

# The phylogenetic position of the Yugoslavian cyprinid fish genus *Aulopyge* Heckel, 1841, with an appraisal of the genus *Barbus* Cuvier & Cloquet, 1816 and the subfamily Cyprininae

Gordon J. Howes

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

## Contents

Introduction . . . . .	165
Methods and materials . . . . .	166
Nomenclature . . . . .	167
Abbreviations used in the figures . . . . .	168
Anatomical characters in <i>Aulopyge</i> and their phylogenetic significance . . . . .	169
The lateral ethmoid and its articulation with the entopterygoid . . . . .	169
Sensory canals and their associated bones . . . . .	174
Vertebral column, dorsal and anal fins . . . . .	177
Other osteological features . . . . .	182
Sexual dimorphism and genitalia . . . . .	186
Discussion . . . . .	186
<i>Aulopyge</i> relationships and barbin classification . . . . .	186
Immediate relationships of <i>Aulopyge</i> . . . . .	190
Acknowledgements . . . . .	192
References . . . . .	192
Appendix 1. The genus <i>Barbus sensu stricto</i> . . . . .	193
Definition and included species . . . . .	193
The systematic positions of <i>Barbus brachycephalus</i> Kessler, 1872 and <i>B. mursa</i> (Güldenstädt, 1773) . . . . .	195
The systematic positions of <i>Barbus andrewi</i> Barnard, 1937 and <i>B. serra</i> Peters, 1864 . . . . .	195
Appendix 2. Characteristics of the subfamilies Cyprininae and Leuciscinae . . . . .	196

## Introduction

*Aulopyge* is a monotypic genus represented by the species *A. huegelii* Heckel, 1841 (Fig. 1), endemic to rivers and lakes of the Yugoslavian karst regions of Dalmatia. Regrettably, there appears to be no published information on the ecology of *Aulopyge*. Populational data are lacking and the species is classified as rare (Lelek, 1980: 122).

*Aulopyge* possesses several unique characters (detailed below) which have led to its being placed in a separate taxonomic category, the Aulopygini (Bleeker, 1863; Karaman, 1971). In Karaman's (1971) view *Aulopyge* represents a relic of an earlier Eurasian barbina assemblage having a close relationship with the schizothoracine cyprinids—a group now confined to high-Asia. Lelek (1980: 122) simply comments '... it is difficult to compare it with other taxa'. Arai (1982: 146) concluded from his study of karyotypes that *Aulopyge*, which is polyploid ( $2n = 100$ ), possesses a 'mosaic of barbina and gobionine characters'.

The recent acquisition by the British Museum (Natural History) of well-preserved specimens of *Aulopyge huegelii* makes possible, for the first time, a detailed anatomical study of the species. The information gained from this study has provided a basis not only for a discussion of the phylogenetic status of *Aulopyge* but also of the classification and relationships of the genus *Barbus* and other cyprinines.

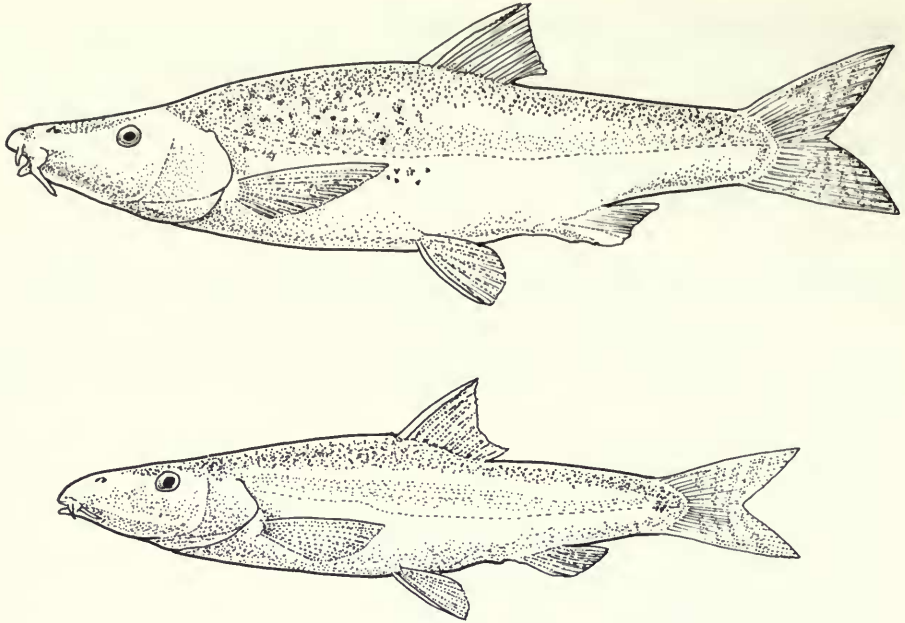


Fig. 1 *Aulopyge huegelii*, female (above) 127 mm SL and male (below) 106 mm SL.

In an earlier paper (Howes, 1981: 47–49) the classification of barbelled and non-barbelled Cyprinidae was discussed. It was reasoned that one lineage, the barbelled cyprinids, could be defined on the synapomorphic presence of paired maxillary barbels each associated with a maxillary foramen (or its suggested past presence) and a rostrally extended supraethmoid. Following the original division of the European Cyprinidae by Bonaparte (1846), the barbelled carps were recognised as the subfamily Cyprininae, while the non-barbelled taxa were ranked as the subfamily Leuciscinae. The latter group was defined simply by absence of maxillary barbels and associated nerve foramen, no synapomorphy having been discovered that would define it as a natural group.

It can be assumed from the outset therefore that *Aulopyge* belongs to the Cyprininae, since it possesses a pair of maxillary barbels supplied by a branch of the VII facial nerve. From this standpoint a more refined hypothesis of the relationship between *Aulopyge* and other cyprinids may be attempted.

### Methods and materials

The osteology of *Aulopyge huegelii* was studied from an alcian-alizarin stained and a dry skeletal preparation (BMNH) 1903.12.4: 41–5), and from X-Radiographs of specimens 106, 112 and 127 mm SL (BMNH 1985.8.20: 1–3; Busko Lake, south Bosnia). Genital anatomy was studied in dissected specimens of this latter series.

Comparative osteology of a wide range of cyprinoids was studied both from alizarin stained and dry skeletal preparations. A principal data source has been the large collection of X-Radiographs of cyprinoid specimens in the BMNH. The following list is of *Barbus* specimens used in this study.

A = alizarin stained preparation; D = dissected specimen; S = dry skeleton. All catalogue numbers are BMNH.

*Barbus ablabes* 1983.3.30: 7–14(D), *B. albanicus* 1970.9.24: 265–67(D), *B. altianalis eduardianus* Uncat., (S), *B. a. radcliffi* 1981.4.9: 42–66(D), *B. altus* 1898.4.2: 196–205(D), *B. amphigramma* 1980.7.18: 319–332(D), *B. andrewi* 1900.11.6: 58(D), 1903.4.27: 94–95(S), *B. antinorii* (type) 1908.10.14: 7, *B. arabicus* 1976.4.7:

201–272(D), *B. argenteus* 1907.6.29: 217(S), *B.* (= *Puntius*) *arulus* 1978.8.31: 234–259(D), *B. aspilus* 1909.4.29: 74(S), *B. barbulus* 1974.2.22: 1275–77(A), *B. barbus* 1864.4.11: 41–42(D), 1908.12.28: 123(S), 1985.10.16: 62–71(A), 1985.10.16: 51, *B.* (= *Puntius*) *bimaculatus* 1981.1.21: 209–217(D), *B. binotatus* 1984.3.3: 39–60(D), 1970.9.3: 56–85(A), *B. biscarensis* 1970.3.1: 100–125(D,A), *B. bocagei* 1980.8.20: 1–6(D), *B. brachycephalus* 1899.7.25: 25–27, *B. burmanicus* 1894.5.21: 46–55(D), *B. bynni* 1861.9.9: 65(S), *B. callensis* 1951.4.10: 1–20(A,D), 1869.1.29: 4(S), *B. camptacanthus* Uncat. (S), *B. canis* 1974.2.22: 1292–94(D), Uncat., (S), *B. cholra* 1935.10.18: 32–46(D), *B.* (= *Puntius*) *collingwoodi* 1892.9.2: 52–56(A), 1982.4.21: 37–38(D), *B. comiza* (syntype) 1909.7.29: 1, *B. conchoni* 1978.8.31: 21–35(D), *B. cummingi* 1978.8.31: 186–222(A), *B. dorsolineatus* 1965.3.15: 406–435(D), *B. esocinus* 1920.3.3: 80–82(D), *B. eutaenia* 1965.3.15: 93–122(D), *B.* (= *Puntius*) *filamentosus* 1981.1.21: 242–260(D), *B. fritschii* 1904.11.28: 59(S), *B. grællsii* 1908.2.12: 21–49(D), *B. grahami* 1907.5.4: 52–57(D), *B. grypus* 1920.3.3: 1–18(D), *B. guirali* 1902.11.12: 119(S), *B. haasianus* 1976.3.18: 892–93(A), *B. harterti* 1902.7.28: 35(S), *B. holotaenia* 1984.7.5: 22–27(D), *B. holubi* 1937.10.4: 12–14(D), *B. hospes* 1980.7.18: 434–438, *B. hypsolepis* 1971.11.26: 28–41(A), *B. intermedius* 1974.1.16: 128–162(A), 166–179(D), 1902.12.13: 338(S), *intermedius australis* 1893.12.2: 36(S), *B. johnstoni* 1975.8.3: 576–80, *B. kersteni* 1978.8.3: 632–84(D), *B. ksibi* 1934.10.25: 1–14(D), *B. leonensis* 1974.9.18: 77–177(A), *B. lineomaculatus* 1974.1.16: 396–411(D), *B. litamba* 1974.1.11: 88–93(D), *B. lithopides* 1889.2.1: 559–61(D), *B. longiceps* 1936.4.6: 5–11, 1949.9.16: 90–92, 1864.8.20: 21(S), *B. luteus* 1874.4.28: 23(S), 1968.12.13: 201–212(D), *B. macrolepis* 1972.11.28: 9–12(D), *B. macrops* 1960.6.7: 111–160(D), *B. mattozi* 1962.8.22: 2–6(D), *B. meridionalis* 1935.10.28: 14–17(D,S), *B. minimus* 1974.1.16: 276–292(D), *B. mursa* 1872.5.30: 67–68, *B. nasus* 1902.1.4: 22(S), *B. natalensis* 1862.8.28: 8(S), *B. neglectus* 1980.7.10: 1–26(D), *B. neumayeri* 1969.3.6: 31–50(D), *B.* (= *Puntius*) *orphoides* 1974.10.10: 865–872(D), *B. oxyrhynchus* 1893.12.2: 31(D), 1906.8.25: 17(S), *B. paludinosus* 1979.3.1: 1–53(D), 1908.1.20: 84(S), cf. *paludinosus* Uncat., (A), *B. paytoni* 1976.2.2: 29–31(D), *B.* (= *Puntius*) *pentazona* 1954.11.23 7–82(A), *B. perince* 1907.12.2: 1268–77(D), *B. plebejus plebejus* 1887.4.5: 15–16, 1982.2.24: 149–155(D), *plebejus peloponnesius* 1964.6.12: 20–26(D), *B. poechii* 1962.7.5: 4–15(D), *B. progenys* 1903.7.28: 155(S), *B. profundus* 1970.5.14: 19–30(D), *B.* (= *Tor*) *putitora* 1884.2.1: 52(S), *B. radiatus* 1982.4.13: 4597–4605(D), *B. reinii* 1903.10.29: 10(S), *B. rocadasi* 1911.6.1: 26(S), *B. rothschildi* 1902.7.28: 22–26(D), *B.* (= *Puntius*) *sarana* 1933.8.19: 7–14(D), *B. schejch* 1931.12.21: 4(D), *B. sclateri* (syntypes) 1861.11.20: 9–13, *B. serra* 1937.10.4: 6–11(D,S), *B. setivemensis* 1905.11.28: 59(S), *B. sharpeyi* 1920.3.3: 71–75(D), *B.* (= *Puntius*) *sophore* 1889.2.1: 777–782(D), *B. subquincunciatus* 1934.10.29: 1(D), *B.* (= *Tor*) *tambroides* 1982.4.21: 39(D), *B. tenuis* 1975.12.29: 250–265(D), *B. thalamakanensis* 1976.3.18: 363–550(D), *B.* (= *Puntius*) *titteya* 1974.6.11: 8–12(A), *B.* (= *Tor*) *tor* 1893.6.30: 31–38(D), *B. trimaculatus* 1907.4.9: 98(S), *B. tropidolepis* 1936.6.15: 599–629(A), *B. xanthopterus* 1973.5.21: 198(D).

Species without a suffix and those cited in the text but not listed above have been examined by X-Radiography only.

## Nomenclature

Because the concept of cyprinid subfamilies and other higher categories used here differs from that of previous authors (see Discussion) I have adopted the following nomenclature.

Subfamily Cyprininae (cyprinines): a monophyletic assemblage (see text) which includes the following subgroups:

\*barbins: a possibly monophyletic group, the members of which possess a foraminate dilatator fossa (see text and Table 3 for included taxa). This group embraces, in part, the Barbinae and Barbini of previous authors.

\*labeins: a monophyletic group *sensu* Reid, 1982 and 1985; includes Labeinae, Labeini, Labeoinae and Garrini of previous authors.

\*squaliobarbins: a monophyletic group *sensu* Howes, 1981.

\*schizothoracins: a supposed monophyletic group (see text); the Schizothoracinae and Schizothoracini of previous authors.

\*other cyprinines: an unresolved assemblage of taxa not included in any of the above categories and lacking a foraminate dilatator fossa (see text and Table 3).

Subfamily Leuciscinae (leuciscines): a possibly non-monophyletic assemblage including Abraminae, Cultrinae etc. of previous authors.

After this paper had been submitted for refereeing, my attention was drawn to a publication by Chen *et al.* (1984). These authors have proposed an hypothesis of cyprinoid relationships whereby they recognise the Cyprinidae as comprising two 'series', the Barbini and Leuciscini. They further recognise two monophyletic groups (tribes) within the Barbini, *viz.* Barbines and Tincanes, of

which the Tincanae, Cyprininae, Barbinae and Labeoninae (*sic*) are the constituent lineages. My concept of Cyprininae corresponds to Chen *et al.* 'Barbini', whilst my subgroups embrace their subfamilies.

The appellations 'small' and 'large' are often given to African *Barbus* species. As used here, 'small' refers to those species in which the striae on the exposed part of the scale are radiate, the fish usually less than 150 mm SL adult size, and the body often marked with spots or lateral stripes; 'large' refers to those species in which the scale striae are more or less parallel, the fish more than 150 mm SL adult size, and the body lacking any noticeable markings.

