

Anatomy and evolution of the jaws in the semiplotine carps with a review of the Genus *Cyprinion* Heckel, 1843 (Teleostei: Cyprinidae)

Gordon Howes

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

Introduction

Scant attention has been paid to the jaw anatomy of cyprinid fishes. Takahasi (1925) described the jaw musculature of various cyprinoids, but only Matthes (1963) and Alexander (1966) have described the osteo-myological anatomy of the cyprinid jaw. These authors, and Ballantijn (1969), have also attempted a functional interpretation of particular jaw types. Howes (1978, 1979, 1980, 1981) described and commented on jaw types of (mostly) non-barbelled carps ('Leuciscinae'). But, in these studies the potential value of the jaws as indicators of phyletic relationship was not recognised. The more diverse jaw morphology of barbelled carps ('Cyprininae') has, however, focussed attention on this aspect of jaw anatomy.

From among the 'Cyprininae' the genus *Semiplotus* is chosen as a model for detailed description because member species possess what is an obviously highly derived osteo-myological jaw structure, manifest externally in the size and shape of the mouth (see below). *Semiplotus* species are large (according to Day (1889) *S. semiplotus* attains at least 2 feet in length), distinctive carps whose geographical range extends through northern India and Burma. The distinctiveness of these fishes lies in the size and shape of the head and extreme body depth (Figs 1A–C). Likewise, the mouth is of great width (probably the widest mouth in relation to head length of any cyprinid fish), the lower jaw is edged with a cornified epithelium and is overhung by the upper jaw (Figs 1B & C).

Many cyprinid taxa possess broad, ventral mouths with cornified cutting edges, the so-called 'sector mouth' (see p. 313 for definition). Only in *Onychostoma*, *Varicorhinus*, *Capoeta* and *Cyprinion* does the morphology of the mouth approach that of *Semiplotus*, both in width and complex development of the lower lip.

Members of these genera are compared here in order to test the hypothesis that a sector mouth is synapomorphic for the group and also to elucidate the possible evolutionary pattern of semiplotine jaw modification.

Nomenclatural note

In the anatomical descriptions, *Scaphiodonichthys burmanicus* is referred to as *Semiplotus burmanicus*. The existence in both 'genera' of synapomorphic osteological and myological characters indicates their generic unity (see p. 312 for a list of characters, and p. 331 for complete synonymy). No specimens of *Semiplotus modestus* have been examined and reference to '*Semiplotus*' in the anatomical text refers only to the species *semiplotus* and *burmanicus*.

List of specimens used in anatomical description

Capoeta capoeta
Capoeta capoeta

BMNH 1968.12.13 : 405–416
BMNH 1879.11.14 : 19 (skeleton)

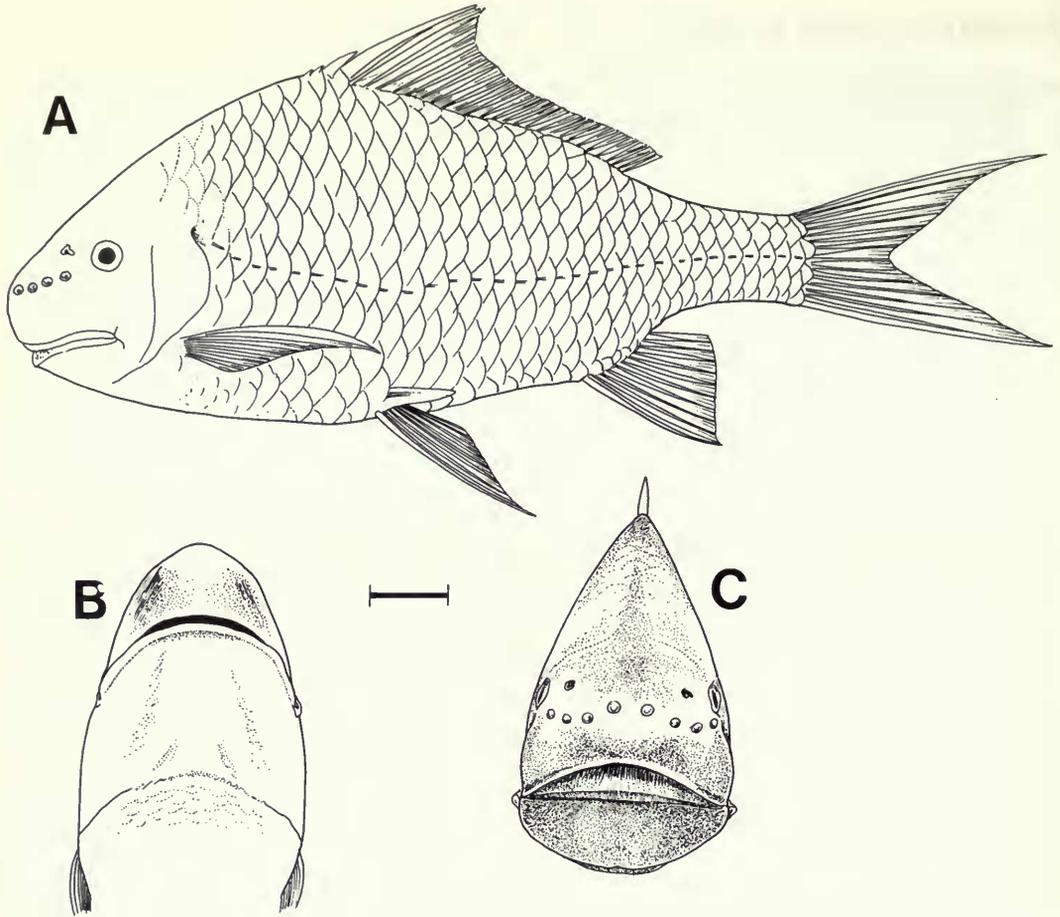


Fig. 1 *Semiplotus semiplotus*. A, in lateral view. B & C, ventral and anterior aspects of the head. Scale = 10 mm. Drawn from specimen 1889.2.1 : 365–6.

<i>Capoeta fusca</i>	BMNH 1899.7.15 : 26
<i>Cyprinion acinaces</i>	BMNH 1977.8.25 : 1–5
<i>Cyprinion kais</i>	BMNH 1974.2.22 : 1115–8
<i>Cyprinion macrostoma</i>	BMNH 1974.2.22 : 118–95
<i>Cyprinion microphthalmum</i>	BMNH 1883.8.2 : 4–9
<i>Cyprinion microphthalmum</i>	BMNH 1977.12.13 : 532–545; 546–556
<i>Cyprinion milesi</i>	BMNH 1889.2.1 : 263–4
<i>Cyprinion watsoni</i>	BMNH 1889.2.1 : 387–396
<i>Cyprinion watsoni</i>	BMNH 1913.4.15 : 90–99
<i>Onychostoma laticeps</i>	BMNH 1969.4.15 : 105–110
<i>Onychostoma varus</i>	BMNH 1935.4.18 : 22
<i>Semiplotus burmanicus</i>	BMNH 1893.2.16 : 32 (skeleton)
<i>Semiplotus burmanicus</i>	BMNH 1889.10.4 : 2
<i>Semiplotus burmanicus</i>	BMNH 1920.9.8 : 1–3
<i>Semiplotus burmanicus</i>	Uncat. Smithsonian Colln.
<i>Semiplotus semiplotus</i>	BMNH 1889.2.1 : 365–6
<i>Semiplotus semiplotus</i>	BMNH 1889.2.1 : 367 (skeleton)
<i>Semiplotus semiplotus</i>	BMNH 1972.7.26 : 10
<i>Squaliobarbus curriculus</i>	BMNH 1888.5.15 : 29 (skeleton)

<i>Varicorhinus beso</i>	BMNH 1968.7.24 : 2
<i>Varicorhinus beso</i>	BMNH 1968.7.24 : 17–19 (alizerins)
<i>Varicorhinus beso</i>	BMNH 1902.12.13 : 377 (skeleton)
<i>Varicorhinus tanganicæ</i>	BMNH 1906.9.6 : 11 (skeleton)

Abbreviations used in text figures

A ₁ a, A ₁ b, A ₂ , A ₃ ,	
A _w	Divisions of the <i>adductor mandibulae</i> muscle
Aa	Anguloarticular
Aamp	Aponeurosis of <i>adductor mandibulae</i> and <i>protractor hyoideus</i> muscles
Aap	Premaxillary anterior ascending process
Afl, 2, 3	Articulatory facets of anguloarticular
Ahy	Anterohyal
Ama	Aponeurosis of <i>adductor mandibulae</i> A1 muscle
Ao	<i>Adductor operculi</i> muscle
Apl, 2	Articulatory processes of anguloarticular
Br	Branchiostegal ray (numbered)
Cm	Coronomeckelian bone
Cp	Coronoid process of dentary
Ctls	Labial shelf connective tissue
Cts-fef	Connective tissue strand linking maxilla to frontal-ethmoid foramen
De	Dentary
Dhy	Dorsohyal
Do	<i>Dilatator operculi</i> muscle
Ect	Ectopterygoid
Elt	Epithelial layer of lower lip
Ent	Entopterygoid
Epo	Epioccipital
Etb	Epithelial tendinous layer
Exo	Exoccipital
Fr	Frontal
Fsef	Frontal-supraethmoid foramen
Hy	Hyomandibula
Ic	Intercalar
Ihy	Interhyal
Im	<i>Intermandibularis</i> muscle
Iop	Interoperculum
Iopf	Interopercular facet
Ke	Kinethmoid
Ks	Keratinized lip surface
Lac	Ligament linking retroarticular with anterohyal
Lai	Ligament linking retroarticular with interoperculum
Lap	<i>Levator arcus palatini</i> muscle
Lapo	Ligament linking retroarticular with preoperculum
Laq	Ligament linking anguloarticular with quadrate
Le	Lateral ethmoid
Lkee	Ligament linking kinethmoid to ethmoid
Lkmx	Ligament linking kinethmoid to maxilla

