucius* in the west and by *R. ansorgii* in the south-west appears to be a morphocline series of taxa. If the descriptions of the west African species given by Boulenger (1911, 1916) are compared closely, the only differences to be found are in lateral line scale counts and some body proportions.

*Raiamas loati* is readily distinguished from the west and south-western species complex by its long maxilla (extending to the posterior third of the orbit), elongate pectoral and pelvic axial fin lobes (half the length of their respective fins), length and shape of the 1st infraorbital bone (equal to eye diameter and with the upper posterior edge slightly extended along the 2nd infraorbital).

In contrast *R. senegalensis*, *R. steindachneri*, *R. buchholzi* and *R. ansorgii* all have a relatively short maxilla, short pectoral and pelvic axial fin lobes, and a short 1st infraorbital bone – the upper border of which extends posteriorly as a narrow triangle.

Regarding *R. macrostoma*, Boulenger (1916) noted ‘... Intermediate between *B. loati* and *B. senegalensis*’. Its elongate axial fin lobes and shape of the 1st infraorbital bone suggest that it is more closely allied to *R. loati*.

Even within the relatively small number of specimens of the west African species examined, ‘intermediates’ between all species can be found.

Two Asian species are included in *Raiamas*, *R. bola* (Hamilton, 1822) and *R. guttatus* (Day, 1869). These species are almost identical in cranial morphology but differ in certain other characters. The lateral line scales in *R. bola* number 88–94 but 44–48 in *R. guttatus*. Barbels are absent in *R. bola* but in *R. guttatus* there are two minute posterior maxillary barbels. Smith (1945) says of *R. bola* that its ‘scales are finer than any known species of *Barilius*’. However, they compare in shape and striation with those of other *Raiamas*, *Opsaridium* and *Barilius* species. According to Hora & Mukerji (1936) *R. bola* is confined to the hilly areas of the Northwest Provinces of India, Assam, Bengal, Orissa and Burma. Fowler (1934) records the species from Thailand but appears to have mistaken *R. guttatus* for *R. bola* (see Smith, 1945). *Raiamas guttatus* occurs in the Shan States, Burma, Thailand, Cambodia (Khmer Republic) and the Malay Peninsula.

#### *LUCIOSOMA* Bleeker, 1855

TYPE SPECIES: *Barbus setigerus* Valenciennes, 1842.

DISTRIBUTION: Thailand, Java, Sumatra, Borneo and Laos.

The following species are included in the genus: *L. setigerum* (Val., 1842); *L. spilopleura* Bleeker, 1865; *L. bleekeri* Steind., 1879; *L. trinema* Bleeker, 1852; *L. pellegrini* Popta, 1905.

*Luciosoma fasciata* Yang & Hwang, 1964 appears from the figure not to belong to this genus. The shape of the head and mouth, the position of the dorsal fin, length of the pectoral fin, and the high number of lateral line scales all indicate a species of *Raiamas*, possibly *R. guttatus*.

#### *PARLUCIOSOMA* Howes, 1980

TYPE SPECIES: *Leuciscus argyrotaenia* Bleeker, 1850.

DISTRIBUTION: India, Thailand, Malay peninsula and Sunda Islands.

Included species: *P. argyrotaenia* (Bleeker, 1850), *P. dusonensis* (Bleeker, 1851), *P. daniconius* (Hamilton, 1822), *P. cephalotaenia* (Bleeker, 1859), *P. volzi* (Popta, 1905).

Species descriptions and details of their distribution are given by Brittan (1954). Species which probably belong to this genus, but which I have not had the opportunity of examining, are: *Rasbora steineri* Nichols & Pope, 1927, *R. hubbsi* Brittan, 1954, *R. myersi* Brittan, 1954, *R. tawarensis* Weber & de Beaufort, 1916.