### Abbreviations used in the figures

aa	anguloarticular	lef	lateral ethmoid facet
abr 1	1st branched anal fin ray	llen	lateral ethmoid-entopterygoid ligament
afsl-3	anal fin rays (unbranched)	loc	lateral occipital fenestra
ah	anterohyal	me	mesethmoid
asn	anterior supraneural	met	metapterygoid
at	anal tube	mp	masticatory plate of basioccipital
bb	basibranchials	nc	neural complex
bh	basihyal	nca	neural canal
bo	basioccipital	ns4	neural spine of 4th centrum
bp	basioccipital process	nspu <sub>2</sub>	neural spines of 2nd preural centrum
bsr	branchiostegal ray	op	operculum
cb	ceratobranchials	os	orbitosphenoid
ccf	coracoid-cleithral foramen	ov	oviduct
cl	cleithrum	pa	parietal
cor	coracoid	pc	parietal canal
csi	cavum sinus imparis	pcl	postcleithrum
ct	connective tissue	pe	preethmoid
de	dentary	ph	posterohyal
df	dilatator fossa	phy	parhypural
dfo	dilatator foramen	po	preoperculum
dfs	dorsal fin rays	poc	preopercular canal (bone enclosed)
dh	dorsohyal	pro	prootic
eb	epibranchials	ps	parasphenoid
ect	ectopterygoid	pte	pteric
enf	ectopterygoid facet	pts	pterosphenoid
ent	entopterygoid	ptt	posttemporal
epf	entopterygoid-palatine facet	qf	quadrate facet
ep	epural	ra	retroarticular
epo	epioccipital	rp	proximal radials
fc	frontal canal	sb	splenic bone
fm	foramen magnum	scc	subcutaneous canal
fr	frontal	sep	scapula
frl	frontal lamina	se	supraethmoid
hb	hypobranchial	so	supraoccipital
hmf	hymandibular fossa	sop	suboperculum
hs	haemal spine	sor	supraorbital
hyo	hyomandibula	sp	sphenotic
hyp	hypurals	spr	sphenotic process
hys	hypurapophysis	srp	supraethmoid rostral process
ic	intercalar	sy	symplectic
ih	interhyal	vh	ventrohyal
int	intestine	vo	vomer
io	infraorbitals	I	olfactory nerve foramen
iop	interoperculum	II	optic fenestra
ip	infrapharyngobranchials	V	trigeminal nerve foramen
lac	lachrymal	VII	facial nerve foramen
lct	lachrymal canal tube	IX	glossopharyngeal nerve foramen
le	lateral ethmoid	X	vagus nerve foramen

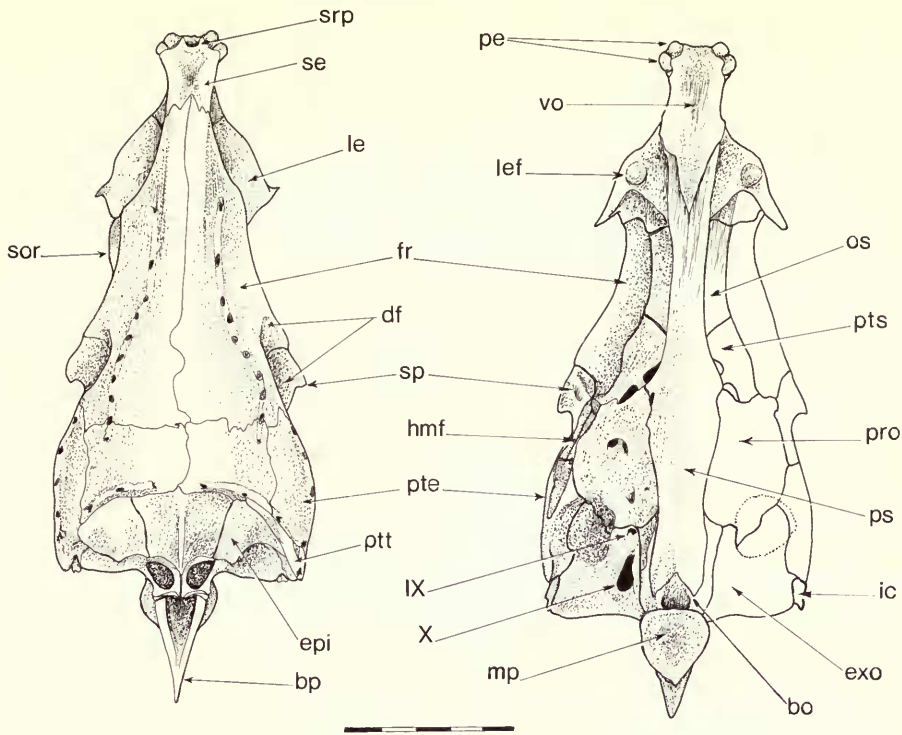


Fig. 2 *Aulopyge huegelii*, neurocranium in dorsal (left) and ventral (right) views. Scale bar in mm.

### Anatomical characters in *Aulopyge* and their phylogenetic significance

The cranium of *Aulopyge* is shown in Figs 2 and 3. In general appearance it is depressed and elongate. The ethmoid region is narrow and shallow, the supraethmoid bearing a sloped, valley-like depression and anteriorly having slight lateral expansions and a short rostral extension which is medially indented (srp, Fig. 2). The kinethmoid (Fig. 4d) is of the rod-shaped type considered by Howes (1978; 1981) as plesiomorphic for cyprinoids. Each lateral ethmoid is extended medially along the parasphenoid and contacts its partner, their being no anterior myodome. Laterally, each bone extends a narrow, posteriorly pointing wing which ventrally bears a well-developed round facet against which the entopterygoid facet articulates (lef, Fig. 2). This is an unusual feature and is discussed further below.

The frontals are narrowed anteriorly and nasal bones are absent; the supraorbital bones are small but not excessively reduced. Otherwise, the cranium of *Aulopyge* exhibits no features which may be regarded as anything but plesiomorphic among cyprinoids, viz.: the prootic is elongate with a long lateral commissure, the subtemporal fossa is round and deep, there is no posttemporal fossa, and the basioccipital has a short posterior process and small, round masticatory plate (Figs 2 & 3).

Likewise the jaws and elements of the suspensorium (Fig. 4), other than the entopterygoid (discussed below), show no departure from the 'generalised' cyprinoid morphology (see Howes, 1978, 1981, 1984).

### The lateral ethmoid and its articulation with the entopterygoid

The presence in *Aulopyge* of a facet, ventrally on the lateral ethmoid, apposing an entopterygoid facet is a feature which has a restricted distribution amongst the Cyprinidae. Ramaswami (1955) drew attention to a mesial entopterygoid facet articulating with the lateral ethmoid in *Labeo*

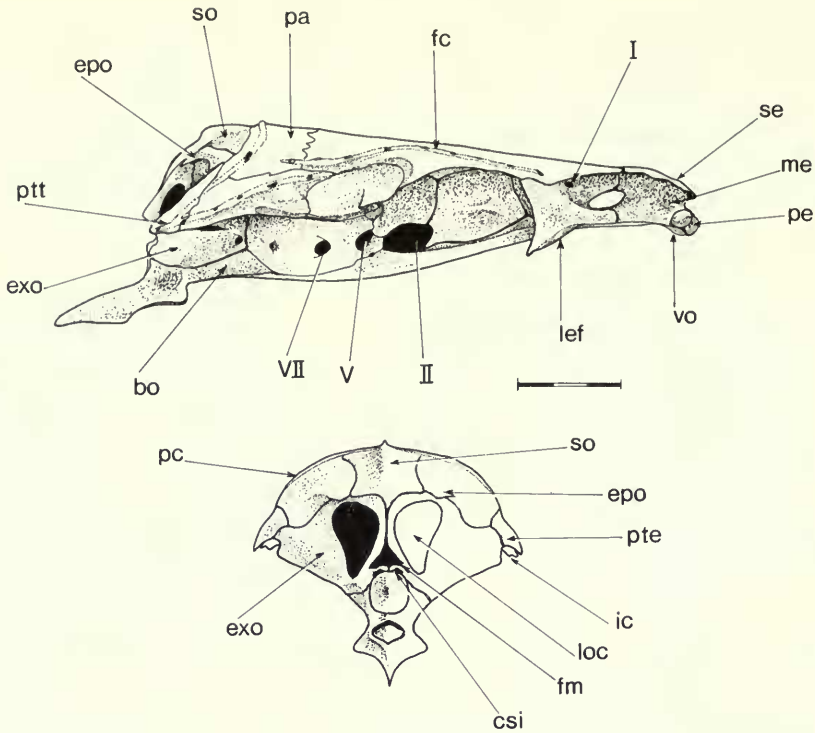


Fig. 3 *Aulopyge huegelii*, neurocranium in lateral (above) and posterior (below) views. Scale bar in mm.

*macrostoma* and *Cyprinus carpio*. Howes (1976: 46) noted that such a facet was variously developed in cyprinids, supposing it best developed in those species with a long ethmoid region and least in those with a short ethmoid. However, further investigation has not endorsed this claim and it appears that the presence of an entopterygoid facet is not positively correlated with the length of the ethmoid. Its presence seems to require a purely phylogenetic rather than a functional explanation. Thus, entopterygoid-lateral ethmoid facets occur only in taxa included in the Cyprininae, being absent, but for a single exception (*Tinca*; see below), in the Leuciscinae, (i.e. all non-barbelled cyprinids). The most highly developed form of this articulation occurs in some species of *Barbus*, *Cyprinus* and in the schizothoracin genus *Diptychus* (Figs 5 & 6).

In *Cyprinus*, the ventral surface of the lateral ethmoid wing is broadly triangular with the ventral articular facet situated antero-medially (Fig. 5b); the facet is sloped posteriorly and articulates against a round facet on the dorso-anterior border of the entopterygoid, just posterior to that bone's articulation with the palatine.

In *Barbus barbatus*, *B. nasus*, *B. plebejus*, *B. bocagei*, *B. meridionalis* and *B. barbulus* the lateral ethmoid facet is a large triangular platform (Fig. 5a). In some 'large' *Barbus* species, e.g. the Asian, *B. grahamsi*, *Barbus* (= *Tor*) *tor* and the North African, *B. setivemensis* the articular, boss-like facet is situated at the midpoint of the lateral ethmoid wing (Figs 6c–e). In all these species the entopterygoid facet is moderately developed. In yet other African and Asian 'large' *Barbus* species the lateral ethmoid facet lies along the posterior margin of the wing and in some taxa, e.g. the majority of 'large' African *Barbus* and *Varicorhinus* species, a distinct facet is barely developed, there being only a bevelling of the posterior border of the wing (Figs 5d & 6f). In these taxa an entopterygoid articulatory surface is feebly developed also (Fig. 5d). However, in the majority of African and Asian *Barbus* examined lateral ethmoid and entopterygoid facets are lacking. This appears to be the condition in all the so-called 'small' African *Barbus* species.

Amongst schizothoracins a lateral ethmoid facet is variously developed (Figs 6k–m), but in

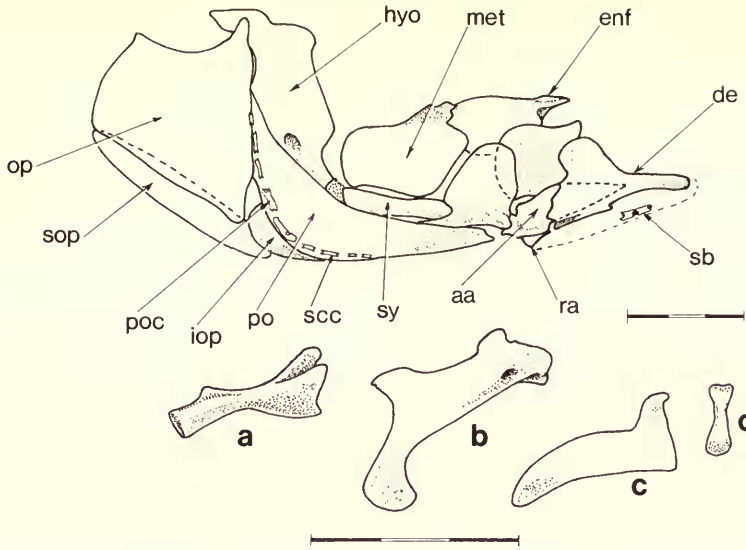


Fig. 4 *Aulopyge huegelii*. (Above) suspensorium in lateral view; (below), (a) palatine; (b) maxilla; (c) premaxilla; (d) kinethmoid. Scale bar in mm.

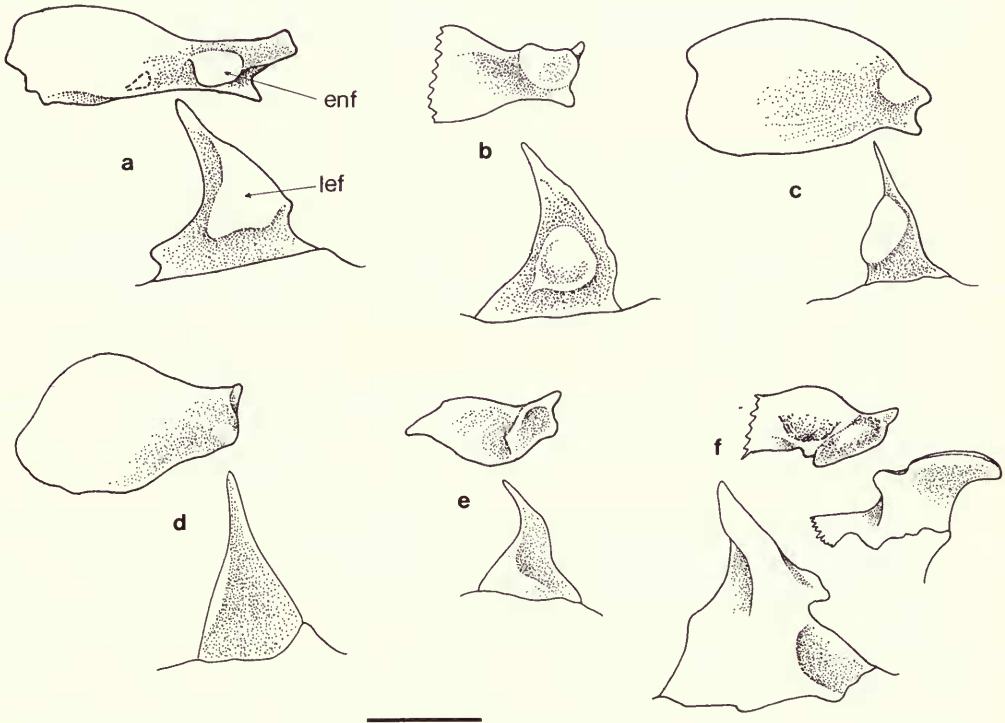


Fig. 5 Articular facets on the ventral surface of the lateral ethmoid wing and antero-dorsal surface of the entopterygoid in: (a) *Barbus barbuis*; (b) *Cyprinus carpio*; (c) *Tor putitora*; (d) *Barbus oxyrhynchus*; (e) *Tinca tinca*; (f) *Labeo coubie*, entopterygoid facet also shown in lateral view. In (a) dashed outline represents attachment area of lateral ethmoid ligament. Anterior to the left. Scale bar = 5 mm.

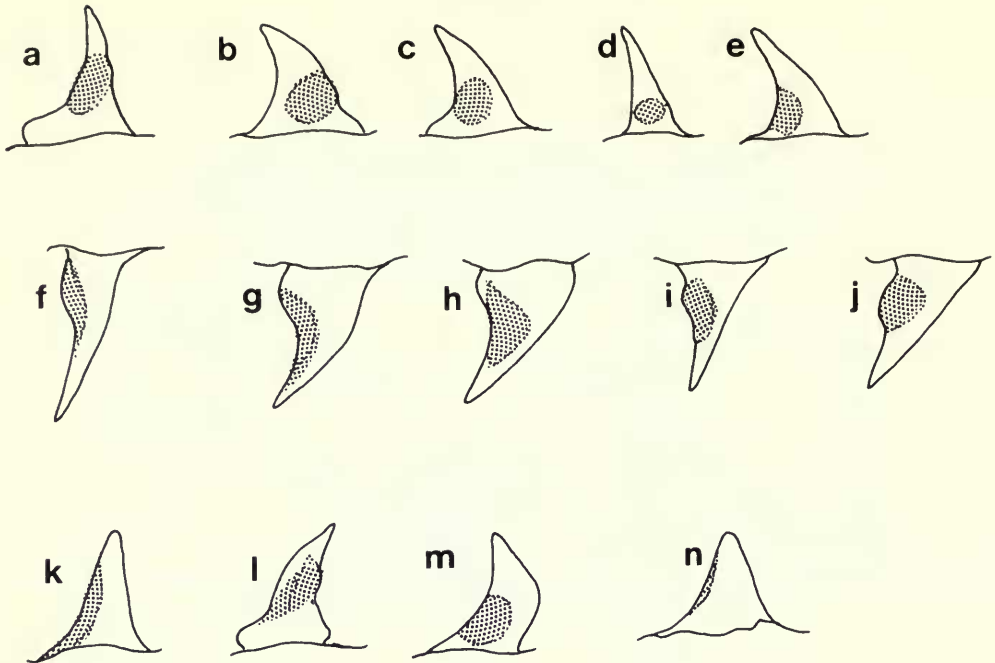


Fig. 6 Lateral ethmoid facets of: (a) *Ditychus dybowskii*; (b) *Barbus nasus*; (c) *B. grahami*; (d) *B. setivemensis*; (e) *B. lithopides*; (f) *Varicorhinus tanganicae*; (g) *Barbus callensis*; (h) *B. serra*; (i) *B. progenys*; (j) *B. canis*; (k) *Schizothorax grahami*; (l) *S. taliensis*; (m) *S. intermedius*; (n) *S. esocinus* and *S. richardsoni*. Semi-diagrammatic; all drawn to same scale; anterior to the left.

none, apart from *Ditychus* (Fig. 6a) is there a condition approaching that in the Eurasian *Barbus* species cited above, and an entopterygoid facet is rarely present.