Lkp	Ligament linking kinethmoid to palatine
Lkpm	Ligament connecting kinethmoid to premaxilla
Ll	Lower lip
Llm	Lateral lamellae
Lo	<i>Levator operculi</i> muscle
Lpe	Ligament linking palatine to ethmoid
Lpm	Ligament linking palatine to maxilla
Lqu	Ligament linking quadrate to interoperculum
Ls	Labial shelf
Mdp	Maxillary distal process
Me	Mesethmoid
Met	Metapterygoid
Mfp	Medial fatty partition
Mkl	Medial keratinized layer of lower lip
Mlp	Maxillary mid-lateral ascending process
Mlt	Medial tissue layer of lower lip
Mmp	Medial maxillary process
Mn	Medial notch
Mv	Maxillary valve
Mx	Maxillary
Mxf	Maxillary foramen
Mxn	Maxillary notch
Nc	Neural complex
Ns	Neural spines
Op	Operculum
Pa	Parietal
Pal	Palatine
Pe	Preethmoid
Ph	<i>Protractor hyoideus</i> muscle
Pha	Medial aponeurosis of <i>protractor hyoideus</i>
Phat	Anterior tendinous segment of <i>protractor hyoideus</i>
Phav	Antero-ventral segment of <i>protractor hyoideus</i>
Phbt	Basal tendinous layer of <i>protractor hyoideus</i>
Phd	Dorsal segment of <i>protractor hyoideus</i>
Phl	Lateral segment of <i>protractor hyoideus</i>
Phlt	Lateral tendon of <i>protractor hyoideus</i>
Phpv	Postero-ventral segment of <i>protractor hyoideus</i>
Phy	Posterohyal
Pop	Preoperculum
Pro	Prootic
Ps	Parasphenoid
Pte	Pterotic
Pty	Pterygiophore (dorsal)
Q	Quadrate
Qaf	Quadrate anterior facet
Qlf	Quadrate lateral facet
Qmb	Quadrate medial buttress
Ra	Retroarticular
Se	Supraethmoid
Sh	<i>Sternohyoideus</i> muscle
Sj	Synarthritic mandibular joint
Sn	Supraneurals (numbered)
Soc	Supraoccipital
Socr	Supraoccipital crest

Stf	Subtemporal fossa
Sy	Symplectic
Syf	Symplectic facet
TA2-1b	Tendon connecting A ₂ with A ₁ ,b
TA3	Insertion tendon of <i>adductor mandibulae</i> A ₃
Ur	Urohyal
V	Vomer
Velt	Ventral epithelial lip tissue
Vhy	Ventrohyal
Vmlt	Ventral medial tissue layer of lower lip

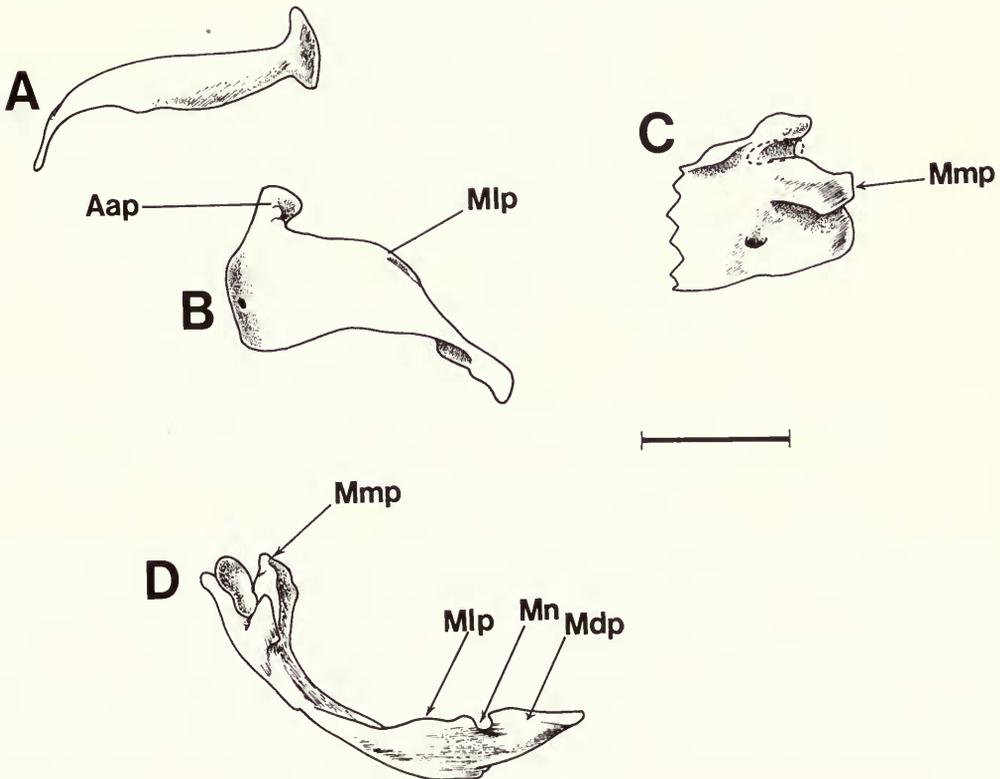


Fig. 2 *Semiplotus semiplotus*, upper jaw bones. A, premaxilla, lateral view. B, maxilla, lateral view. C, maxilla, medial view of symphyseal portion; dashed line indicates meniscus. D, maxilla, dorsal view. Scale = 10 mm.

Jaw anatomy of *Semiplotus semiplotus* (McClelland, 1839)

Upper jaw bones

The *premaxilla* (Fig. 2A) is exceedingly thin and shallow, with only a slight anterior ascending process. The posterior portion of the bone is directed ventrally at a right angle to its anterior part, with its tip compressed and shallowly bifurcated.

The *maxilla* (Fig. 2B) is deep, its dorsal border convex. The anterior ascending process (Aap) is shallow and thick, its dorsal border notched (the palatine ligament lies across this notch). The upper symphyseal border of the ascending process is turned so that its face forms a 45° angle to the midline. The lower portion is strongly concave and extends antero-medially to form the symphyseal part to the maxilla, syndesmotically contacting its partner. The medial (rostral) maxillary process (Mmp, Fig. 2C) is almost square and it too makes

syndesmotomic contact with its partner. A mid-lateral ascending process is represented by a slight convexity of the maxillary dorsal border (Mlp). This part of the maxilla is separated from the posterior part by a medial notch (Mn). The posterior rim of the notch acts also as the leading border of a broad medial triangular ledge.

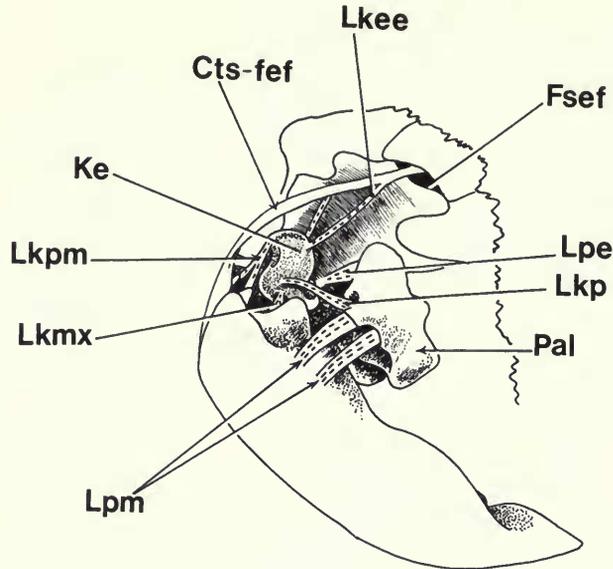


Fig. 3 *Semiplotus semiplotus*, upper jaw articulation in oblique dorso-lateral aspect. Scale = 5 mm.

Articulation of the upper jaw (Fig. 3)

The upper jaw bones articulate with the cranium *via* the kinethmoid, the palatine and the premaxillary meniscus.

The *kinethmoid* (Ke) is attached *via* a thick ligament from its head to the ascending process of the premaxilla (Lkpm). A broad, bifurcated ligament (Lkee) extends from the posterior face of the kinethmoid to attach to the lateral edges of the supraethmoid and, dorsally, to the connective tissue overlying the ethmoid region. A strand of this connective tissue (Cts-fef) inserts onto the rim of the foramen between the frontals and the supraethmoid. A mid-lateral ligament (Lkp) attaches the kinethmoid to the palatine, and a ventro-lateral ligament (Lkmx) links it to the maxilla.

A paired ligament (Lpm) attaches the lateral face of the maxilla with the lateral shelf of the palatine (Pal). The palatine, in turn, is connected with the mesethmoid by a thick medially directed ligament (Lpe).

Interposed between the medial face of the maxilla, the preethmoid and part of the vomer is a cartilaginous meniscus (*sensu* Alexander, 1966). This is thick and ellipsoidal and lies between a ventral prominence of the premaxillary ascending process and the medial (rostral) process (Fig. 3).