Mention may be made at this point of *Rasbora zanzibarensis* Günther, 1866 reportedly collected from the Rovuma river, East Africa, and to date the only known representative of the genus in Africa. Day (1877) placed the species in the synonymy of *Rasbora daniconius*, an action followed by Brittan (1954). Neither author made particular mention of the African locality of the species. I have examined the unique type of *R. zanzibarensis* and find that it is a *Rasbora*, but I am doubtful that it belongs to the species *daniconius*. I also doubt the provenance of the fish in Africa and I suspect that there has been an error concerning the locality citation. For the present *R. zanzibarensis* must remain a *species inquirendum*.

### **MEGARASBORA** Günther, 1868

TYPE AND ONLY KNOWN SPECIES: *Cyprinus elanga* Hamilton, 1822.

DISTRIBUTION: Bengal, Assam and western Burma.

The species has been described by Brittan (1954) and an osteological description is given above, p. 183.

## **Appendix 2**

### **A note on the taxa formerly included in Engraulicypris**

As *Engraulicypris* is now restricted to the type species, *E. sardella* (see p. 182), the species previously included must be referred to another genus. A preliminary review of the anatomy of these species has indicated on the basis of synapomorphic characters that they belong to three genera, namely *Neobola*, *Rastrineobola* and *Chelaethiops*. The apomorph characters defining the genera and their contained species are as follows:

### **NEOBOLA** Vinciguerra, 1895

TYPE SPECIES: *Neobola bottegi* Vinciguerra, 1895.

APOMORPH CHARACTERS: Deep, narrow ethmoid block, the dorsal surface (supraethmoid) channelled, elongate nasal, raised frontal sensory canal, narrow infraorbitals, separation of the dermo- and autopterotic by a posttemporal fossa, long anterior premaxillary processes, attenuated opercular border, rounded anterior articular face of 1st vertebra.

INCLUDED SPECIES: *N. bottegi* Vinc., 1895, *N. fluviatilis* (Whitehead, 1962), *N. brevianalis* (Blgr, 1908), *N. bredoi* (Poll, 1945), *N. spinifer* (Bailey & Matthes, 1971), *N. stellae* (Worthington, 1934), *N. moeurensis* (Blgr., 1915).

### **RASTRINEOBOLA** Fowler, 1934

TYPE SPECIES: *Neobola argentea* Pellegrin, 1904.

APOMORPH CHARACTERS: Long, ventrally directed medial maxillary processes, long post-coronoid dentary border.

INCLUDED SPECIES: *R. argentea* (Pellegrin, 1904).

### **CHELAETHIOPS** Boulenger, 1899

TYPE SPECIES: *Chelaethiops elongatus* Blgr, 1899.

APOMORPH CHARACTERS: Supraethmoid narrow, channelled and overlapped by the frontals, raised

frontal sensory canal, elongate jaws, maxillaries contacting one another medially, separation of the dermo- and autopterotic by a posttemporal fossa, anterior articular face of 1st vertebra rounded with caudally directed lateral processes, elongate pectoral axial scale, numerous olfactory lamellae. In addition the jaw musculature shows derived features.

INCLUDED SPECIES: *C. elongatus* Blgr, 1899, *C. bibie* (Joannis, 1835), *C. congicus* (Nichols & Griscom, 1917), *C. minutus* (Blgr, 1906).

I have examined the type specimens of both *Chelaethiops congicus* and *C. katangae* Poll, 1948, and it is my opinion that the latter is a synonym of the former. Specimens catalogued in the BM(NH) collections as *C. congicus* are not this species and represent an undescribed taxon (or taxa). Ricardo (1939) described from Lake Rukwa a subspecies of *C. congicus*. However, her description was based on the examination of the misidentified comparative material noted above. Although *rukwaensis* is indeed a discrete taxon it is not closely related to *C. congicus*, although it is related to the undescribed taxa from Lake Tanganyika and the Malagarasi river. Thus, Ricardo's subspecies is here recognized as a species, *Chelaethiops rukwaensis* Ricardo, 1939.

The relationships of *Neobola*, *Rastrineobola* and *Chelaethiops* remain to be investigated, but my preliminary observations indicate that all three genera form a monophyletic assemblage related to middle Asian and European groups as represented by *Phoxinellus* (of which there are two African species, *P. chaigoni* and *P. callensis*). There is thus no close relationship with the bariliine group.

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