In the squaliobarbins (*Squaliobarbus*, *Ctenopharyngodon* and *Mylopharyngodon*), a group considered as primitive cyprinines (see Howes, 1981, and Fig. 21), the lateral ethmoid articular surface is elongate, with a bevelled anterior margin against which abuts the posterior edge of the palatine. The entopterygoid articulates only with the posterior rim of the lateral ethmoid wing as in some 'large' African *Barbus* described above.

In labeins, *Labeo* (*sensu* Reid, 1985) has an extensive lateral ethmoid whose ventral surface bears a fossa which cups an entopterygoid condyle (Fig. 5f). *Garra*, on the other hand, has a narrow lateral ethmoid wing, which is only connected ligamentously with the entopterygoid.

Lateral ethmoid and entopterygoid facets are also lacking in *Cyprinion*, *Gibelion* and *Capoeta*; whether this condition represents secondary loss or a plesiomorphic state is uncertain in the absence of recognised synapomorphies indicating the relationships of these taxa.

That there is a phylogenetic rather than a functional basis for the various types of articulatory surfaces among cyprinines is seemingly supported by the following observations.

In those taxa where there is a well-developed articulation between the two bones, e.g. *Cyprinus* and some Eurasian *Barbus* species, the anterior portion of the entopterygoid is almost horizontal (Figs 8a & b), and it is also horizontal in those taxa which have only a moderate articulation between these bones, e.g. some 'large' African *Barbus* and *Varicorhinus* species (Fig. 8c). In *Aulopyge*, where there are well-developed lateral ethmoid and entopterygoid facets, the entopterygoid slopes at an angle similar to that in taxa which lack such close articulation, e.g. *Schizothorax esocinus* (Fig. 8d). Thus, whilst the slope of the entopterygoid is correlated with cranial width (being horizontal in those taxa with the widest crania) there is apparently no correlation between slope (both in the horizontal and vertical planes) and the presence or absence of



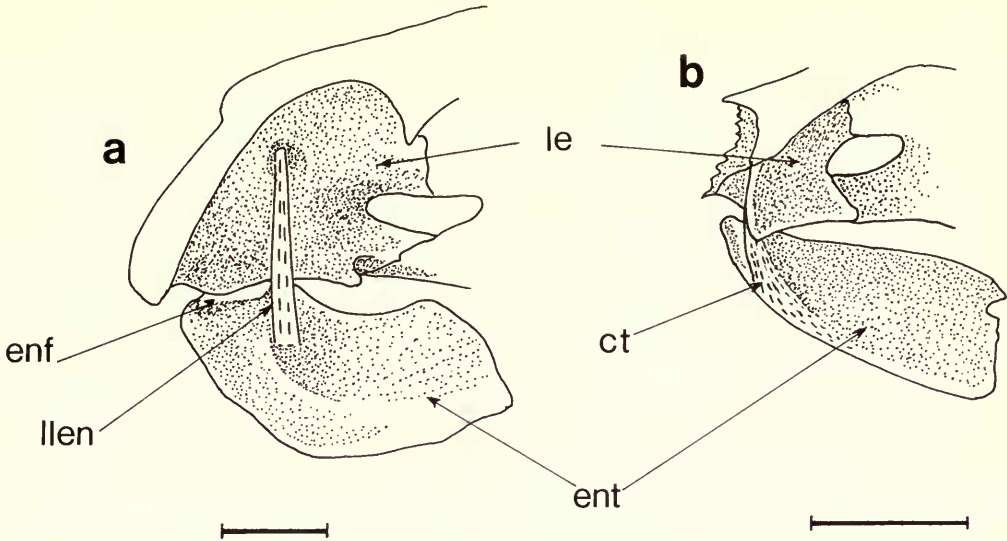


Fig. 7 Connection between the lateral ethmoid and entopterygoid in, (a) Cyprininae; *Barbus barbatus*, and (b) Leuciscinae; *Raiamas loati*. Scale bars = 3 mm.

articulatory surfaces. Even if one accepts this as evidence for the apomorphic status of articulatory facets, there is nothing to suggest which type of facet morphology is the more derived, be the extensive well-developed articulation of the Eurasian *Barbus* and *Cyprinus* or the less intimate connection of the African *Barbus* and *Varicorhinus* species.

It was noted above that all but one leuciscine taxon lack an articular connection between the lateral ethmoid and entopterygoid. Instead, the two bones are ligamentously connected and often the entopterygoid extends anterior to the lateral ethmoid (Fig. 7b). *Tinca* is the exception amongst leuciscines, in that the entopterygoid bears a distinct and deep fossa which articulates with a lateral ethmoid facet (Fig. 5e).

That articulatory lateral ethmoid and entopterygoid facets occur only amongst cyprinines further supports an internal division of the Cyprinidae, but whether this represents the derived condition, and if so, whether it is synapomorphic for those taxa in which the articulation occurs is problematic (see remarks above).

The types of ligamentous connection between the lateral ethmoid and the entopterygoid support the subfamilial division of the Cyprinidae (see p. 166 and Appendix 2). The widespread ostariophysan condition is for there to be a strong ligament running from the upper medial face of the lateral ethmoid wing to the dorsolateral surface of the entopterygoid (Fig. 7a; see also Vanderwalle, 1977, Fig. 4 of *Barbus barbatus*).

In all members of the subfamily Cyprininae investigated, apart from *Ctenopharyngodon*, there is a single, slender ligament connecting the bones; in *Ctenopharyngodon* a broad ligamentous band connects the bones. In the subfamily Leuciscinae a ligament of the type found in the Cyprininae is absent and connection between the lateral ethmoid and entopterygoid is via undifferentiated connective tissue. Vandewalle (1977) showed in *Leuciscus leuciscus* a ligament (labelled Li18) running from the edge of the lateral ethmoid to the entopterygoid. I find no such discrete ligament, but instead thickened connective tissue running to the lateral edge of the entopterygoid (Fig. 7b).

The widespread occurrence and constant position of the lateral ethmoid-entopterygoid ligament amongst ostariophysans suggests it is plesiomorphic and thus its absence in the Leuciscinae is considered a derived loss. It is interesting to note in this group, as compared with the Cyprininae, what appears to be an anterior shift of the entopterygoid head, and its somewhat looser connection with the palatine, features which may be associated with the absence of a ligamentous connection.

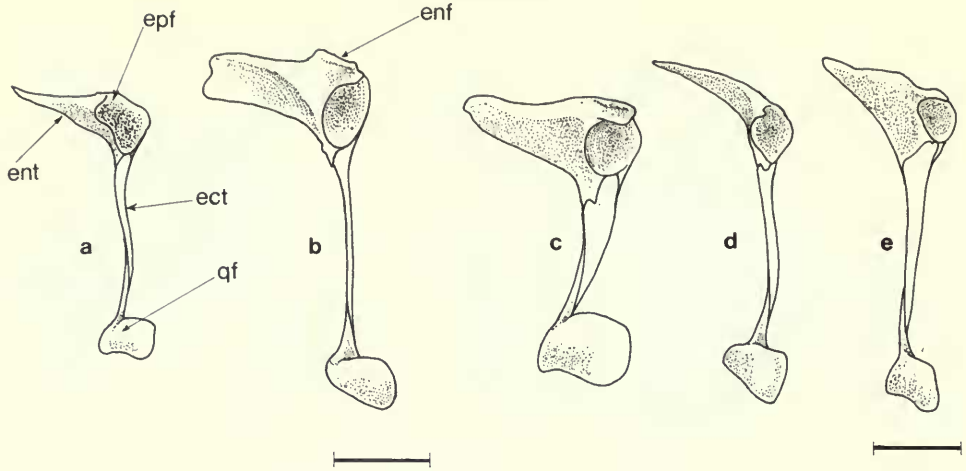


Fig. 8 Anterior views of the right suspensorium in; (a) *Cyprinus carpio*; (b) *Barbus barbatus*; (c) *Varicorhinus tanganicus*; (d) *Schizothorax esocinus*; (e) *Aulopyge huegelii*. Scale bar for a–d = 5 mm, for e = 1 mm.

### Sensory canals and their associated bones

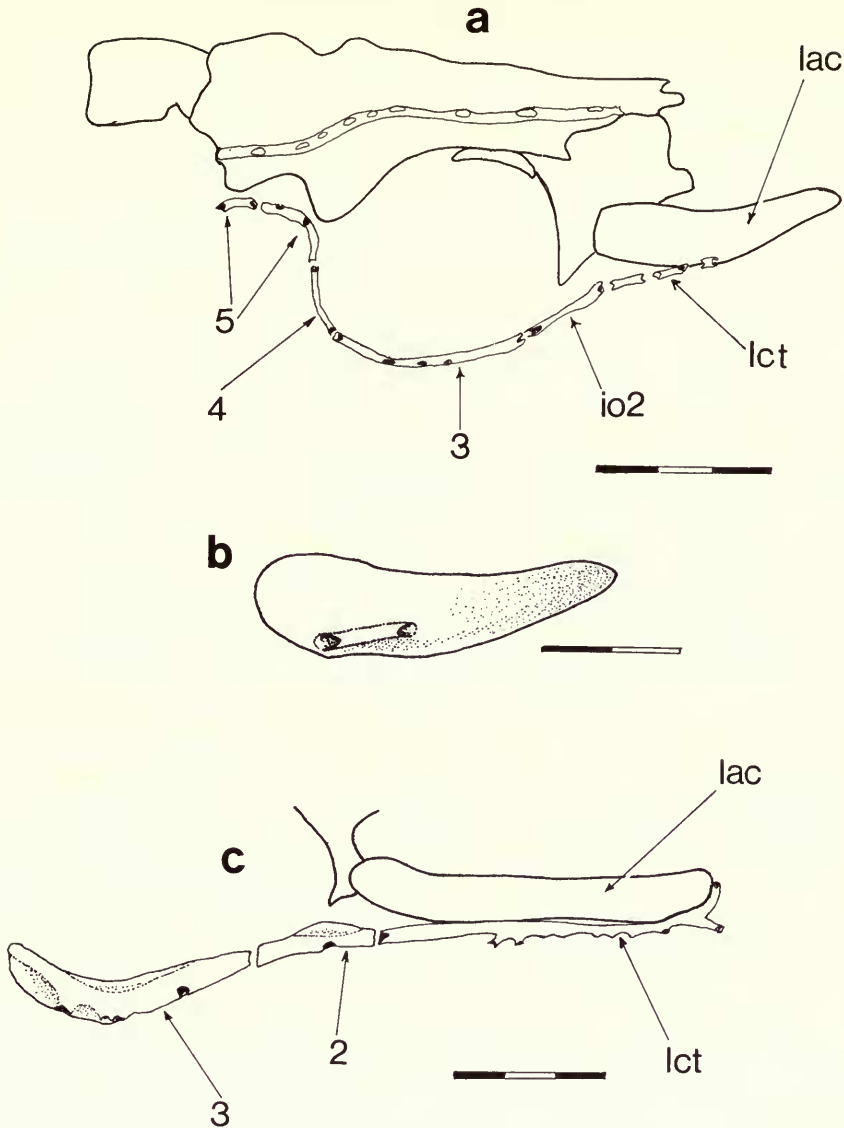
*Aulopyge* possesses the pattern of supraorbital canals corresponding to Illick's (1956) group IVAA, where a marked gap separates the supraorbital and infraorbital canal systems; the frontal and parietal canals are distant and the parietal canals are separated from one another by a midline gap. The dorso-cranial canals are bony tubes lying on the surface of their respective bones; the frontal canal contains 9–10 pores. The infraorbital series is reduced to bony tubes, the first and last infraorbitals being fragmented into several elements (Fig. 9a).

The most unusual feature of the *Aulopyge* infraorbital canal is its disassociation from the lachrymal (1st infraorbital, lac, Fig. 9a). In an alizarin stained specimen of 52 mm, the weakly ossified canal lies somewhat ventral to the well-developed elongate 'lachrymal' bone. This situation is evident in all the specimens of *Aulopyge* examined (60–127 mm SL) with the exception of an 84 mm SL female, where a bony canal tube is attached to the face of the lachrymal (Fig. 9b). Those portions of the canal posterior and anterior are epidermal.

The mandibular-preopercular canal is incomplete. Only a single, small tube lies below and separate from the dentary (Fig. 4). There is a short groove along the ventro-lateral border of the dentary, but no sign of a canal associated with the anguloarticular. The canal reappears as a series of weakly ossified, epidermal tubes along the posterior part of the preoperculum; at the point of curvature, the canal runs through the bone (poc, Fig. 4), then continues in three or four epidermal tubes, the last terminating close to the dorsal tip of the preoperculum.

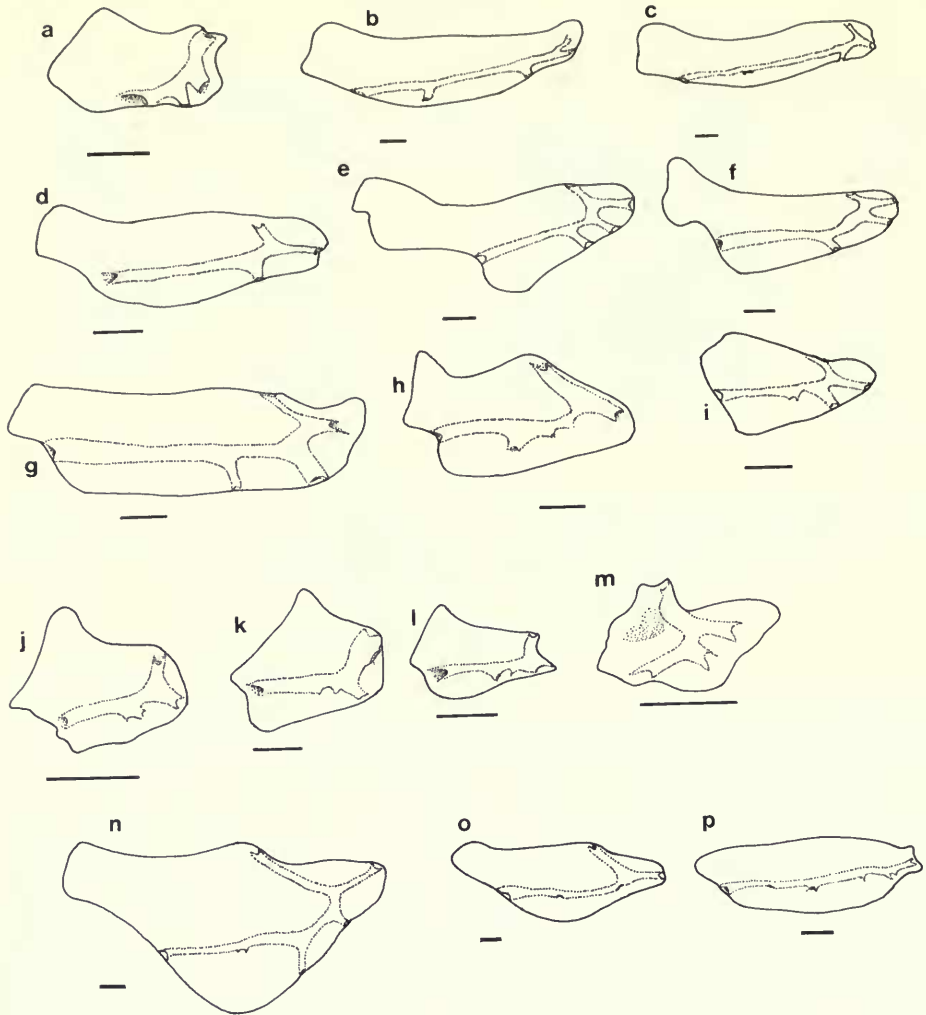
The development of cyprinoid sensory canals was studied by Lekander (1949) who summarised the results and theories of previous authors. Lekander showed that the sensory canals can, from the earliest ontogenetic stages either be united with their respective bone, later fuse with it, or remain separate from it. He drew particular attention to the 'antorbital' (= lachrymal of most authors) noting that in some cypriniforms, the canal remains separate from its lamellar portion. Such is the case in the Cobitidae, where there is apparently an antorbital, i.e. a bone lying antero-dorsal to the 1st infraorbital, while the elongate lachrymal is by-passed ventro-laterally by the subcutaneous sensory canal (Lekander, 1949; Parshall, 1983).