Muscles attaching to the upper jaw (Fig. 4)

The *adductor mandibulae* A₁ muscle occupies only the lower half of the cheek, the area below the orbit and between it being filled with fatty connective tissue. The muscle is divisible into ventral and dorsal sections. The lower section, A_{1b}, originates from the lower border of the preoperculum, is thin and triangular, but with its ventral border thickly tendinous. Fibre alignment varies from 45° (ventrally) to almost horizontal (dorsally). At the posterior tip of the maxilla, the muscle section is constricted into a bifurcated tendinous

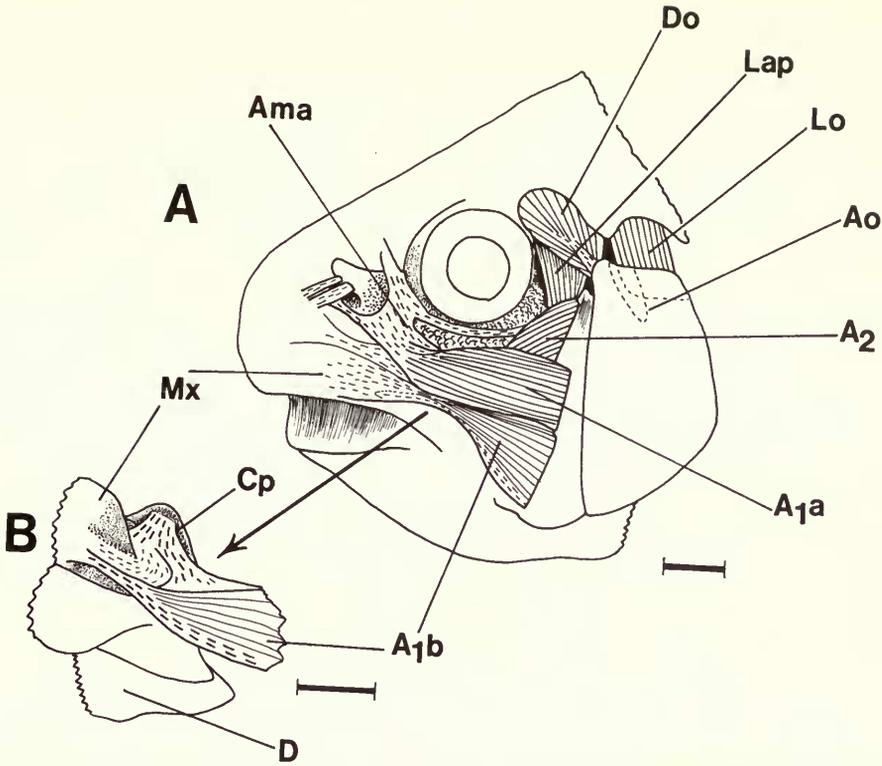


Fig. 4 *Semiplotus semiplotus*. A, lateral view of superficial jaw and cranial musculature. B, detail of jaw muscle insertions. Scale = 5 mm.

area, the outer tendon inserting on a small lateral maxillary process, the inner on the medial maxillary notch (see above, p. 304). The lateral border of the inner tendon (Fmd, Fig. 4B) extends mesially to attach to the lateral face of the dentary coronoid process. The medial fascia of adductor A_{1b} is connected with the lateral body of *adductor mandibulae* muscle A_2 by a thick tendon (see below).

The dorsal section of the *adductor mandibulae*, A_{1a} , originates from the central area of the preoperculum. This portion of the muscle is even thinner than A_{1b} , being only a few fibres in thickness at its origin. The segment is oblong, with an almost parallel arrangement of fibres. The muscle terminates *via* a narrow tendon which forms the lateral segment of a broad, thick aponeurosis (see below). The tendon of insertion reaches the first of the palatine-maxillary ligaments.

The aponeurosis into which muscle A_{1a} inserts is complex (Ama, Fig. 4). Laterally it is joined to the medial face of the 1st infraorbital, and medially to the lateral ethmoid and to the palatines. Ventro-medially the sheet has a posterior extension in the form of a tendinous band which joins onto the anterior edge of the entopterygoid and then expands to become continuous with the medial fascia of muscle A_3 (Fig. 8A).

Upper lip and buccal cavity (Fig. 9)

Epithelial tissue covering the upper jaw is thin and lacks a cornified edge. The inside of the mouth is bordered by a single row of leaf-like lamellae; above this row is a thin, narrow maxillary valve (Mv). The tissue covering the antero-lateral buccal roof is formed into a near longitudinal series of broad leaf-like lamellae (Llm). The surfaces of these lamellae are highly papillose. The vomerine tissue is transversely rugose; there is no vomero-palatine organ (*sensu* Matthes, 1963).

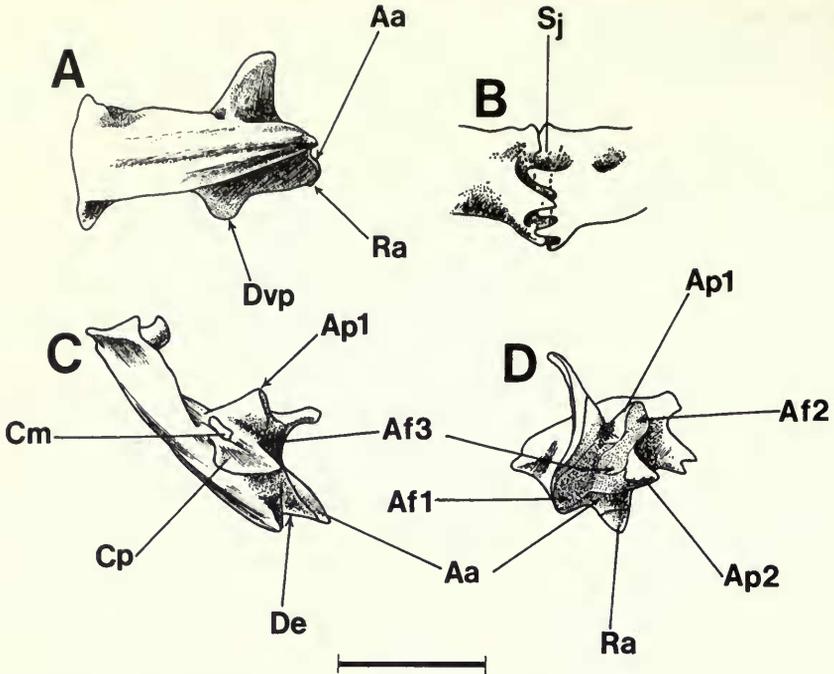


Fig. 5 *Semplotus semplotus*, lower jaw bones. A, lateral; C, dorsal; and D, posterior views. B, medial aspect of dentary joint. Dotted lines indicate the course of a ligamentous connection. Scale = 10 mm.

Lower jaw bones (Fig. 5)

Each *dentary* (Figs 5A & B) articulates with its partner *via* a complex symphyseal joint (Sj). This is basically a peg and socket joint, the central peg being on the dentary of the right side and inserting into a deep notch in the left dentary. Above the joint there is a strong ascending process on each bone, joined syndesmotically to that of its partner. Ventrally, the articulation is more complex (Fig. 5B). Each dentary is extended as a ventral process which is joined to its counterpart *via* a bifurcated, curved articulation. Strong, vertical ligaments connect each facet of this joint.

The wall of the dentary is thick, its dorsal part tapering to a thin edge and curving mesially so as to form a sloped labial surface. On the medial underside of this lip is a deep cavity into which the *intermandibularis* muscle inserts. The lateral face of the dentary bears a deep ridge which tapers posteriorly to a V-shaped process. The coronoid process is high and almost square, its anterior edge curved outward so that when viewed dorsally (Fig. 5C) the plane of the dorsal margin of the coronoid is coincident with that of the body axis. The posterior border of the dentary is blunt with a rounded ventral process corresponding in position to the coronoid process (Dvp, Fig. 5A).

The *anguloarticular* (Aa, Figs 5C & D) is a large, triangular bone, its posterior dorsal edge extending somewhat up the medial face of the dentary coronoid process, following that processes' outward curvature. The articular surface is complex. Postero-laterally there is a triangular facet (Af1, Fig. 5D), its posterior border extending only slightly beyond that of the dentary. The medially directed portion of the anguloarticular is bifurcated. The dorsal process (Ap1) is thickly rounded and directed somewhat dorsally, its posterior face forming a facet (Af2). The ventral process (Ap2) is triangular and is directed slightly ventrally. The medial dorsal process (Ap1) is separated from the outer wall of the bone by a deep, concave channel. The posterior aspect of the anguloarticular is V-shaped and there is a large, figure of 8-shaped facet situated between the dorsal and ventral medial processes (Af3). In lateral

view, only a narrow portion of the anguloarticular is visible beyond the posterior dentary margin.

The *retroarticular* (Ra, Fig. 5D) is a thick wedge lying below the ventral anguloarticular process (Ap2). Laterally, the retroarticular is almost entirely covered by the ventral process of the dentary and only a narrow portion is visible (Fig. 5A).

The *coronomeckelian* (Cm, Fig. 5C) is an almost oblong bone with a rounded posterior border. Its anterior portion projects medially to form a deep, sloped shelf. There is a slight depression on the shelf into which insert the tendons of the *adductor mandibulae* musculature.

Articulation of the lower jaw (Fig. 6)

The complex articular surface of the anguloarticular is matched by an equally complex *quadrate* surface.

The quadrate facet occupies the lateral anterior and medial portions of the bone (Figs 6B & C). The lateral facet (Lqf) is aligned at 45° to the horizontal and apposes the medial face of the lateral anguloarticular process (Afl). The anterior facet is also aligned at 45° and apposes

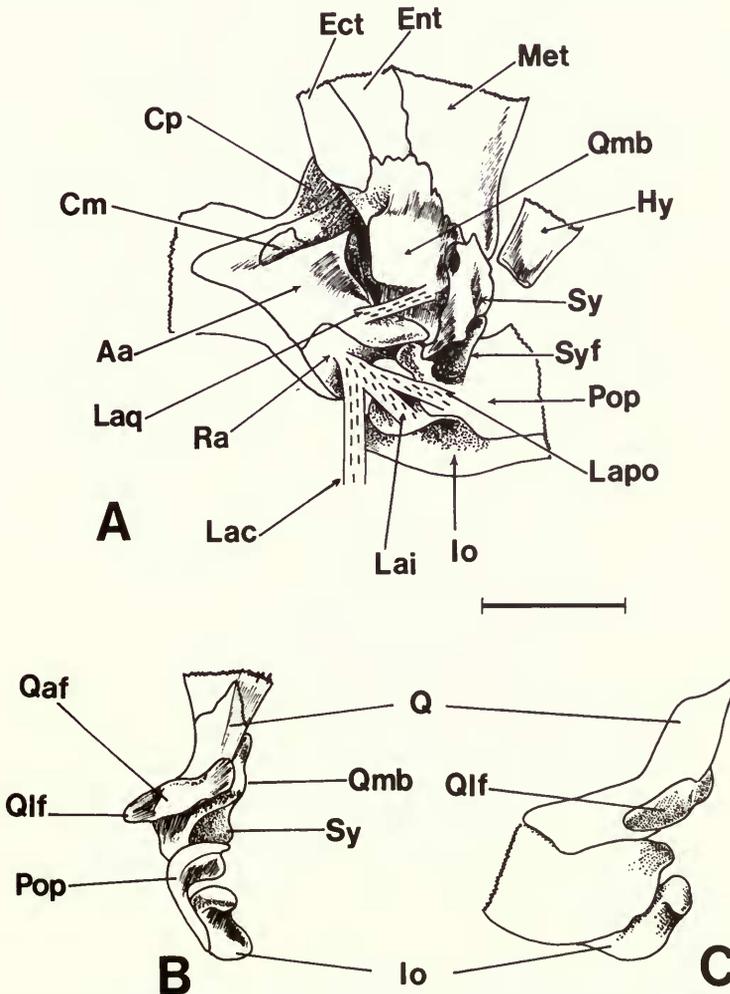


Fig. 6 *Semiplotus semiplotus*, lower jaw articulation. A, medial view of posterior jaw elements and their connections with suspensorial and opercular bones. B, anterior and C, lateral aspects of quadrate and inferior opercular elements. Scale = 5 mm.

the central anguloarticular facet (A_{f3}). The medial part of the quadrate is formed into a buttress with an elliptical anterior face which apposes the dorso-medial anguloarticular facet (A_{f2}). The ventro-medial process of the anguloarticular (A_{p2}) lies below the medial quadrate buttress and is attached to it by a thick ligament (L_{aq}).

Ventrally a complexly divided ligament attaches the jaw to certain opercular and hyal elements. Immediately from its point of attachment to the posterior face of the retroarticular the ligament trifurcates and attaches, (1) to the anterior face of the interoperculum (L_{aio}) which is medially curved and formed into a facet; (2) to the medial face of the preoperculum (L_{apo}) which is formed into a condyle; and (3) to the posterohyal *via* a fascial attachment to the ceratohyal (L_{ac}).

The lateral articulations between the anguloarticular, preoperculum and interopercular bones is covered by a broad ligament which stems from the ventro-lateral face of the quadrate (L_{qi}, Fig. 8A).

Muscles attaching to the lower jaw (Fig. 7)

The muscles having their attachment to the lower jaw are the *adductor mandibulae* A₂ and A₃ (Fig. 7B). The upper portion of muscle A₂ originates from the hyomandibula and the

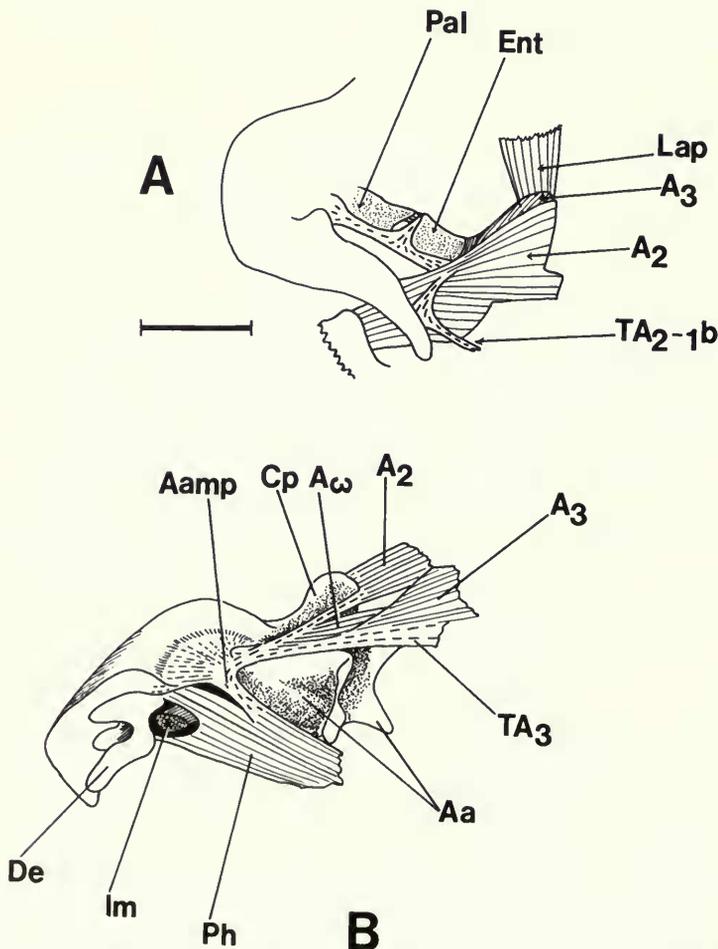


Fig. 7 *Semiplotus semiplotus*, lower jaw musculature. A, lateral view of the deeper muscle elements. B, medial view of jaw muscle insertions and their connection with hyoid musculature. Scale = 5 mm.

lower lateral portion of the preoperculum. All its fibres insert into a medial aponeurosis. From the lateral part of this aponeurosis a narrow tendon runs antero-ventrally into the medial fascia of the adductor muscle (A₁b (Fig. 7A). A bundle of fibres continues forward from the aponeurosis and almost immediately inserts into a thick tendon which terminates on the coronomeckelian bone (sesamoid articular). Insertion of A₂ is *via* a broad tendon onto the dorso-posterior rim of the dentary coronoid process. A thin, inner branch of the tendon continues ventrally down the medial face of the coronoid process to insert on the coronomeckelian bone. Attaching to this tendon is a triangular sheet of muscle fibres crossing from A₃; this most probably represents section A_w of the *adductor mandibulae* series (see Fig. 7B & p. 313).

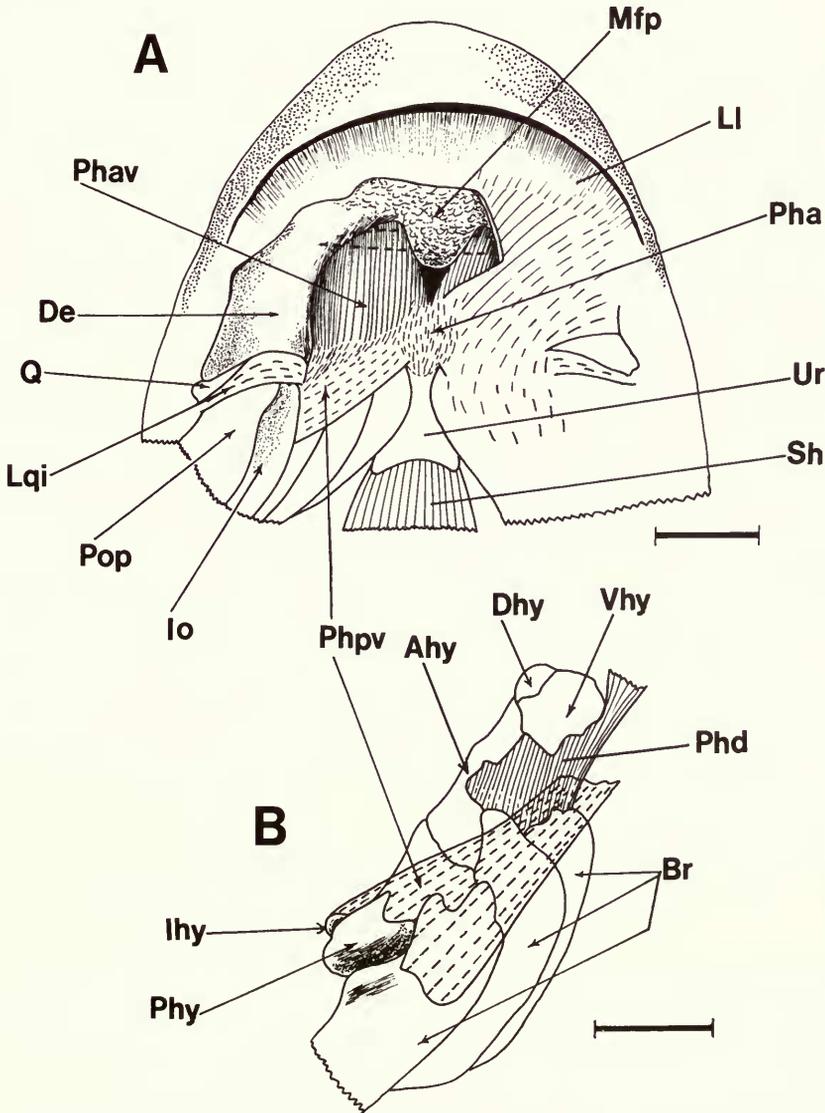


Fig. 8. *Semiplotus semiplotus*, hyoid musculature. A, ventral aspect of head with right side dissected to display major hyoid muscle elements. Dotted lines indicate path of the *intermandibularis* muscle. B, detailed view of *protractor hyoideus* insertions on hyoid elements of the right side. Scale = 5 mm.