As in the adult *Aulopyge*, the developing infraorbital canals in some cyprinids often appear irregularly spaced and remain unfused to one another; a 'splenial' bone may be present (Lekander, 1949: 81), and the preopercular latero-sensory canal tubes remain separated from one another and from the preoperculum (Lekander, 1949: 95; 102; 112).



**Fig. 9** Infraorbital bones of *Aulopyge huegelii*; (a) complete series of 52 mm SL specimen; (b) the lachrymal of an 84 mm SL specimen with canal attached to the bone. (c) *Barbus barbulus*, showing disassociated lachrymal canal. Scale bars in mm.

Lekander (1949: 113) makes the point that sensory canals in cyprinids develop later than in most other teleosts he examined. Whether this is so or not, I observe a temporal difference in the development of the infraorbital canals between two species of *Barbus*. In specimens of *Barbus* cf. *paludinosus* of 17 mm SL the sensory canal of the 1st infraorbital (lachrymal) is present in the bone although it does not become completely enclosed until 24 mm SL. However, in *Barbus barbulus* of 25 mm SL, the canal is subcutaneous and well-separated from the membranodermic part of the lachrymal. These species are respectively, tropical and temperate, and small and large sized. Thus, the variation in canal development may reflect the different temperature and hormonally controlled growth rates. In an adult specimen of *Barbus barbulus*, the posterior part of the canal lies subcutaneously, whereas the anterior part is attached to the lachrymal (Fig. 9c).



**Fig. 10** Lachrymal (1st infraorbital) bones of; (a) *Barbus barbatus* of 66 mm SL; (b) *B. barbatus*, adult; (c) *B. comiza*; (d) *B. plebejus*; (e) *B. capito* (also in *B. sclateri*); (f) *B. bocagei* (also in *B. albanicus*); (g) *B. longiceps*; (h) *B. grypus* (also in *B. canis*, *B. sharpeyi*, *B. reinii*); (i) *B. intermedius intermedius*; (j) *B. trimaculatus*; (k) *B. altus*; (l) *B. callipterus*; (m) *Labeo coubie*; (n) *B. mursa*; (o) *B. serra*; (p) *B. andrewi*. Scale bars = 1 mm.

If Lekander (1949) is correct in recognising three distinct types of association between the laterosensory and membranodermic parts of the canal bones (at least amongst cypriniforms), then it may be that these represent arrest at successive ontogenetic stages. In this case, that exhibited by *Aulopyge* and some cobitids where the sensory and membranodermic components are separate represented the earliest, whilst that in which they are united, as in *Leuciscus*, would represent the most advanced ontogenetic stage.

The lachrymal in *Aulopyge* is virtually oblong in lateral view being somewhat tapered anteriorly. In most cyprinids the lachrymal is a deep, triangular or pentagonal bone, as in *Cyprinus*, *Labeo* and the majority of *Barbus* species (Figs 10i–m). In some Eurasian *Barbus* species, however, the lachrymal has the same oblong shape as in *Aulopyge*, and the sensory canal also runs in the ventral part of the bone. In this latter respect the Eurasian species also differ from other African and Asian *Barbus* where the canal runs centrally through the lachrymal (Fig. 10k). In *Barbus barbatus*, one of

the species with an oblong lachrymal in adults, there is a marked ontogenetic change in the bone's shape. In a specimen of 66 mm SL, it is almost square with a short, dorsally curved sensory canal (Fig. 10a). In adults, the bone is elongated, with a greatly lengthened canal (Fig. 10b), the anterior part of the canal having become more deeply forked and an additional pore developing at the posterior elongation of the canal.

The adult lachrymal morphology of *Barbus barbatus* resembles that characteristic of certain other Eurasian species (Figs 9c, 10c, d, f & g). A variant of this condition is found in the Middle-eastern species *B. canis*, *B. sharpeyi*, *B. grypus*, *B. reinii* and the Asian *Barbus* (= *Tor*) *tor*, where the anterior part of the sensory canal runs close to the anterior border of the bone, and the dorsal border is concave (Fig. 10h).

It is difficult to evaluate the shape of the lachrymal as a phylogenetic character. Skelton (1980) pointed out that the South African West Cape species *Barbus andrewi* and *B. serra* possess a lachrymal of the same elongate form as that of the Eurasian species. However, the lachrymal of these two species differs from that in the Eurasian taxa in having the ventral border convex rather than straight (Figs 10o & p); see also p. 195.

My own comparisons permit the following generalisations:

\*in all Leuciscinae the lachrymal has a square or even rounded, never elongate shape, even in those species with a relatively long ethmoid region (e.g. *Elopichthys bambusa*; Fig. 12A in Howes, 1978).

\*in *Barbus* there is some degree of 'intermediacy' in shape between such forms as *B. trimaculatus* and *B. altus* (Figs 10j & k) and the *B. canis* type (Fig. 10h) exemplified by *B. oxyrhynchus* and *B. intermedius* (Fig. 10i).

\*there is a distinct (?apomorphic) type characterising a group of Eurasian *Barbus* species; see above.

### Vertebral column, dorsal and anal fins

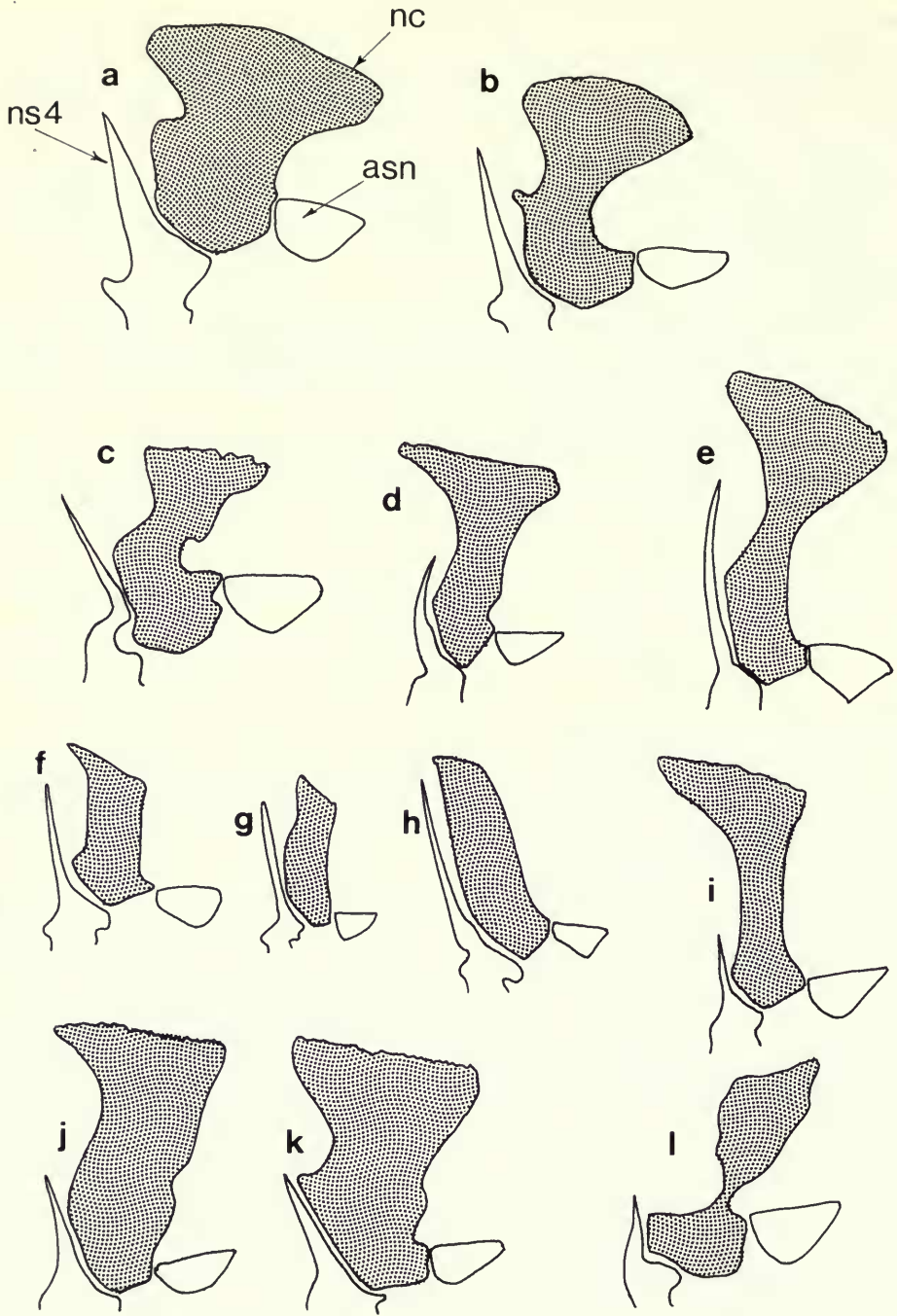
The general morphology of the Weberian ossicles and centra of *Aulopyge* resembles that of *Barbus barbatus*. In both taxa the neural complex is low, with a concave anterior border. Its posterior border is irregular and widely separated from the 4th neural spine, which is almost half the height of the neural complex and is inclined posteriorly.

*Neural complex.* The comparative morphology of the cyprinid neural complex has not been subject to any detailed treatment and from the following perfunctory observations appears worthy of closer study. The so-called 'neural complex' in cypriniforms is a supraneural having synchondral contact with the 3rd and 4th neural arches. There is usually a long gap between the supraoccipital and the neural complex and only rarely are they in close contact (see Reid, 1985). Within the Cyprinidae, two morphotypes of neural complex are recognisable (briefly described in Howes, 1981: 29–30; see also Chen *et al.*, 1984); these can be correlated with the subfamily division already recognised as Cyprininae and Leuciscinae (see above and Appendix 2).

In Cyprininae, the neural complex is most often tall, axe-shaped and lamellate, with a vertical or forwardly inclined anterior border and without a grooved dorsal surface. The 4th neural spine is rarely as high as the neural complex, most often being half or less than half its height and narrowly separated from it. The first free supraneural never articulates directly with the neural complex.

In Leuciscinae, the neural complex is most often low, oblong or square, vertically or backwardly inclined; its dorsal surface contains a groove, and in some taxa, the neural complex is deeply forked (Howes, 1981, Fig. 22); the 1st free supraneural articulates with the groove (Howes, 1978: 19; Fig. 13). The 4th neural spine is most often as tall as the neural complex and may be widely separated from it.

The morphology of the neural complex is variable within the Cyprininae, but from the data at hand it is possible to make a broad and tentative classification. Within *Barbus*, the 'small' species examined (*B. radiatus*, *B. paludinosus*, *B. perince*, *B. leonensis*, *B. hulstaerti*) and some Asian taxa (including *B.* (= *Puntius*) *sophore*) possess a tall, oblong neural complex, either vertical or sloping backward and narrowly separated from the 4th neural spine which is the same height as the neural complex (Figs 11f–l).



**Fig. 11** Neural complex (shaded) and position of 4th neural spine in (a) *Aulopyge huegelii*; (b) *Barbus barbuis*; (c) *B. plebejus*; (d) *B. altianalis radcliffi*; (e) *Cyprinus carpio*; (f) *Barbus paludinosus*; (g) *B. perince*; (h) *Puntius sophore*; (i) *Barbus marequensis* ('long-head morph'); (j) *Varicorhinus steindachneri*; (k) *V. ensifer*; (l) *Schizopygopsis stoliczkae*. Drawings made from radiographs, all to approximately the same scale.

Within the 'large' *Barbus* species, as in other Cyprininae, the neural complex is tall and axe-shaped. Its relationship to the 4th neural spine is variable. In some taxa the spine is short and curved forward, e.g. *B. intermedius*, *B. arabicus*, *B. altianalis* (Fig. 11d), *B.* (= *Tor*) *putitora*, *Carassius auratus*, or long and curved forward, e.g. *Cyprinus carpio* (Fig. 11e), *Cyclocheilichthys*, or short, vertical or sloping backward, e.g. majority of 'large' African *Barbus* (Fig. 11i), and some Asian *Barbus*. In some *Varicorhinus* species the spine is minute and barely developed as is also the case in *Cyprinion* species (see Howes, 1982). In all these taxa, however, the 4th neural spine is closely apposed to the posterior border of the neural complex (Fig. 11j).

As noted above, the neural complex of *Aulopyge huegelli* and *Barbus barbatus* exhibit another morphotype (Figs 11a & b), being squat to oblong with a concave anterior border and an indented posterior border leaving a wide gap between it and the 4th neural spine. Other taxa with this morphology are the Eurasian, Middle-eastern and Chinese *Barbus* species *plebejus*, *nasus*, *meridionalis*, *barbulus*, *schejch*, *subquincunciatus* and *grahami*. An exaggerated variant of this condition occurs among the schizothoracin genera *Schizocypris* (Fig. 11l), *Diptychus*, *Gymnocypris* and *Schizothorax*, where the neural complex is irregularly shaped and widely separated from a small 4th neural spine.

From this limited survey it cannot be said which of these is a derived morphotype. That characteristic of *Aulopyge*, some Eurasian and Middle-eastern *Barbus* and schizothoracins may simply be a correlate of the generally elongate and depressed bodies of those taxa. There is also a degree of intraspecific and ontogenetic variability. For example, the ontogenetic sequence of neural complex development in the 'large' African *Barbus intermedius* is at 21.5 mm SL (Fig. 12a) that of the adult morphology (almost identical to that of *B. altianalis*, shown in Fig. 11d) in which the complex is narrowly separated from the 4th neural spine. At 25 mm SL the neural complex is tilted forward, is relatively taller and has a large gap separating it from the neural spine. At 31 mm SL the neural complex is upright and the 4th neural spine is tall and narrowly separated from it.

The four ontogenetic stages shown in Fig. 12 of specimens 21.5, 23.5, 25.0 and 31.0 mm SL seem to reflect four of the similar adult morphotypes described above.

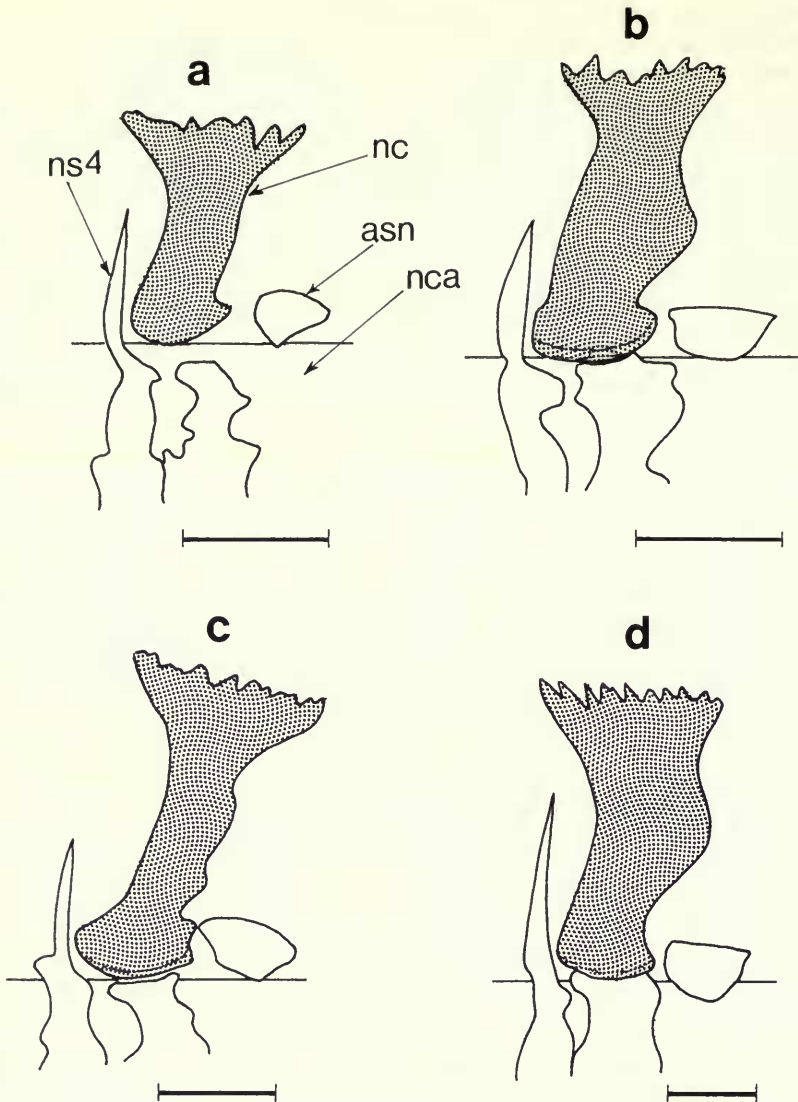
To summarise the conditions of the neural complex among cyprinines:

- \*tall and oblong with long 4th neural spine—in 'small' African *Barbus* and (?all) Asian *Puntius*
- \*tall and axe-shaped with 4th neural spine closely apposed—in 'large' African and Asian *Barbus* and most other cyprinines, subgrouped as:
  - 4th neural spine short—some African *Barbus* and other cyprinines
  - 4th neural spine long—most African and Asian *Barbus*
  - 4th neural spine minute—*Varicorhinus* and *Cyprinion*
- \*low, oblong or square with irregular anterior and posterior borders and with 4th neural spine widely separated posteriorly—in *Aulopyge*, Eurasian *Barbus* and schizothoracins

*Vertebral number.* *Aulopyge* has a total of 37–38 vertebrae, of which 10 (including the four Weberian vertebrae) are pre-dorsal, i.e. the neural spine of the last vertebra in the set lies in front of the 1st dorsal pterygiophore. This total vertebral number lies within the modal range for Cyprininae.

In a sample of 46 'large' African *Barbus* species the range is 36–42, of which 20 species have a range of 9–11 pre-dorsal vertebrae, 4 species have 11–12 (*oxyrhynchus*, *somereni*, *mariae* and *ethiopicus*) and the remaining 22 species have 13–17. These latter species, apart from the South African Cape *B. serra* and *B. andrewi*, are European and Middle-eastern species (Table 1). Schizothoracin genera have both higher total (46–48) and pre-dorsal (13–17) vertebral numbers (Table 2). In other Cyprininae, the numbers of pre-dorsal vertebrae rarely exceed 10; in *Cyprinion* there are 8–12, in *Cyprinus* 9–10, *Gibelion* 8 and *Catlacarpio* 8–9. In labeins, *Garra* has 9–12, and *Labeo* has 8–9. Squaliobarbin taxa also have a high pre-dorsal number, 10–12.

Skelton (1976) recorded the vertebral numbers in four groups of African *Barbus*, groupings made on the basis of scale striae pattern and degree of ossification in the last unbranched dorsal fin ray. He found higher counts in the group with parallel striated scales and with the dorsal fin ray ossified and smooth, a group to which belong the 'large' African *Barbus* species cited above.



**Fig. 12** *Barbus intermedius* Ontogenetic development of the neural complex, at (a) 21.5 mm SL; (b) 23.5 mm; (c) 25 mm; (d) 31 mm. Scale bars = 0.5 mm.

Following Lindsey's (1976) broader discussion of pleomerism, Skelton (1980) pointed out that Jordan's rule (the correlation of increased vertebral number with higher latitudes) may be a factor when considering, for example, the endemic high-latitude, high-altitude redfin '*Barbus*' which have a more frequently occurring range (36–38) than species of 'small' African *Barbus* (31–38). Skelton argues that such specialisation signifies that the higher vertebral number represents a synapomorphy, one he uses to recognise the redfin '*Barbus*' as a monophyletic group.

In the Cyprininae, the total vertebral number never exceeds 48, and the modal range is 38–40; in the Leuciscinae the total range is greater, being 33–61, as is the modal range of 40–45 (see Howes, 1978, Table 1). Perhaps more significant is the consistently higher range of pre-dorsal vertebrae in Leuciscinae, 10–19 *versus* 9–14 in Cyprininae. Howes (1978; 1984) considered a high number of vertebrae as a synapomorphy for the aspinin group of leuciscine cyprinids, since the range for this group exceeds that of other leuciscines in both abdominal and caudal vertebrae.

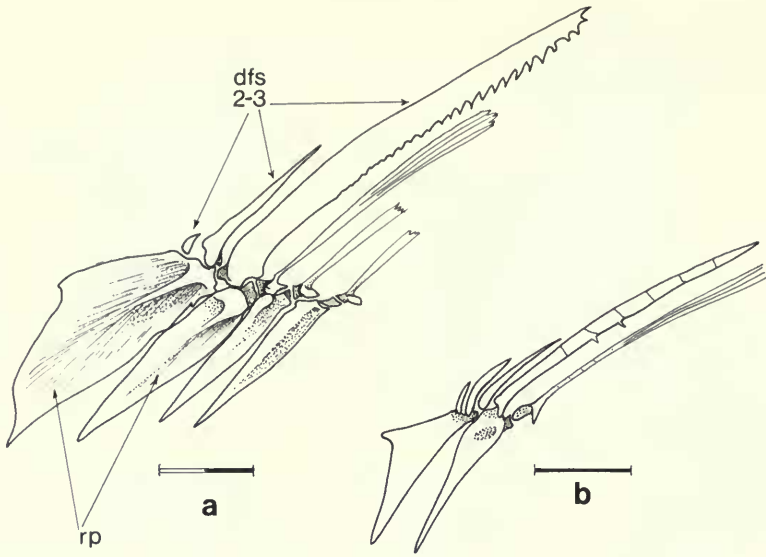


**Table 1** Vertebral and lateral line counts in *Barbus* species having high total and pre-dorsal numbers of vertebrae and lateral line scales, and having a serrated last unbranched dorsal fin ray. In '*Barbus*' species with a pre-dorsal vertebral count of 9–11, the total count rarely exceeds 43.

Species	Total	Pre-dorsal	Lateral line scales
<i>albanicus</i>	44	14	57
<i>andrewi</i>	38–40	14–16	38–40
<i>barbulus</i>	44	13	52–54
<i>barbus</i>	46	14	55–63
<i>bocagei</i>	42–44	14–15	45–49
<i>brachycephalus</i>	47	11	63
<i>capito</i> (including specimens labelled as <i>kersin</i> )	42–45	13	57–65
<i>comiza</i> (syntypes)	43	12	48–50
<i>esocinus</i>	48	14	76–78
<i>graellsii</i>	42–43	14	47–52
<i>grypus</i>	44–47	13–14	40
<i>lacerta</i>	43	13	55–63
<i>longiceps</i>	43–44	13–14	51–60
<i>meridionalis</i>	40	13	48–60
<i>mursa</i>	43	14	90–97
<i>nasus</i>	43–44	13–14	49–78
<i>plebejus</i>	41–42	13–14	49–78
<i>rajanorum</i> (including specimens labelled as <i>schejch</i> )	45–46	13–14	57–65
<i>sclateri</i> (syntypes)	42	12	46–47
<i>serra</i>	39–41	14–17	42–43
<i>sharpeyi</i> (lacks serrated last dorsal spine)	40–42	13–14	30–31
<i>subquincunciatus</i>	45	13–14	80–84
<i>xanthopterus</i>	44	13	58–60

**Table 2** Vertebral counts in a selection of schizothoracins.

Species	Total	Pre-dorsal
<i>Diptychus dybowski</i>	48	13
<i>Diptychus maculatus</i>	49	14
<i>Gymnocypris</i> sp.	46	14
<i>Schizothorax dipogon</i>	49	15
<i>Schizothorax esocinus</i>	46–47	16
<i>Schizothorax chrysochlorus</i>	42	14
<i>Schizothorax grahami</i>	47	16
<i>Schizothorax intermedius</i>	48	14
<i>Schizothorax richardsoni</i>	46	15
<i>Schizothorax prenanti</i>	46	15
<i>Schizothorax sinuatus</i>	48	16–17
<i>Schizothorax yunnanensis</i>	46	15
<i>Schizopygopsis stoliczkae</i>	48	15



**Fig. 13** Unbranched dorsal fin rays of, (a) *Aulopyge huegeli*, 115 mm SL; (b) *Barbus barbatus*, 24 mm SL (cartilage stippled); scale = 1 mm.

It is difficult to assign polarity to vertebral number for other groups of cyprinids because,

\*there is a continuum from the relatively low numbers in Cyprininae to the higher numbers in Leuciscinae

\*there is the phenomenon of pleomerism (see Lindsey, 1975)

\*vertebral numbers may be influenced by latitudinal position and temperature changes (see Lindsey, 1975; Lindsey & Arnason, 1981).

Lindsey (1975) commented that the Catostomidae display significant pleomerism among its species, but not in the family as a whole. The same observation can be applied to the Cyprinidae, where deep-bodied genera such as *Cyprinion* and *Megalobrama* have similar maximum lengths to those of cylindrical, depressed or compressed and slender forms, but possess lower vertebral numbers.

*Dorsal fin and serrated unbranched dorsal fin ray.* In *Aulopyge* the first (reduced) dorsal fin ray lies on a vertical just anterior to the base of the pelvic fin and above the 15th vertebra.

In those *Barbus* with a high number of pre-dorsal vertebrae the 1st dorsal fin ray lies above the 16th–18th vertebra and above or somewhat anterior to the origins of the respective fins. In the majority of the Cyprininae, the dorsal fin lies:

\*above or anterior to the origin of the pelvic fins.

\*rarely posterior to the pelvic fin origin, (e.g. '*Labeo*' *stoliczkae*, *Barbus paludinosus*, *B. serra*, some *Puntius* species).

In the Leuciscinae, however, only exceptionally does the dorsal fin originate in advance of the pelvics, (e.g. *Pogonichthys*). In both Cyprininae and Leuciscinae there are several taxa where the dorsal fin origin is immediately above the pelvic fin insertion. Such a situation occurs in both basal leuciscines with short, cylindrical bodies, (e.g. *Opsariichthys*, *Zacco*) and those with elongate, compressed bodies, (e.g. *Salmostoma*, *Macrochirichthys*). In cyprinines, this generalised position of the dorsal fin is present in many 'large' and 'small' African *Barbus* species. Skelton (1980) considered a dorsal fin posteriorly placed in relation to the pelvics as a synapomorphy uniting serrated-dorsal fin rayed redfin *Barbus* species. However, if one assumed the Cyprininae to be the derived sister-group of the Leuciscinae, such a posterior dorsal fin position may indicate the

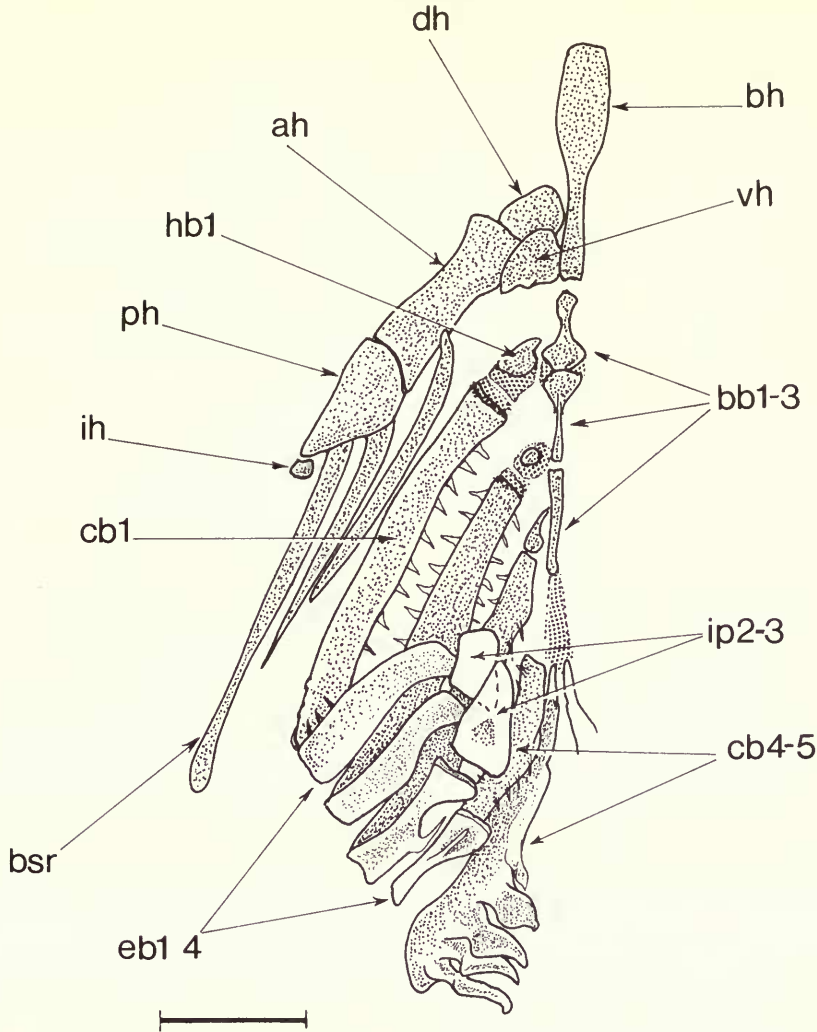


Fig. 14 *Aulopyge huegelii*, branchial arches of left side in dorsal view. Scale = 2 mm.

plesiomorphic condition. The forward placement of the dorsal fin in the Cyprininae, seen in its most extreme form amongst labeines, is more likely to be the derived state.

An analysis of the position of the 1st dorsal fin ray in relation to the vertebral column again reflects the major taxonomic grouping of the Cyprininae and Leuciscinae. In the majority of cyprinines, the 1st dorsal ray lies above the 11–18th vertebra (14–15th in *Aulopyge*), whereas in leuciscines, it may lie above any from the 16th to the 31st vertebra (modally between the 18th and 21st). The furthest posterior position of the 1st dorsal fin ray occurs in the chelin assemblage, where it lies above the 21st–26th vertebra in *Salmostoma* and the 30th–31st in *Macrochirichthys*. In the schizothoracins the 1st dorsal ray lies above the 17th–21st vertebra.