Adductor mandibulae muscle A_3 originates partly from the hyomandibula (where it is separated from A_2 by the *levator arcus palatini* muscle) and partly from the deeply concave lateral face of the metapterygoid. Its fibres run almost at right angles to the midline to join the aponeurosis of muscle A_2 . Antero-ventrally, A_3 inserts via a strong tendon which runs through the deep cleft between the medial and lateral portions of the anguloarticular, to join an aponeurosis on the coronomeckelian bone (Fig. 7B). Extending anteriorly from this aponeurosis is a set of thin, tendinous fibres which spread along the inner aspect of the dentary upper margin. These tendinous bands are connected by fibrous tissue to the overlying loose, fatty connective tissue of the lower lip (see below). From the lateral part of the aponeurosis a tendon extends ventro-posteriorly, across the medial face of the anguloarticular, to join the lateral portion of the *protractor hyoideus* muscle (Tcph, Fig. 7B).

The *protractor hyoideus* muscle is a short and thick element divisible into dorsal and ventral sections (Fig. 8A). The ventral portion is X-shaped, the two anterior arms separated by a thick nodule of fatty tissue and each attaching to the medial face of the dentary. Their posterior junction is a thick pad (Pha) from which radiate wide, tendinous bands to form the ventral face of the muscle. These bands insert into the posterior margin of the tissue forming the lower lip (see below). The posterior arms of the muscle are almost entirely tendinous and attach to the branchiostegal rays, and the inner faces of the posterohyal and the interhyal. Each dorsal section of the *protractor hyoideus* is broad and extends from the ceratohyal and the 1st branchiostegal ray to join the ventrohyal. The more medial fibres run into the body of the muscle and insert into the tendinous area just anterior to the ventrohyal (Fig. 8B).

The *intermandibularis* is a thin, cylindrical muscle crossing between the dentaries where it is contained in a small cavity. The muscle separates, transversely, the anterior portions of the *protractor hyoideus* (Figs 8B & 9B).

The lower lip (Fig. 9)

The lower lip of *Semiplotus semiplotus* is a complex structure composed of several tissue types which extend well beyond the outer face of the dentary. Its core is a deep shelf of dense collagenous tissue that surrounds the dentary (Ls). This labial shelf is enveloped in loose, stratified epithelium. The tissue that covers the dorsal surface of the labial shelf is comprised of a thick, fatty epidermal layer (Elt), and an underlying, more fibrous tissue (Mlt). The ventral surface of this tissue adheres to tendinous bands originating from the aponeurosis that incorporates the insertions of the *adductor mandibulae* and *protractor hyoideus* muscles (see above). Thus, toward the lateral part of each dentary the labial epidermis becomes united with jaw and hyoid tendinous elements and only at the symphysis is it firmly attached to each dentary. Anteriorly, where it passes around the leading edge of the labial shelf, the epidermis is thin and cornified, forming a chisel-edge to the jaw (Ks). Ventrally, the epidermis is attached to the labial shelf by thin strands of connective tissue. As it passes beneath the dentary the tissue becomes tendinous and contiguous with the ventral face of the *protractor hyoideus* (see above).

Apomorphic jaw characters in *Semiplotus*

Before considering whether, or to what degree, the jaws of *Semiplotus semiplotus* may be a derived feature, it is necessary to present a model of the plesiomorph cyprinid jaw and its associated articular elements for comparison. The following model is modified from Howes (1980, 1981) and is reckoned to be the plesiomorph type on grounds of its wide-spread occurrence amongst various cyprinid taxa.

The plesiomorph *maxilla* has a well-developed mid-lateral ascending process with convex anterior and concave posterior borders; the *premaxilla* L-shaped with a moderately developed anterior ascending process; *dentary* with a vertical, high, long coronoid process situated posteriorly; the *anguloarticular* with its dorsal border confluent with that of the dentary coronoid process but not extending to cover the medial face of that process, its

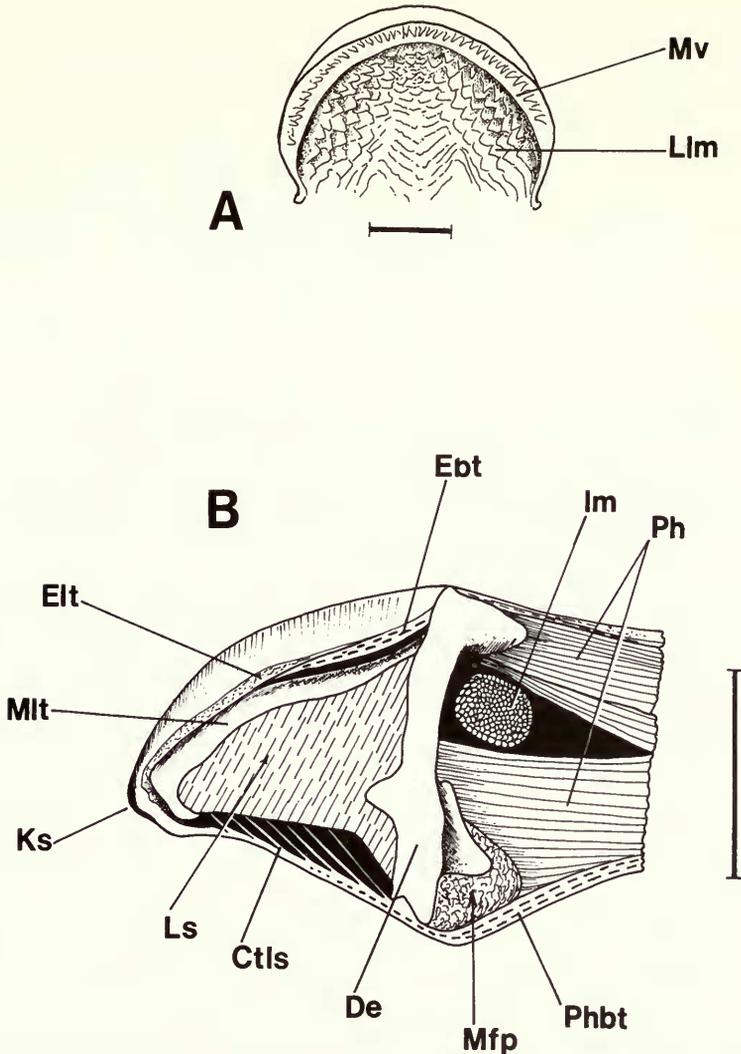


Fig. 9 *Semiplotus semiplotus*. A, ventral view of upper lip and buccal cavity. B, sagittal section through the lower lip and associated hyoid musculature. Scale = 5 mm.

posterior border reaching to well beyond the posterior margin of the dentary, its articular facet transversely concave. All those features are found in the jaws of *Squaliobarbus*, Fig. 10.

The plesiomorph cyprinid *quadrate* is regarded as one essentially broadly triangular in outline and with an anteriorly positioned articular facet.

The plesiomorphic condition of the *adductor mandibulae* A_1 muscle in cyprinids would appear an undivided element having its insertion on the outer, posterior portion of the maxilla (as in aspinine cyprinids; see Howes, 1979). Commonly in cyprinids there are two medial sections of the *adductor mandibulae*. The outer (A_2) inserting on the rim of the coronoid process of the dentary, and the inner (A_3) inserting on the coronomeckelian bone (see Takahasi, 1925 : 20). Primitively, the *mentalis* section (A_w) of the adductor complex is present as a well-developed element (as in the bariliines, chelines, aspinines and cultrines) but in the majority of cyprinid taxa it is reduced or lacking entirely (see Takahasi, 1925 : 20).

According to Takahasi (1925) and Matthes (1963) the *protractor hyoideus* (= *geniohyoideus*) muscle is usually attached to the 1st and/or 2nd branchiostegal rays, rarely to the

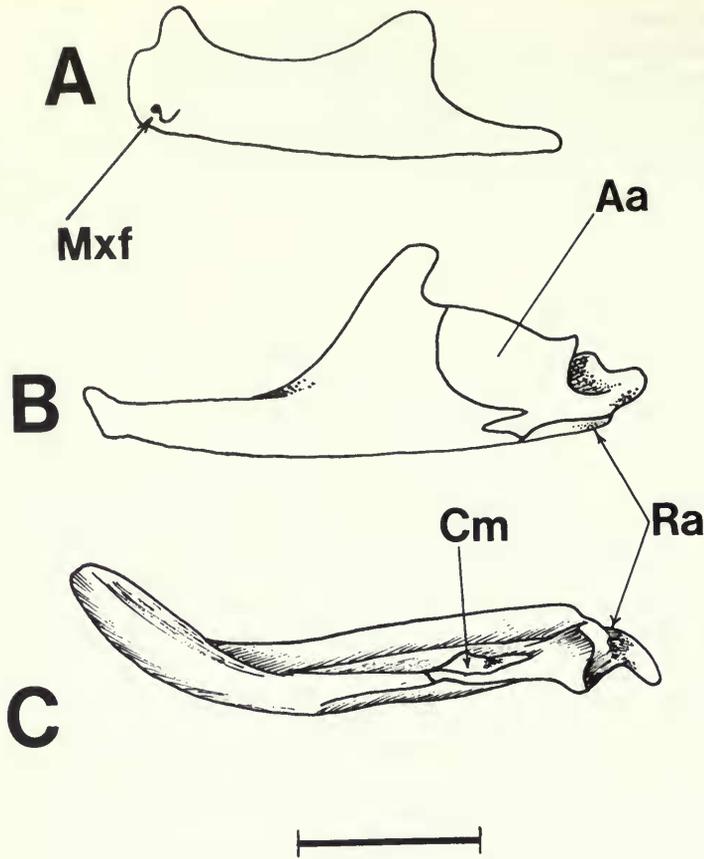


Fig. 10 *Squaliobarbus curriculus*, jaw bones. A, maxilla. B & C, dentary in lateral and dorsal views. Scale = 5 mm.

3rd and never to the interhyal. A tendinous lateral border of the muscle is not uncommon in cyprinids and in many taxa the lateral part of the muscle appears as a separate element.