In *Aulopyge* there are 3 unbranched dorsal fin rays, the last being moderately serrated along its distal posterior border; there are 7–8 branched dorsal fin rays.

The number of unbranched dorsal fin rays preceding the 1st branched ray varies in the Cyprinidae from 2–6. Gosline (1978) found some significance in the numbers of unbranched dorsal

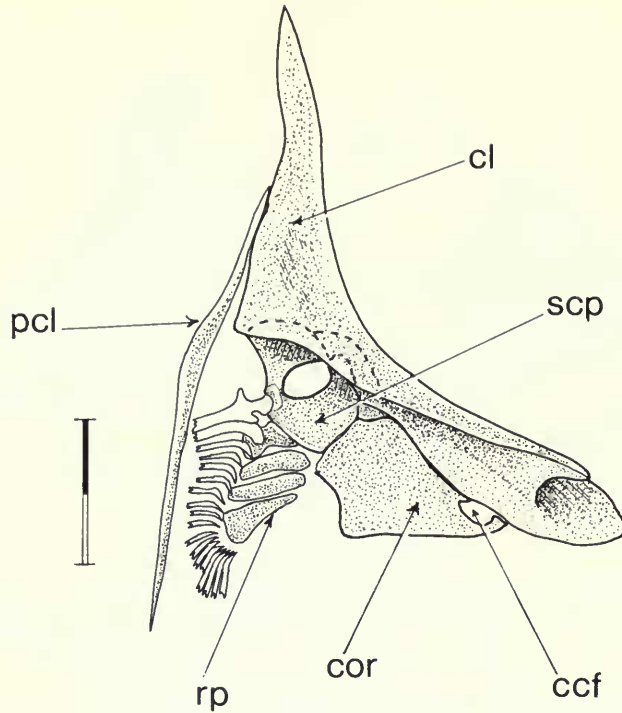


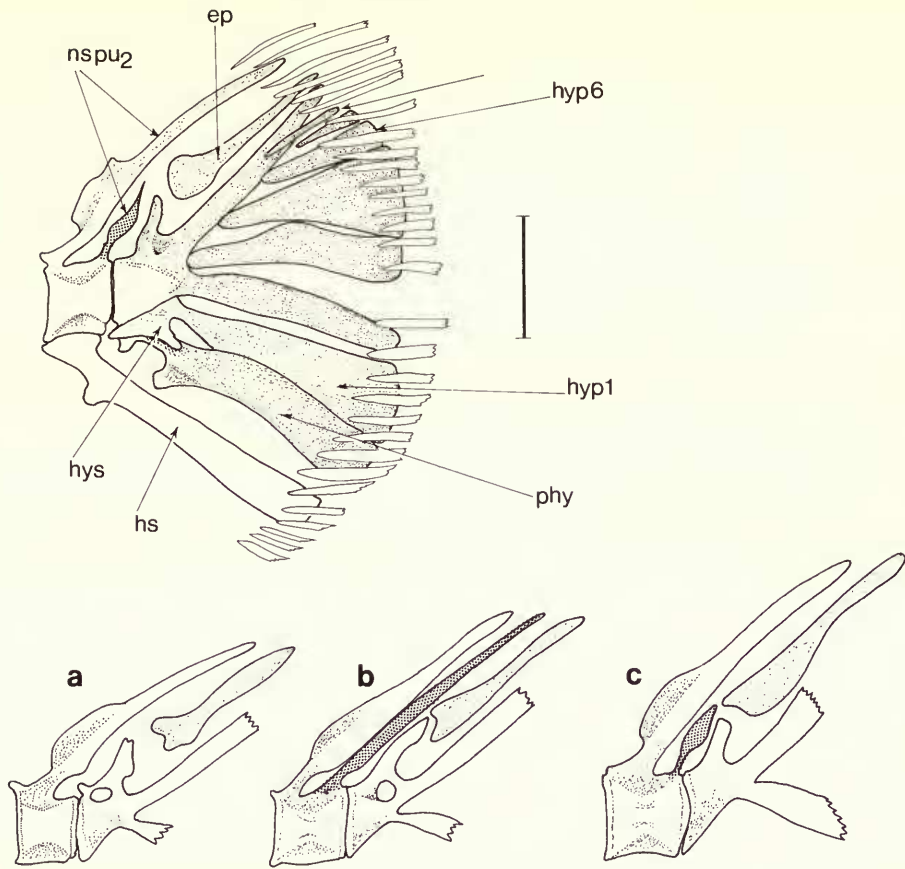
Fig. 15 *Aulopyge huegelii*, right pectoral girdle in lateral view. The (medial) positions of the mesocoracoid and part of the scapula are indicated by dashed lines.

fin rays, believing a modal count of 4 to be representative of the Cyprininae whilst 3 was present in '... other cyprinid subfamilies'. Although Gosline's subfamily concept differs from that presented here, I find his statement justified. A possible reason for there being a high number of unbranched dorsal fin rays in cyprinines may be correlated with the often marked ossification of the last such element. A large heavy spine-like ray, in order to remain rigid may require some anterior bracing in the form of several and strong elements in the fin.

Highly ossified dorsal rays rarely occur in the Leuciscinae, (e.g. *Capoetobrama*) and never bear serrations.

In the Cyprininae the last unbranched ray is always the largest but varies from flexible to heavily ossified, and may be smooth or serrated along its posterior margin. When present, a serrated ray may bear serrae over its entire or partial proximal length. A serrated dorsal ray occurs only in some species of the genera *Barbus*, '*Puntius*', *Schizothorax* and *Mystacoleucus*, while in other genera, such as *Acrossocheilus*, *Cyclocheilichthys* and *Cyprinus*, all species possess a serrated last unbranched dorsal ray.

Based principally on the classification of Boulenger (1911), Skelton (1976) recognised four group of *Barbus*, of which only one (Group III) contained species with a serrated dorsal fin ray. Within this group, the subgroup (IIIA) comprises the 'large' African *Barbus* and contains those species which also have relatively high total and pre-dorsal vertebral counts (see above, p. 179 and Table 1). The ranking of serrated dorsal fin rays as a synapomorphy is dubious since the feature has an irregular distribution among genera recognised as monophyletic, (e.g. *Cyprinion*; see Howes, 1982). However, it would be possible to test for the plesiomorphic nature of dorsal fin ray serrations by observing their presence in some ontogenetic stage of those taxa whose adults lack them. In *Barbus barbus*, in which the last unbranched dorsal ray bears serrations, they begin to appear at 23.5 mm SL when that ray is still segmented (Fig. 13b).



**Fig. 16** *Aulopyge huegelii*. (above) caudal fin skeleton of 52 mm SL specimen. Scale = 1 mm; (below) variation on second neural spine (dark shading) on  $PU_2$  of specimens (a) 106 mm, (b) 112 mm, (c) 127 mm SL.

### Other osteological features

*Aulopyge* is conservative in its other skeletal elements.

The *gill arches* are of a generalised cyprinid type except for the complete absence of gill-rakers on the outer margin of the 1st ceratobranchial and only 3 or 4 rakers on the 1st epibranchial. The pharyngeal bone (5th ceratobranchial, Fig. 14) is broad and bears a single row of four teeth, the first somewhat globular with a prominent cusp, the others having bevelled or chisel-like crowns.

The *pectoral girdle* has a tall, upright cleithral limb and a short horizontal limb with a narrow lamina (Fig. 15). The cleithral-coracoid foramen is minute and the coracoid is small. The size of the cleithral-coracoid foramen is variable amongst cyprinids, both intra- and interspecifically (see Howes, 1979: 180), and appears to have little worth as a phyletic character. There is a single, long postcleithrum in *Aulopyge*.

The *caudal fin skeleton* is of a generalised type with 6 hypurals, a well-developed hypurapophysis, paired uroneurals and a long, proximally expanded epural (Fig. 16). There is, however, variable development in the neural arch on  $PU_2$ . In the smallest specimen available (52 mm SL) there are two neural arches on  $PU_2$ , the posterior arch having only a short spine (Fig. 16). In a specimen of 106 mm SL there are two arches with fully developed spines, and in the largest, 127 mm SL, the condition resembles that of the smallest specimen, namely, the second, posterior arch having a small neural spine (Figs 16a-c).

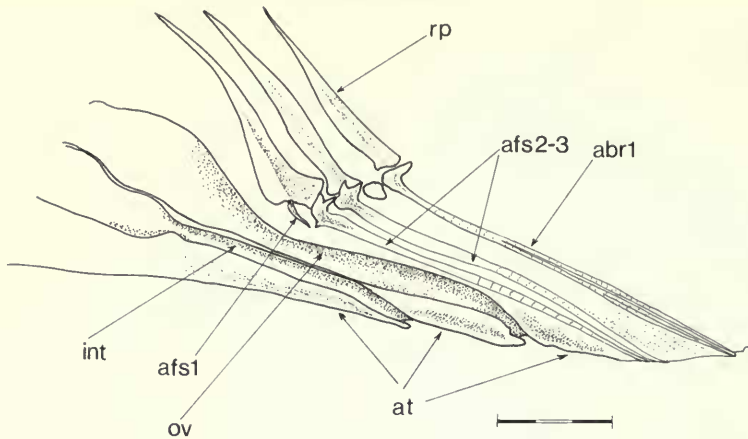


Fig. 17 *Aulopyge huegeli*, anal tube and anal fin of female. Drawn from dissection and X-Radiograph of 116 mm SL specimen.

Radiographs of a wide range of cyprinines reveal the presence of a second neural arch on  $PU_2$  to be of not infrequent occurrence, although when it does occur, the neural spine is usually fully developed, (e.g. *Barbus plebejus*, *Barbus canis*, *Barbus micropogon*, *Barbus barbulus*, *Acrossocheilus yunnanensis*, *Carassius auratus*). A reduced second  $PU_2$  neural spine is found in *Barbus comiza*.

The significance, phyletic or otherwise, of a second neural arch and spine on  $PU_2$  is unknown. Its mosaic and wide distribution in cyprinines make polarity assignment impossible. It is of interest to note, however, that in leuciscines, it is the 3rd preural centrum which bears a double neural arch rather than the 2nd as in cyprinines (see Howes, 1984: 296). Variability of neural arches on the posterior caudal centra may be a plesiomorphic feature of teleosts; Greenwood (1970: 134) noted such variability in Elopiformes.

### Sexual dimorphism and genitalia

Seeley (1886) pointed out the marked sexual dimorphism of *Aulopyge* exhibited in the morphology and position of the anal and genital openings and in the smaller body size of the male.

In the male *Aulopyge*, the anus and genital opening are separated, the genital orifice being posterior in position and lying in front of the first unbranched anal fin ray. In the female, both openings and their respective ducts are contained in a fleshy tube which is adnate to the 2nd unbranched anal fin ray. The oviduct is firmly joined to the flexible 2nd ray for part of its length (Fig. 17). In both males and females the 1st unbranched anal fin ray is vestigial and does not project from the body surface. The genital morphology of *Aulopyge* is unique among cypriniforms.

## Discussion

### *Aulopyge* relationships and barbin classification

*Aulopyge* exhibits a condition well known to cyprinid systematists, namely the possession of several unique features (autapomorphies) and few, if any, recognisable synapomorphies with other cyprinid taxa. Too few published comparative anatomical data exist for barbelled carps (Cyprininae) and the comparisons made during this study are of limited taxonomic scope. However, some information has emerged which may signpost useful characters for determining subgroups amongst barbines. The phylogenetic position of *Aulopyge* can only be discussed in the context of these wider issues.

It was stated in the Introduction that *Aulopyge* is a member of the Cyprininae. This subfamily was one of the divisions recognised by Howes (1981) on the basis of:

\*a maxillary barbel associated with a foramen in the maxillary bone through which the barbel is supplied by a branch of the VII facial nerve.

\*a rostrally extended supraethmoid with a laterally convex border.

At present only two monophyletic assemblages have been identified within the Cyprininae, viz. the *squaliobarbin* group (Howes, 1981) and the *labein* group (Reid, 1982; 1985). The former is a group of three seemingly plesiomorphic genera (*Ctenopharyngodon*, *Mylopharyngodon* and *Squaliobarbus*) having a native distribution restricted to China. The labeins are a speciose assemblage of c. 16 genera with an Afro-Asian distribution. *Aulopyge* shares none of those derived characters listed by Howes (1981) and Reid (1982; 1985) as defining either group.

The Cyprininae may be subdivided on the basis of the morphology of the dilatator fossa (Howes, 1981: 15). There are two conditions of the fossa; 1) it indents the dorso-lateral cranial surface, or 2) it is a foramen in the ventral lamella of the frontal, and in the case of the labeins, the sphenotic as well.

It is assumed from its widespread occurrence in teleosts, and its universal presence in all non-barbelled cyprinids (Leuciscinae) and other cyprinoids, that the dorsal cranial dilatator fossa represents the plesiomorphic condition. That the ventral, foraminate dilatator fossa is a derived condition is reinforced by its ontogenetic history.

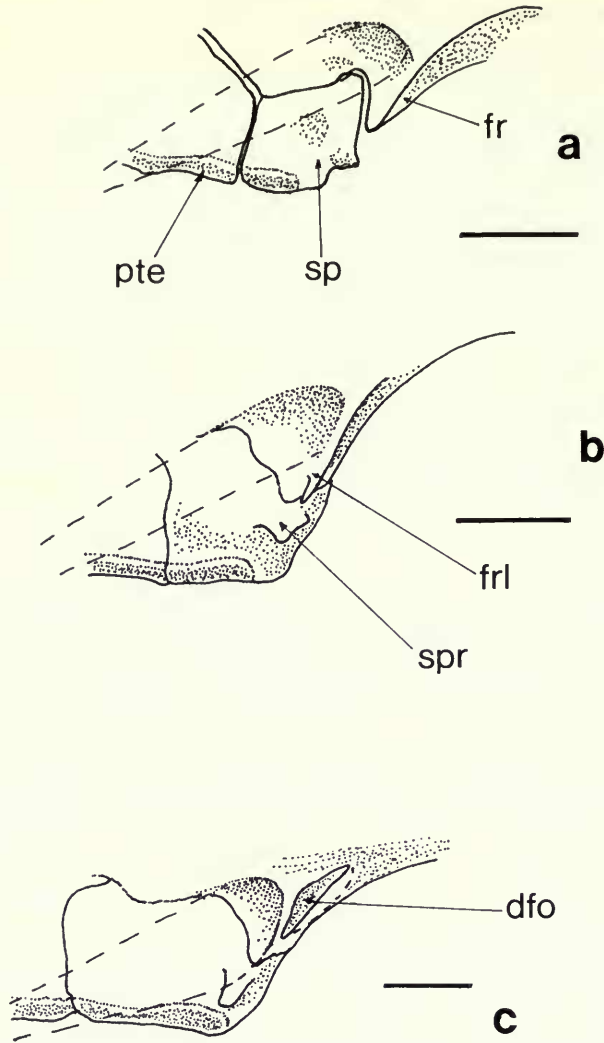
The development of the foraminate fossa was traced in a series of *Barbus intermedius* specimens 20–55 mm SL. In the smallest specimens the fossa is of the plesiomorphic type, (i.e. dorso-laterally placed and indenting the surfaces of the sphenotic and frontal); the *dilatator operculi* muscle is a narrow band-like element. At 29 mm SL there is a lateral process on both the frontal and sphenotic; the indentation for the muscle in the frontal has deepened. By 31 mm SL the sphenotic process has curved downward and the frontal lamella is perforated; the anterior part of the dilatator muscle runs through the foramen and fibres also originate from its lateral rim and the sphenotic process (Figs 18a–c). By 55 mm SL the foramen is well-formed and increased in size by medial attrition of the frontal lamella.

In the smallest specimens of *Barbus barbus* available (25 mm SL) there is no sign of a foraminate dilatator fossa and the condition resembles that in the smallest specimen of *Barbus intermedius*. It is reasonable to assume that the development of the fossa in this species proceeds along much the same course as that described in *B. intermedius*. In the two closely related species *Barbus litamba* from Lake Malawi and *B. mattozi* from the Limpopo, the fossa is foraminate only in specimens above 103 mm SL, and then only has a small opening.

Although it may be argued that a foraminate dilatator fossa could have been derived independently within different cyprinine lineages, it will be accepted as a working hypothesis that it is the principal synapomorphy for one group of Cyprininae. Since *Aulopyge* lacks a foraminate dilatator fossa it must be included with the squaliobarbins, schizothoracins, several *Barbus* species and other taxa listed in Table 3. Of these, the most likely candidate for sister-group relationship to *Aulopyge* is the schizothoracin assemblage. Some schizothoracin genera lack scales, possess a narrow ethmoid, serrated last unbranched dorsal fin ray and have a well-developed ventral facet on the lateral ethmoid, all derived characters shared with *Aulopyge*. However, these characters are mosaically distributed amongst schizothoracin species, no one taxon possessing all together, and so a relationship between *Aulopyge* would involve only certain species, thus making the schizothoracins a paraphyletic group. Previous authors, in recognising the subfamily Schizothoracinae *sensu* Berg, 1912, have tacitly assumed monophyly. Such an assumption is based on the possession by all included taxa of 'tile' scales, i.e. a row of regular, oblong scales at the base of the anal fin. This synapomorphy is supported by another, namely the presence of a bony strut extending from the parasphenoid to contact the prootics in the midline and thus dividing the posterior myodome. As such, this feature resembles the basisphenoid present in other teleosts, but which is absent in ostariophysans. These two characters indicate the monophyly of the schizothoracins and as such exclude *Aulopyge*, which lacks both of them.

*Aulopyge* also shares the character of well-developed lateral ethmoid and entopterygoid facets with some species of *Barbus*. This character distribution immediately raises the question; what is meant by *Barbus*?

At the present time *Barbus* includes c. 800 nominal species distributed in Eurasia and Africa,



**Fig. 18** *Barbus intermedius intermedius*, ontogenetic development of dilatator fossa; (a) at 21.5 mm; (b) at 25 mm; (c) at 31 mm SL. Dashed line indicates position of *dilatator operculi* muscle; all in ventro-lateral view. Scales = 0.5 mm.

many of which, even to the non-specialist, bear scant resemblance to the type species of the genus, the European *Barbus barbus* (Linn.). Some authors have opted to recognise separate genera, (e.g. *Puntius*, *Tor*) for Indian and South East Asian species, a solution which does little to elucidate relationships since these 'genera' are not defined on derived characters. The definition of *Barbus* can only be approached through an adequate anatomical comparison of the Eurasian and African species.

Comparisons and character analyses made during this study have demonstrated that a 'group' including the type species *Barbus barbus* and other Eurasian species can be defined on a suite of five characters:

- 1) shield-shaped supraethmoid (Fig. 19a)
- 2) oblong lachrymal with ventral sensory canal (Fig. 10b)
- 3) enlarged lateral ethmoid facet articulating with a well-developed entopterygoid facet (Fig. 5a)
- 4) 13–15 pre-dorsal vertebrae



**Table 3** Distribution of the dilatator fossa morphotypes amongst examined Cyprininae.**Foramen present:**

## Single foramen

*Acrossocheilus*  
*Barbichthys*  
*Barbus* (part; see Table 4)  
*Capoeta*  
*Carassius*  
*Cyprinus*  
*Probarbus*  
*Varicorhinus*

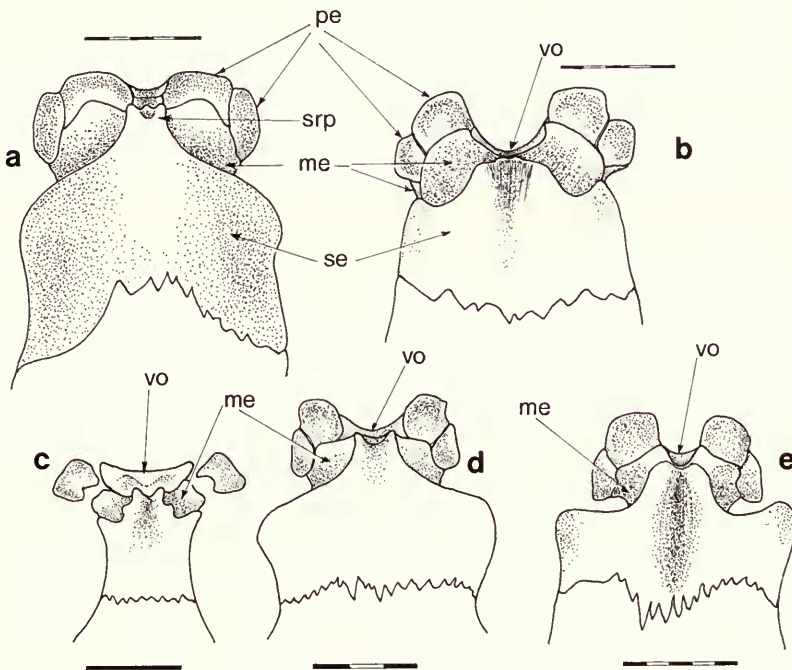
## Double foramen

*Catla*  
*Cirrhhina*  
*Crossocheilus*  
*Garra*  
*Labeo*  
*Labiobarbus*  
*Lobocheilos*  
*Osteocheilus*  
*Semilabeo*  
*Tylognathus* (*sensu* Reid, 1985)  
*Typhlogarra*

**Foramen absent:**

*Ageniogarra*  
*Aulopyge*  
*Barbus* (part; see Table 4)  
*Cyprinion*  
*Mystacoleucus*  
*Onychostoma*  
*Prolabeo*

and in the squaliobarbins  
*Squaliobarbus*  
*Mylopharyngodon*

**Fig. 19** Ethmoid region in dorsal view of, (a) *Barbus barbus*; (b) *B. altianalis altianalis*; (c) *B. leonensis* (scale bar = 0.5 mm); (d) *B. serra*; (e) *Tor putitora*.

**Table 4** Condition of the dilatator fossa in 80 species of '*Barbus*'.**Foramen present**

African species: *altianalis* (all subspecies), *andrewi*, *biscarensis*, *callensis*, *camptacanthus*, *fritschi*, *guirali*, *intermedius* (all subspecies), *jacksoni*, *johnstoni*, *litamba* (some, see text), *macrolepis*, *marequensis* (all morphs), *natalensis*, *nigrodorsalis*, *oxyrhynchus*, *progenys*, *reinii*, *rothschildi*, *serra*, *setivemensis*, *somerini*, *trimaculatus*, *tropidolepis*.

Eurasian species: *barbus*, *barbulus*, *bocagei*, *canis*, *comiza*, *douronensis*, *graellsii*, *grahami*, *hexagonolepis*, *longiceps*, *meridionalis*, *nasus*, *plebejus*, *sharpeyi*, *tambroides*, *tor*, *xanthopterus*.

**Foramen absent**

African species: *ablaves*, *amphigramma*, *argenteus*, *aspilus aurantiacus*, *dorsolineatus*, *eutaenia*, *holotaenia*, *hospes*, *hypsolepis*, *kersteni*, *leonensis*, *lineomaculatus*, *macrops*, *mimus*, *neglectus*, *neumayeri*, *paludinosus*, *paytoni*, *perince*, *poechi*, *profundus*, *radiatus*, *tenuis*, *thalamakanensis*.

Asian species: *aurilius*, *bimaculatus*, *binotatus*, *burmanicus*, *chola*, *collingwoodi*, *conchoni*, *filamentosus*, *pentazona*, *lithopides*, *orphoides*, *sarana*, *sophore*, *titteya*.

5) low neural complex widely separated from the 4th neural spine (Fig. 11b)

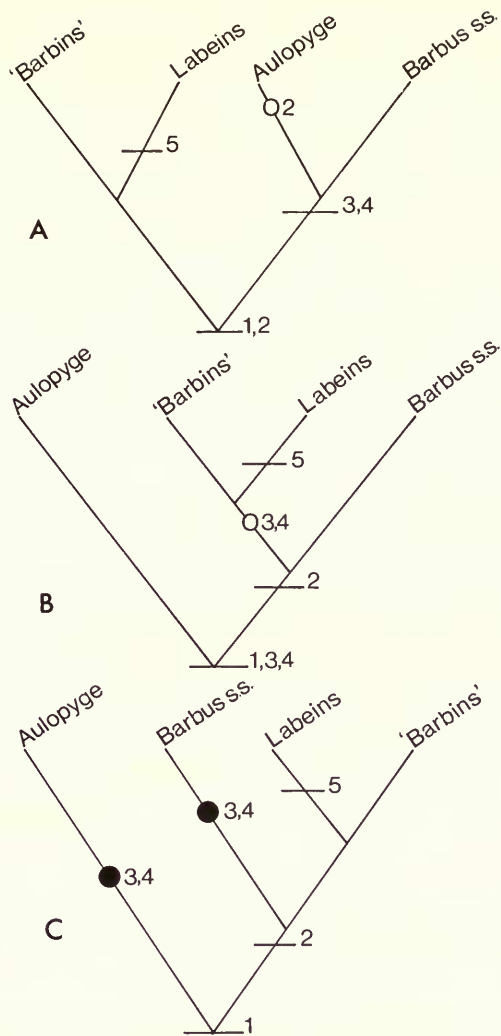
Of these only characters 1 and 2, because of their restricted distribution, can be treated as synapomorphies (character 2 is also shared with *Aulopyge*; see below). Characters 3–5, when viewed in the context of cyprinoid distribution are apparently derived. Their disparity among cyprinines, however, does not make them highly corroborated synapomorphies. Nonetheless they are congruent with characters 1 and 2.

If, on the basis of this character suite, *Barbus* is restricted to only some Eurasian species (see Appendix 1) then it remains to be determined how closely related it is to those African and Asian species presently included in *Barbus*, *Tor* and *Puntius*. From the distribution of the foraminate dilatator fossa (see above) it is clear that African and Asian barbines do not constitute a monophyletic assemblage. Of 80 African and Asian '*Barbus*' species selected at random, virtually 50% possess the character (41 with, 39 without; Table 4). Also emerging from this analysis is that almost none of the 'small' African *Barbus* examined possess a foraminate fossa. Thus, on the basis of the synapomorphic foraminate fossa, some *Barbus* species are more closely related to labein and other cyprinine genera such as *Capoeta*, *Cyprinus*, *Varicorhinus* and *Acrossocheilus* than to other *Barbus* species.

**Immediate relationships of *Aulopyge***

Although it lacks a foraminate dilatator fossa, *Aulopyge* shares with some Eurasian *Barbus* species (termed from hereon *Barbus sensu stricto*) well-developed lateral ethmoid and entopterygoid articular facets and an oblong lachrymal with a ventral sensory canal (although in *Aulopyge* the canal is not fused with the bone; see p. 174. The lack of a foraminate fossa may be interpreted either as a loss or as a plesiomorphic condition, in which case the lateral ethmoid-entopterygoid facets and oblong lachrymal must be viewed as having been independently derived. Fewer assumptions are required to support the 'loss' of the derived dilatator fossa in *Aulopyge* than are demanded by other schemes of relationship (Figs 20A–C). Support for 'loss' is that *Aulopyge* exhibits heterochrony in the late development and fusion of infraorbital sensory canals and in the absence of scales. It may be that the dorso-lateral dilatator fossa is also the retention of an early ontogenetic stage (see p. 187). Outright dismissal of independent origin on grounds of parsimony must be treated with caution, however, since it is noted that amongst the schizothoracins a lateral ethmoid facet is present in some taxa (p. 170). Since the schizothoracins are almost certainly a monophyletic group within the Cyprininae (see p. 187) it follows that this feature has been derived independently from that in *Aulopyge*, *Barbus sensu stricto* and other barbines (including *Cyprinus*).

Whether *Aulopyge* is recognised as the sister-group to *Barbus sensu stricto*, or to *Barbus sensu*



**Fig. 20** Three possible schemes of relationship between *Aulopyge* and other cyprinines. A, the most parsimonious, involves the loss of character 2 in *Aulopyge*. B, involves the loss of characters 3 and 4 in 'Barbins' and Labeins. C, involves independent derivation of characters 3 and 4 in *Aulopyge* and *Barbus sensu stricto*.

Character 1. lateral ethmoid articular facet; 2. foraminat dilatator fossa; 3. expansion of lateral ethmoid facet and presence of entopterygoid facet; 4. oblong lachrymal; 5. double-foraminate fossa (additional characters defining Labeins are given in Reid, 1985). 'Barbins' include those taxa listed in Table 3, under 'foramen present'.

*stricto* plus other barbines and labeins cannot be resolved on those characters considered here. However, no synapomorphies have been identified that would suggest *Aulopyge* is more closely related to any cyprinine taxon lacking a foraminat dilatator fossa, including the schizothoracins.

Karaman's (1971) hypothesis of an intermediate taxonomic position for *Aulopyge* between 'barbine' and 'schizothoracine' subgroups (see above, p. 165) is not supported by this study. Schizothoracins do share with *Barbus sensu stricto* high total and pre-dorsal numbers of vertebrae (Table 2), but the polarity of this character is uncertain (see p. 182) and if treated as a synapomorphy in a scheme of relationship involving *Aulopyge*, *Barbus* and 'other cyprinines' it is incongruent with other synapomorphies.

I have found no evidence in support of Arai's (1982) contention that *Aulopyge* possesses some gobionine characters.

From the data analysed two hypotheses are available:

\**Aulopyge* is a derived member of the *Barbus sensu stricto* lineage, with specialisation through reduction and 'loss' (Fig. 20A)

\**Aulopyge* is a member of the 'stem-group' of Eurasian plus African barbines (Figs 20B & C).

### Acknowledgements

I am most grateful to my colleagues Keith Banister, Humphry Greenwood, Alwyne Wheeler and Peter Whitehead for their critical comments on the manuscript, and for their many enlivened discussions over the years on the taxonomy of *Barbus*. To Gordon Reid of the Horniman Museum, I am particularly indebted for his critical refereeing, his sound advice and continuing encouragement. Paul Skelton of the J. L. B. Smith Institute of Ichthyology has my gratitude for providing specimens and so much stimulating discussion.

My sincerest thanks are due to Primoz Zupancic of Dolsko, Yugoslavia, for obtaining the specimens of *Aulopyge* upon which most of this work is based, and for providing me with photographs and information on their habitat; and to Keith Easton of the Severn Trent Water Authority for providing juvenile specimens of *Barbus barbus*.

Special thanks go to my colleague Mandy Holloway for preparing the radiographs.

After this paper had been submitted for publication, Dr Friedhelm Krupp of the Senckenberg Museum generously provided me with additional information which has been added to the text.