Semiplotus semiplotus and *S. burmanicus* show markedly derived states of the above hypothesized plesiomorph jaw and muscle morphology. The following features uniquely characterize the jaws of *Semiplotus*:

Upper jaw

1. Premaxilla: shallow, thin, with acute posterior curvature and reduced ascending process.
2. Maxilla: deep, with broad anterior ascending process, reduced mid-lateral process and depressed, notched posterior portion.
3. Bifurcated tendon of muscle A₁ attaching to lateral and medial faces of the maxilla. Some amplification of this character is required. It was noted above that the plesiomorph condition is for muscle A₁ to insert on the outer face of the maxilla. Most often this insertion is tendinous but in bariliine, cheline and aspinine cyprinids it may be musculose across a broad fascia that cover both the dorsal rim of the dentary as well as its lateral aspect (see Howes, 1976 Fig. 23). This, often tendinous, fascia may represent the 'ligamentum primordium' as might the connective tissue in other cyprinids which links the maxilla to the face of the anguloarticular and enwraps the insertion area of the lower jaw musculature. A divided tendinous insertion of the superficial adductor muscle is present in *Cyprinus*, *Carassius* and *Gobio*. However, unlike the semiplotine

condition, the tendons cross over so that the insertion of the lower element (A_{1b}) is above that of the upper (A_{1a}). Takahasi (1925) regarded *Cyprinus* and *Carassius* as representing 'Transitional stages . . .' between the simple bariliine (*Opsariichthys*) and complex gobioid (*Gobio*) types of insertion. Crossing of A_1 tendons also occurs in *Aspidoparia*, a genus with bariliine affinities (see Howes, 1980), *Cosmocheilus*, *Cyclocheilichthys*, *Puntioplites* and *Amblyrhynchichthys*. Whilst it is possible that these four latter genera are closely related, such a relationship appears unlikely between them and *Aspidoparia*. All five taxa have a short, deep ethmoid region and the mouth is inferior in position. It is likely that the crossed tendon arrangement is functionally more efficient, in activating jaws of this kind and has been derived independently in the various taxa.

4. Kinethmoid attached to connective tissue overlying the ethmoid bloc.

Lower jaw

5. Dentary: with a sloped labial surface, lateral ridge, outwardly curved coronoid process, ventral posterior process and a synarthritic joint.
6. Anguloarticular rising dorsally to cover the medial face of the dentary coronoid process, only a small portion of the bone extending beyond the posterior border of the dentary; the medial portion extended and formed into stout and complex articular processes.
7. A medial tendon of muscle A_2 to which is attached muscle A_w . Some amplification of this character is required: As noted above, the common, and presumed plesiomorph condition in cyprinids is for muscle A_2 to insert on the rim of the coronoid process of the dentary. In *Semiplotus* and some *Cyprinion* species (see p. 309) the muscle is bifurcated (see above) with both an outer tendinous insertion on the coronoid process and an inner one on the coronomeckelian bone. A segment of muscle stretches from the lower part of the tendon of muscle A_3 to the anguloarticular and should almost certainly be identified as an A_w . Although a similarly developed muscle stems from the tendon of A_3 in *Varicorhinus beso* (p. 317) and some *Barbus* species (Banister, pers. comm.) it does not insert on a medial tendon of A_2 but on the medial face of the anguloarticular.
8. *Protractor hyoideus* muscle connected anteriorly, via an aponeurosis, with the *adductor mandibulae* insertions; its posterior part tendinous, attaching to all branchiostegal rays, posterohyal and interhyal.
9. Lateral quadrate facet apposing lateral anguloarticular process. Quadrate short and tall.

Comparisons of the jaws in *Semiplotus* with those in *Onychostoma*, *Varicorhinus*, *Capoeta* and *Cyprinion*

Taxa with 'sector mouths', i.e. an inferior mouth which is wide and has an exposed cornified mandibular cutting edge; the dentary invariably has a broad, sloping or deflected labial surface, occur frequently amongst the Cyprinidae. Examples are *Onychostoma*, *Varicorhinus*, *Capoeta*, *Cyprinion*, *Barbus* and some species of *Schizothorax*. Although a cornified lower jaw occurs in *Labeo* and *Garra* it is invariably covered by a thick labial fold.

The jaw morphology of *Onychostoma*, *Varicorhinus*, *Capoeta* and *Cyprinion* species is remarkably similar to that of *Semiplotus*. The similarities may be independently derived, i.e. they are convergent, or inherited through a shared common ancestor, i.e. they are synapomorphic. These hypotheses are tested by comparative analysis.

Onychostoma laticeps Günther, 1896 (Figs 11A–C)

The *premaxilla* is deeper than that of *Semiplotus* and has no distal ventral curvature, its ventral border is also thick and lacks the sharp, thin edge of the semiplotine bone.

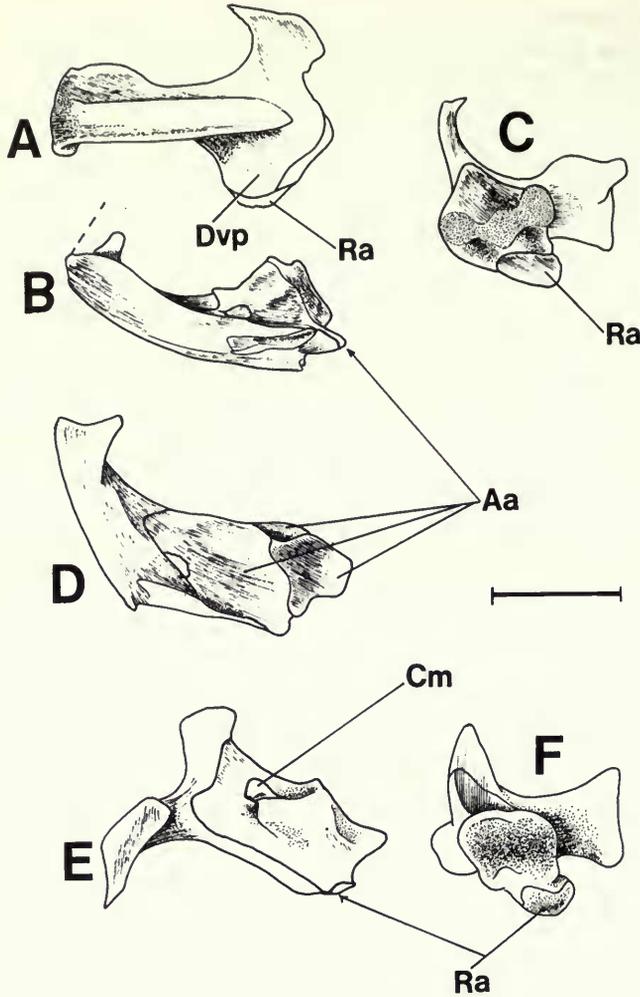


Fig. 11 Lower jaw bones of A, B & C, *Onychostoma laticeps* in lateral, dorsal and posterior views; D, *Varicorhinus beso*, dorsal view; E & F, *Capoeta capoeta* in medial and posterior views. Scale = 5 mm.

The *maxilla* is deep with a broad anterior ascending process. As in *Semiplotus* the mid-lateral process is curved mesially, and although there is a posterior depression of the premaxilla there is no medial notch.

The lower jaw resembles that of *Semiplotus* in a number of features, cf. Figs 5 & 11A. The *dentary* has a bevelled labial surface, a prominent lateral ridge and a postero-ventral process. The coronoid process differs from the semiplotine one and that in other compared taxa in having a markedly concave anterior edge with a long dorso-anterior process. There is no synarthritic joint. The *anguloarticular* is broad, its posterior face shaped into a figure-8 facet. Although the medial portion of the bone forms an articular surface it is not posteriorly extended, nor does it appose a separate facet.

The superficial *jaw musculature* is more complex than in *Semiplotus*. *Adductor mandibulae* A_{1b} is extensive, its lower, preopercular part almost entirely tendinous; insertion is *via* a thick tendon to the lateral maxillary face. Muscle A_{1a} is a parallel fibred element that inserts musculosly on the maxilla above A_{1b}. The anterior part of the adductor

muscle complex is crossed by a band of ligamentous tissue attached dorsally to the inner face of the 1st infraorbital and ventrally to the skin covering the preoperculum (Fig. 12A). Muscle A_2 is a narrow element, its posterior part overlying A_{1a} (Fig. 12B). The muscle's ventral border is tendinous and insertion is *via* a thick tendon on to the posterior rim of the coronoid process. The area of insertion is invested by a thick connective tissue sheath which extends around the coronoid process and laterally attaches to the maxilla. Muscle A_3 can be distinguished from A_2 by its posterior separation by the *levator arcus palatini* muscle, and its separate insertion onto the coronomeckelian bone.

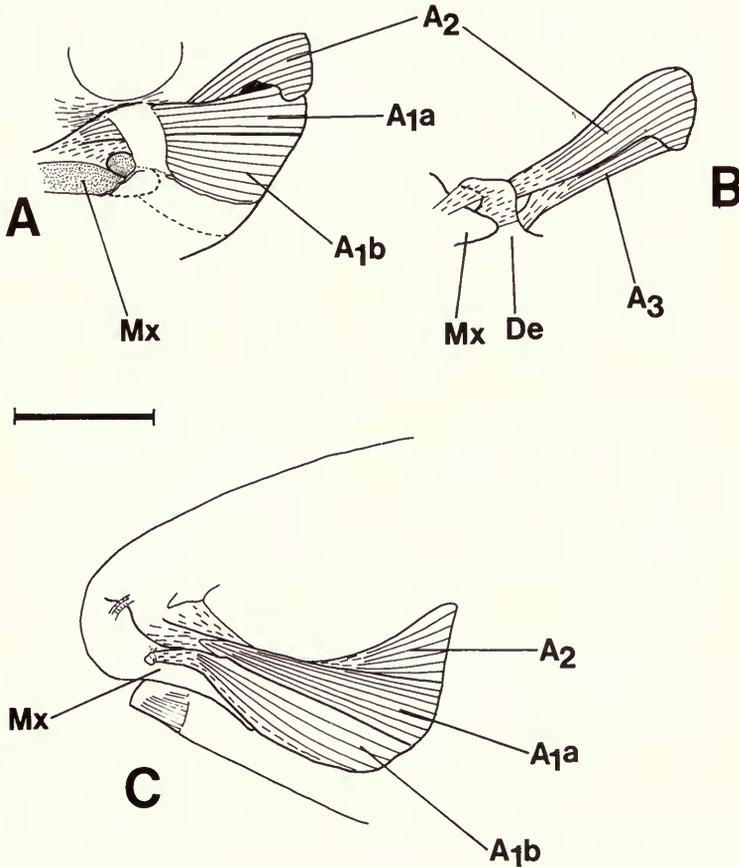


Fig. 12 Jaw musculature of A & B, *Onychostoma laticeps*, A, superficial and B, deeper muscle layers; C, *Cyprinion microphthalmum* superficial musculature. Scale = 5 mm.