### References

- Almaça, C. A. S. 1967. Estudo das populações portuguesas do Gen. *Barbus* Cuvier, 1817 (Pisces, Cyprinidae). *Revista da Faculdade de Ciências* 2<sup>a</sup> ser., 14(2): 151–400.
- 1972. Sur les systématique des barbeaux (genre et sous-genre *Barbus*) de la péninsule Iberique et de l'Afrique du Nord. *Arquivos do Museu Bocage* 2<sup>a</sup> ser., 3(10): 319–330.
- 1981. La collection de *Barbus* d'Europe du Muséum national d'Histoire naturelle (Cyprinidae, Pisces). *Bulletin du Muséum national d'Histoire naturelle*, Paris, 4e ser., 3, Sect. A. No. 1: 277–307.
- 1983. Re-examination of the types of *Barbus haasi* Mertens 1924. *Senckenbergiana Biologica* 63(1–2): 33–38.
- Arai, R. 1982. A chromosome study on two cyprinid fishes, *Acrossocheilus labiatus* and *Pseudorasbora pumila pumila*, with notes on Eurasian cyprinids and their karyotypes. *Bulletin National Science Museum, Tokyo (Zool.)* 8(3): 133–152.
- Banister, K. E. 1980. The fishes of the Tigris and Euphrates rivers. In: *Euphrates and Tigris, Mesopotamian ecology and destiny*. (Eds Rzoska, J., Talling, J. F., Banister, K. E.). Junk. The Hague-Boston-London: 95–108.
- Bleeker, P. 1863. Systema Cyprinoideorum revisum. *Nederlandsch Tijdschrift voor de Dierkunde* 1: 187–218.
- Berg, L. S. 1912. *Faune de la Russie*: Poissons 3(1): 1–336. St Petersburg.
- Bonaparte, C. L. 1846. Catalogo metodico dei pesci Europei. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale*, Milano: 1–95.
- Boulenger, G. A. 1911. *Catalogue of the fresh-water fishes of Africa in the British Museum (Natural History)* 2: 529pp.
- Chen Xiang-Lin, Yue Pei-Qi & Lin Ren-Duan. 1984. Major groups within the family Cyprinidae and their phylogenetic relationships. *Acta Zootaxonomica Sinica* 9(4): 424–440.
- Gosline, W. A. 1978. Unbranched dorsal-fin rays and subfamily classification in the fish family Cyprinidae. *Occasional papers of the Museum of Zoology, University of Michigan* No. 684: 1–21.
- Greenwood, P. H. 1970. Skull and swimbladder connections in the fishes of the family Megalopidae. *Bulletin of the British Museum of Natural History (Zoology)* 19(3): 119–135.
- Howes, G. J. 1978. The anatomy and relationships of the cyprinid fish *Luciobrama macrocephalus* (Lacepède). *Bulletin of the British Museum of Natural History (Zool.)* 34(1): 1–64.
- 1979. Notes on the anatomy of *Macrochirichthys macrochirus* (Valenciennes). 1844 with comments on the Cultrinae (Pisces, Cyprinidae). *Bulletin of the British Museum of Natural History (Zool.)* 36(3): 147–200.
- 1981. Anatomy and phylogeny of the Chinese Major Carps *Ctenopharyngodon* Steind., 1866 and *Hypophthalmichthys* Blkr., 1860 *Bulletin of the British Museum of Natural History (Zool.)* 41(1): 1–52.

- 1982. Anatomy and evolution of the jaws in the semiplotine carps with a review of the genus *Cyprinion* Heckel, 1843 (Teleostei: Cyprinidae). *Bulletin of the British Museum of Natural History* (Zool.) **42**(4): 299–335.
- 1984. Phyletics and biogeography of the aspinine cyprinid fishes. *Bulletin of the British Museum of Natural History* (Zool.) **47**(5): 283–303.
- Illick, H. J.** 1956. A comparative study of the cephalic lateral-line system of North American Cyprinidae. *American Midland Naturalist* **56**(1): 204–223.
- Jayaram, K. C.** 1981. *The freshwater fishes of India. A handbook*. Calcutta. 475pp.
- Karaman, M. S.** 1971. Süswasserfische der Türkei 8. Revision der Barben Europas, Vorderasiens und Nordafrikas. *Mitteilungen aus den Hamburgischen Zoologischen Museum und Institut*. **67**: 175–254.
- Lekander, B.** 1949. The sensory line system and the canal bones in the head of some ostariophysii. *Acta Zoologica* **30**: 1–131.
- Lelek, A.** 1980. *Threatened freshwater fishes of Europe* Council of Europe Nature and Environment Series No. 18, Strasbourg. 269pp.
- Lévêque, C. & Daget, J.** 1984. Cyprinidae. In: *Check-list of the freshwater fishes of Africa*. **1** ORSTOM, Paris and MRAC, Tervuren: 217–343.
- Lindsey, C. C.** 1975. Pleomerism, the widespread tendency among related fish species for vertebral number to be correlated with maximum body length. *Journal of the Fisheries Research Board of Canada* **32**(12): 2453–2469.
- & **Arnason, A. N.** 1981. A model for responses of vertebral numbers in fish to environmental influences during development. *Canadian Journal of Fisheries and Aquatic Sciences* **38**(3): 334–347.
- Menon, M. A. S.** 1956(1960). On a third collection of fish from Iraq. *Records of the Indian Museum* **54**(3–4): 139–157.
- Parshall, A. M.** 1983. *A reassessment of the phylogenetic position of the family Cobitidae* (Ostariophysii). Ph.D. Thesis, University of London. 369pp.
- Ramaswami, L. S.** 1955. Skeleton of cyprinoid fishes in relation to phylogentic studies: 6. The skull and Weberian apparatus of the subfamily Gobioninae (Cyprinidae). *Acta Zoologica* **36**(2): 127–158.
- Reid, G. M.** 1982. The form, function and phylogentic significance of the vomero-palatine organ in cyprinid fishes. *Journal of Natural History* **16**: 497–510.
- 1985. A revision of African species of *Labeo* (Pisces: Cyprinidae) and a re-definition of the genus. *Theses Zoologicae*, **6**: 1–322.
- Seeley, H. G.** 1886. *The freshwater fishes of Europe*. Cassell, London, Paris, New York and Melbourne. 444pp.
- Skelton, P. H.** 1976. Preliminary observations on the relationships of *Barbus* species from Cape coastal rivers, South Africa (Cypriniformes, Cyprinidae). *Zoologica Africana* **11**(2): 399–411.
- 1980. *Systematics and biogeography of the redfin *Barbus* species (Pisces, Cyprinidae) from Southern Africa*. Ph.D. Thesis, Rhodes University. 417pp.
- Vandewalle, P.** 1977. Particularités anatomiques de la tête deux Poissons Cyprinidés *Barbus barbuis* (L.) et *Leuciscus leuciscus* (L.). *Bulletin Academie Royale de Belgique* 5e ser., **63**: 469–479.

Manuscript accepted for publication 11 April 1986

## Appendix 1

### The genus *Barbus sensu stricto*

#### Definition and included species

Banister (1980) placed the majority of Middle-eastern *Barbus* into two groups—the ‘European’ and ‘Afro-Indian’, which he characterised on overall morphology, scale type and serrated or smooth last dorsal fin ray. Banister stated that both groups might be monophyletic and so tacitly restricted *Barbus* to the ‘European’ group.

Lévêque & Daget (1984) stated that ‘Strictly speaking the generic name *Barbus* shall be restricted to European and some north-African species’. These authors’ remarks are supported by this study and reference has been made in the text to *Barbus sensu stricto*. Only a thorough comparative anatomical study of ‘barbins’ will provide a strict diagnosis (based on synapomorphies) of *Barbus*. The definition of *Barbus* used here is based on the characters analysed above and forms a working

hypothesis for a more critical evaluation. Those taxa not embraced by this definition are referred to as '*Barbus*' or *Barbus sensu lato*; in the case of the Asian species, the generic names *Puntius* and *Tor* are already widely used (see for example, Jayaram, 1981). For African '*Barbus*' several generic names are available (see synonymy in Lévêque & Daget, 1984).

*Barbus sensu stricto* is defined on the basis of its members having a total vertebral count of 40–48 of which 13–15 are pre-dorsal vertebrae; a well-developed, centrally to anteriorly situated ventral lateral ethmoid facet articulating with a well-developed anterodorsal entopterygoid facet; a 'shield'-shaped supraethmoid with (usually) a prominent rostral process (Fig. 19a); neural complex low with a deeply indented anterior border, its posterior border (usually) well-separated from the 4th neural spine which is at least half the height of the neural complex; lachrymal elongate, often oblong with tapered anterior tip and sometimes an indented posteroventral border, sensory canal running through the lower half of the bone; 49–90 scales in the lateral line, (cf. 20–55 in African and Asian '*Barbus*').

Almaça (1981) distinguished three groups of Eurasian *Barbus* on the basis of lateral line scale counts but he pointed out the lability of this character due to influences of temperature and latitudinal variation (see similar remarks under 'vertebrae', p. 182).

The following species are considered to constitute *Barbus sensu stricto*:

*Barbus albanicus* Steindachner, 1870 (including *B. graecus* (Steindachner, 1895))

Distribution: Albania–Greece

*Barbus barbuis* (Linnaeus, 1758), type species of the genus.

Distribution: Europe (see Almaça, 1981 for detailed distributional data and recognition of subspecies)

*Barbus barbuis* Heckel, 1846

Distribution: Tigris

*Barbus bocagei* Steindachner, 1865

Distribution: Iberia

*Barbus capito* (Güldenstädt, 1773)

Distribution: Caspian and Aral Sea basins; Amu Darya

*Barbus comiza* Steindachner, 1865

Distribution: Iberia

This species is included in *Barbus* on the basis of its possessing a high vertebral number, and a typical oblong lachrymal (Fig. 10c). However, it differs from other species in its longer and narrower head (see Almaça, 1967; 1972), concave dorsal profile, lower number of pre-dorsal vertebrae (12, cf. 13–15), tall neural complex narrowly separated from the 4th neural spine, and the absence of a fleshy overhanging upper lip. In its striking dorsal and lateral head profiles, and narrow ethmoid *B. comiza* greatly resembles *Aulopyge*. However, no synapomorphies have been identified that would suggest these features are anything other than homoplasies.

*Barbus esocinus* (Heckel, 1843)

Distribution: Tigris-Euphrates

*Barbus graellsii* (Steindachner, 1866)

Distribution: Portugal

*Barbus lacerta* Heckel, 1843

Distribution: Tigris-Euphrates and Qwarq rivers

*Barbus longiceps* Valenciennes, 1842

Distribution: Jordan River system

*Barbus lorteti* Sauvage, 1882

Distribution: Orontes R.

*Barbus microcephalus* Almaça, 1967

Distribution: Iberia

*Barbus meridionalis* Risso, 1826 (including *B. peloponnesius* Val., 1842).

Distribution: NE Spain—S. France—Yugoslavia—Greece

*Barbus nasus* Günther, 1874

Distribution: Morocco

*Barbus pectoralis* Heckel, 1843

Distribution: Orontes R.

*Barbus plebejus* Bonaparte, 1839 (including the subspecies recognised by Almaça, 1981; 1983)

Distribution: N. Italy–Greece

*Barbus rajanorum* Heckel, 1843

Distribution: Tigris-Euphrates

Karaman (1971) considers *B. schejch* (Heckel, 1843) and *B. barbulus* Heckel (listed here as a separate species), to be synonyms of *B. rajanorum*. This synonymy is doubtful and the 'rajanorum complex' requires a taxonomic reappraisal. In Dr F. Krupp's opinion (pers. com.) *B. rajanorum* is a hybrid between *B. pectoralis* and *Capoeta damascinus*.

*Barbus sclateri* Günther, 1868

Distribution: Iberia

*Barbus subquincunciatus* Günther, 1868

Distribution: Tigris-Euphrates

*Barbus steindachneri* Almaça, 1967

Distribution: Iberia

*Barbus xanthopterus* Heckel, 1843

Distribution: Tigris-Euphrates

Although the Middle-eastern species *Barbus grypus* and *B. sharpyei* have relatively high vertebral numbers (Table 1), they lack the elongate lachrymal of the other species listed and possess, in common with *B. canis* and *B. reinii* what is considered to be another derived form of lachrymal in which the sensory canal runs along the anterodorsal border (see p. 177). *Barbus canis* and *B. reinii* both have low vertebral numbers, respectively 38–39 and 37 (totals) and 10 and 10–11 predorsal elements. *Barbus sharpyei* differs from other species of this group in having only 30–31 lateral line scales.

#### The systematic positions of *Barbus brachycephalus* Kessler, 1872 and *B. mursa* (Güldenstädt, 1773)

The generic placements of these two south Central Asian species (respectively the Aral and Caspian Seas and the Kura system) are problematical. Both species although having high vertebral counts differ in several ways from *Barbus sensu stricto* and other species of '*Barbus*'.

*Barbus brachycephalus* has rather slender barbels, unlike the thick, often papillate barbels of 'typical' species of the genus, and 7 branched dorsal fin rays, cf. 8 in the majority of *Barbus sensu stricto* and also in *Barbus sensu lato*. The cranium is broad and flat, lacking the transverse convexity of most barbins. There are a total of 47 vertebrae, but only 11 are predorsal, cf. 13–15 in *Barbus sensu stricto*.

*Barbus mursa* has a deep lachrymal with an anterior branching pattern resembling that of *Barbus canis* and related species discussed above (Fig. 10n). However, it possesses a series of preanal scales and a prominent genital papilla more reminiscent of schizothoracins.

#### The systematic positions of *Barbus andrewi* Barnard, 1937 and *B. serra* Peters, 1864

These two species are restricted to the South African Western Cape. On the basis of the characters given for *Barbus sensu stricto* both species should be included. Both, however, have a higher predorsal vertebral count than other *Barbus sensu stricto*, viz.: 14–17, cf. 13–15, but, a relatively low total vertebral number, viz.: 38–41, cf. 40–47. The supraethmoid has the same 'shield'-shaped appearance as in *Barbus sensu stricto* (Fig. 19d), but the vomer is broader anteriorly and extends further dorsally in *B. serra* and *B. andrewi*. Again, the lachrymal bones of the two species, while having the same overall appearance of that bone in the Eurasian *Barbus* have a sloped, rather than a perpendicular posterior margin and more convex ventral border. Because of these differences I am hesitant to include the Cape species in *Barbus sensu stricto*. According to Skelton (1980), *Barbus serra* and *B. andrewi* are sister-taxa, not closely related to any African '*Barbus*' he examined.

## Appendix 2

## Characteristics of the subfamilies Cyprininae and Leuciscinae

CYPRININAE

LEUCISCINAE

(including 'Schizothoracinae')

1	Maxillary barbel present	No maxillary barbel
2	Maxillary foramen	No maxillary foramen
3	Supraethmoid with medially indented rostral process	No supraethmoid rostral process
4	Articular facets present on lateral ethmoid and entopterygoid in some taxa	Articular facets absent (except in <i>Tinca</i> )
5	Single, strong ligament connecting posterior face of lateral ethmoid with dorsomedial surface of entopterygoid	Connection between lateral ethmoid <i>via</i> connective tissue sheet, sometimes thickened laterally
6	Lachrymal (1st infraorbital) sometimes elongate and oblong	Lachrymal never elongate or oblong
7	<i>Dilatator operculi</i> muscle sometimes originating from ventral surface of the frontal and passing through a frontal-sphenotic foramen	<i>Dilatator operculi</i> muscle confined to cranial surface; fossa never foraminate
8	Neural complex lacking grooved dorsal surface; sometimes close to, or even contacting the cranium (supraoccipital)	Neural complex with grooved dorsal surface, never contacting the cranium
9	1st free supraneural not contacting neural complex	1st free supraneural articulating with neural complex
10	Dorsal fin origin lies above or anterior to that of the pelvics (rarely posterior)	Dorsal fin origin rarely above or in advance of the pelvics
11	1st unbranched dorsal fin ray lies above the 11th–18th vertebra	1st unbranched dorsal fin ray lies above 16th–31st vertebra
12	Last unbranched dorsal fin ray often serrated	Last unbranched dorsal fin ray never serrated
13	Modal number of vertebrae 38–40 (never exceeding 48)	Modal number of vertebrae 40–45 (range 33–61)

Note: The genus *Tinca* is included here in the Leuciscinae, although possessing a cyprinine feature (character 4). Chen *et al.* (1984) consider *Tinca* to be the sister-group of the Cyprininae (their 'Barbines'). Although for the most part, these authors appear to base their hypothesis on differences rather than on shared homologies, their cladogram requires serious consideration and offers a much needed, testable classification of the Cyprinidae.