The *protractor hyoideus* (Fig. 13A) is complex and composed of several sections. The muscle is organised around a tendon that originates from the interoperculum and meets its partner at a median raphe. The anterior part of the muscle runs from the transverse tendon to the inner rim of the dentary. The symphyseal area of the muscle grades into a thick, fatty connective tissue which becomes confluent with the lower lip tissue. Laterally, there is a separate segment of the *protractor* running to the hyoid arch. A dorsal portion of the muscle extends from the anterohyal and becomes confluent with the ventral section of the muscle. The posterior body of the *protractor* extends from the branchiostegal rays to the central, transverse tendon; it is dense, with its fibres, or strands of fibres widely separated by a fatty and tendinous tissue. The basal layer of the muscle strongly adheres to the dermis of the hyoid area.

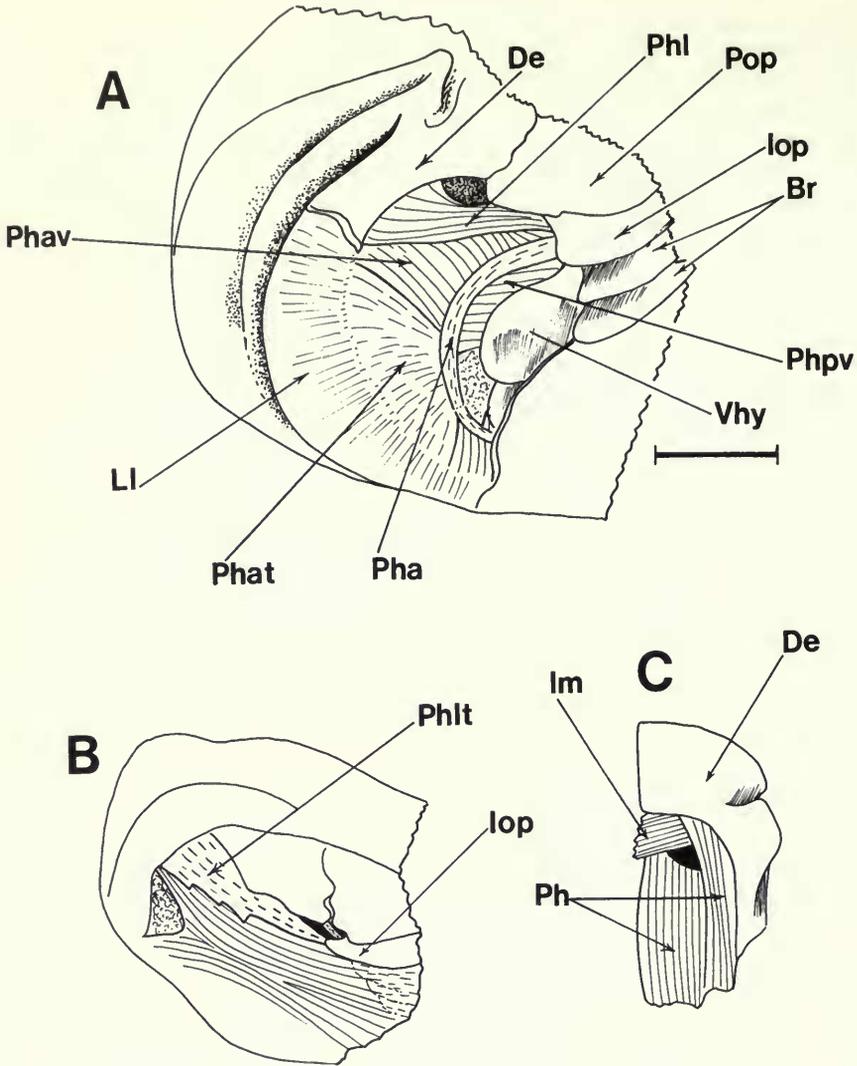


Fig. 13 Hyoid musculature of A, *Onychostoma laticeps* in oblique ventral view. Scale = 10 mm; B, *Varicorhinus beso* in oblique ventral view, and C, *Capoeta capoeta* direct ventral view of left side. B & C are semi-diagrammatic.

The lower lip (Fig. 14)

As in *Semiplotus*, the core of the lip is a deep, broad labial shelf of dense tissue, its dorsal layer (Dls) being of a more fibrous nature. Overlying, and completely free from its dorsal and anterior surfaces is a thick tissue envelope composed of a thin basal layer (Mlt) and a thicker, denser upper layer (Elt) whose lingual portion rises above the dentary rim. Anteriorly the epidermal layer is transformed into a keratinized sheath. Sandwiched between the labial shelf and the basal layer is a thin keratinized band (Mkl) that extends along the central portion of the labial shelf. Ventral to the shelf are layers of tissue which are the counterparts of those lying dorsally. The ventral dermal and epidermal layers (Vmlt, Velt) are, however, firmly attached to the shelf. Unlike *Semiplotus*, there are no tendinous bands connecting the dorsal lip tissue directly with the *protractor hyoideus* muscle and neither, apart from the epidermis, is the ventral tissue contiguous with that muscle.

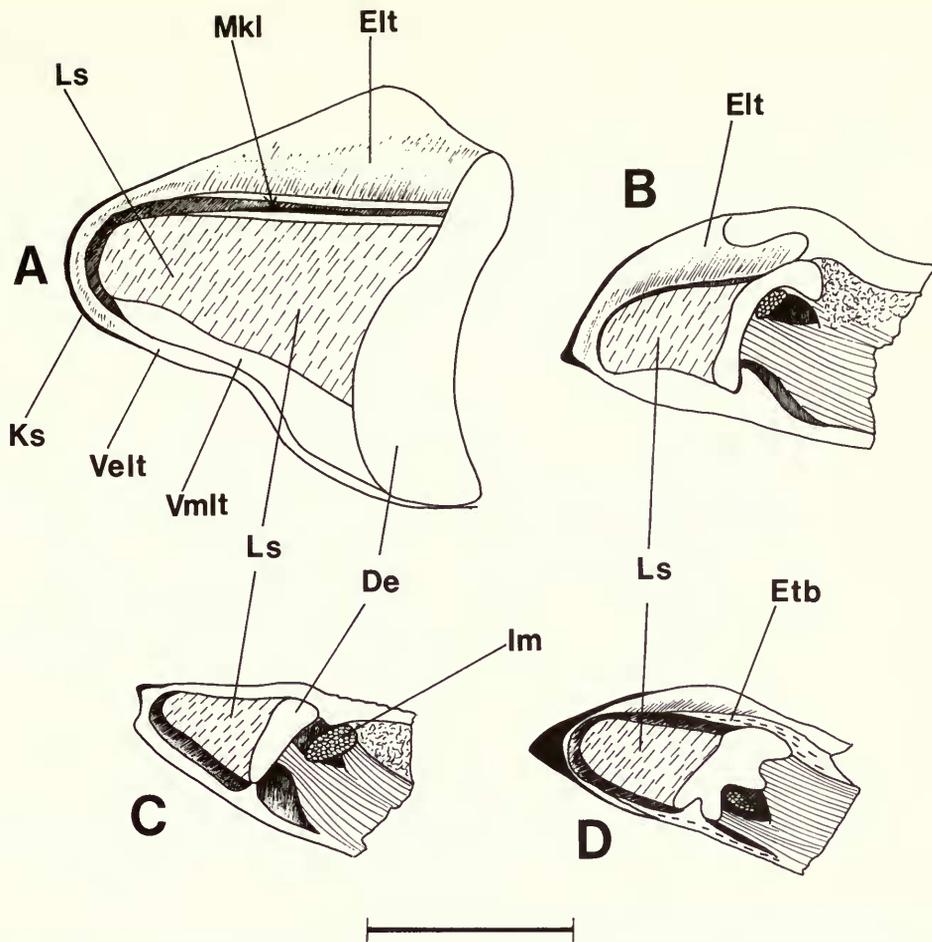


Fig. 14 Sagittal sections through the lower lips of A, *Onychostoma laticeps*; B, *Varicorhinus beso*; C, *Capoeta capoeta*; D, *Cyprinion macrostomum*. Scale = 10 mm.

Varicorhinus beso Ruppell, 1836

The *premaxilla* is shallow and lacks a prominent anterior ascending process; the *maxilla* has broad and thick anterior, and long, mesially curved mid-lateral processes. Unlike *Semiplotus*, the posterior portion of the maxilla is not expanded, compressed or medially notched.

The *dentary* (Fig. 11D) has an abrupt mesial curvature with a broad labial surface and a laterally protruding process at the rictus; its coronoid process is tall and slopes outward. The *anguloarticular* is short and broad, its anterior tip extending beyond the base of the coronoid process. Unlike *Semiplotus* the articular facet is not developed into medial processes, and it is transversely aligned.

The *quadrate*, like that in *Semiplotus*, is short and deep with an expanded articulatory facet. The facet is a double ellipsoid inclined at 45° to the transverse horizontal. In contrast to *Semiplotus* the facet is confined to the anterior face of the bone, no part extending to the lateral surface.

The jaw musculature differs from *Semiplotus* in that *adductor mandibulae* muscle A_1 has a single tendinous insertion on the maxillary outer face. A small A_w portion fans out from the tendon of A_3 across the anguloarticular and part of the coronoid process. The *protractor hyoideus* is strongly developed, its main portion attaching tendinously to the 1st and 2nd

branchiostegal rays and to the posterohyal (Fig. 13B). A lateral part attaches *via* a strong tendon (almost ossified in large specimens) to the anterior tip of the interoperculum, a feature not found in *Semiplotus*. Its anterior part becomes tendinous and fans out to attach along the posterior rim of the dentary (Fig. 13B).

The *lower lip*, although having the same basic structure as in *Semiplotus* has a less complex histological structure (Fig. 14B). The differences are a shallower labial shelf, lack of a basal dermal tissue layer, the dermis united at its central portion with the labial shelf, and more extensive keratinization of the anterior epidermis. There are no tendinous connections between the lip tissue and the *protractor hyoideus* muscle.

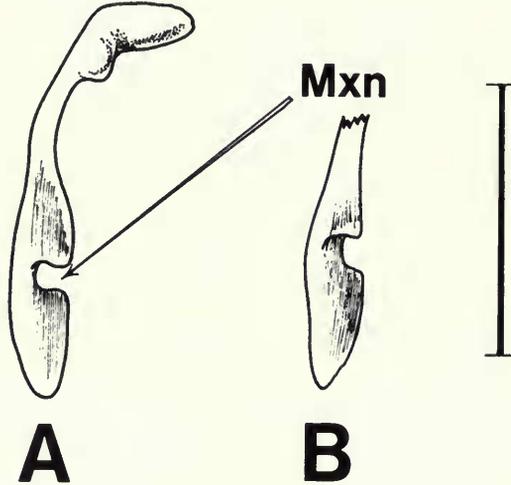


Fig. 15 Premaxillae in dorsal view of A, *Cyprinion watsoni*; B, *Capoeta capoeta* posterior portion only. Scale = 5 mm.

Capoeta capoeta Guldenstadt, 1773

The *premaxilla* lacks an anterior ascending process; the *maxilla* has a marked mesial curvature, a thick and wide anterior and a shallow mid-lateral ascending process. The posterior arm of the maxilla, as in *Semiplotus*, is compressed and medially notched (Fig 15).

The *dentary* has the same abrupt medial curvature and antero-ventrally sloped labial surface as in *Varicorhinus beso* (Fig. 11E). Unlike *Semiplotus*, *Onychostoma* and *Varicorhinus*, the coronoid process is aligned at 45° to the midline, so that it is set at the curve of the dentary. The ventro-posterior surface of the dentary is broad, as is the depressed anguloarticular which overlies it. The articular facet is ovate and transversely aligned (Fig. 11F).

The jaw musculature of *Capoeta* is similar to that of *Semiplotus* and *Varicorhinus*. *Adductor mandibulae* A₁ is a single muscle with a central anterior aponeurosis; insertion is *via* a thick tendon onto a lateral maxillary process. A thin tendinous strip of tissue runs from the dorso-anterior part of the muscle to insert on the connective tissue covering the medial face of the maxilla. Muscle A₂ inserts entirely on the posterior border of the dentary coronoid process; a separate group of fibres leaves the main tendon to run ventrally across the medial coronoid face. Tendon A₃ inserts on the coronomeckelian bone.

The *protractor hyoideus* is extensively tendinous in its posterior part and it is attached to all the hyoid elements except the interhyal. There is no lateral portion stemming from the interoperculum as in *Varicorhinus*. Anteriorly the left and right arms of the muscle are widely separated so that the *intermandibularis* is exposed (Fig. 13C).

The *lower lip* differs from that in the other taxa compared here in having a narrow labial shelf, no layered organisation of the tissue overlying the shelf, and this tissue continuous with

that lining the mouth. The outer, keratinized sheath lies along the upper edge of the labial shelf rather than around its anterior face.

Cyprinion Heckel, 1843

In *Cyprinion* species, the *premaxilla* usually lacks an ascending process, and when one is present it is but slightly developed. Maxillary shape is interspecifically variable and in only one species, *C. watsoni*, does it closely resemble *Semiplotus* in having a reduced, medially directed mid-lateral ascending process and a depressed, medially notched posterior arm (Fig. 15).

The lower jaw of *C. macrostomum* and *C. microphthalmum* resembles that of *Semiplotus* more closely than does that of any other *Cyprinion* species. This resemblance is in the

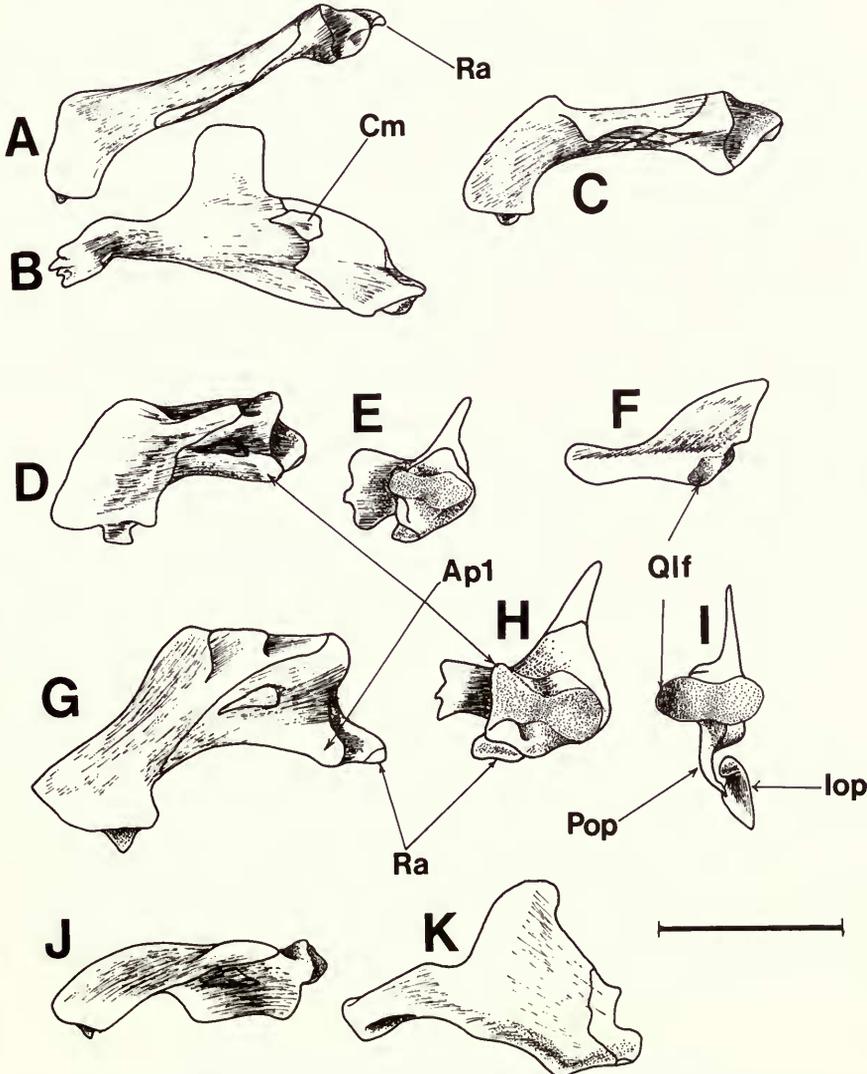


Fig. 16 Lower jaw bones (right side) of A & B, *Cyprinion acinaces* in dorsal and medial views; C, *Cyprinion watsoni* in dorsal view; D & E, *Cyprinion microphthalmum* in dorsal and posterior views; F, quadrate in lateral view; G & H, *Cyprinion macrostomum* in dorsal and posterior views; I, quadrate in anterior view; J & K *Cyprinion kais* in dorsal (right jaw bone) and lateral (left jaw bone) views. Scale = 5 mm.

curvature of the dentary, a complex synarthritic joint and the broad articular surface of the anguloarticular. There is a slight medial process, equivalent to process Ap1 in *Semiplotus*, separated from the lateral part of the bone by a deep cleft. Both *Cyprinion* species also possess a quadrate bearing part of its articular facet laterally (Fig. 16F). *Cyprinion watsoni* has a more elongate jaw than *C. microphthalmum* and *C. macrostomum*, but the anguloarticular has a similar broadening of its facet.

With the exception of *C. microphthalmum* the muscles attaching to the upper jaw are undivided or only partially divided. In that species the *adductor mandibulae* A_{1a} is separated from A_{1b} for almost its entire length but shares a common insertion with it on both the outer and inner aspects of the maxilla (Fig. 12C). The lower jaw muscles are also interspecifically variable with respect to their proportions and fibre orientation, but their insertions are essentially similar. There is some variability in the size of muscle A_w. In *C. microphthalmum* and *C. macrostoma*, as in *Semiplotus* it inserts on a medial tendon of muscle A₂.

The lower jaws of *C. acinaces*, *C. milesi* and *C. watsoni* are less derived with respect to their labial and articular surfaces but all have a synarthritic joint of varying complexity, the weakest being in *C. acinaces* (Fig. 16A). The jaw of *C. acinaces* is regarded as the most plesiomorph of all *Cyprinion* species with respect to its moderately expanded labial surface, mid-laterally placed coronoid process and small, transverse articular facet. The lower jaw of *C. kais* is deeper posteriorly than in any other *Cyprinion* species, and its labial surface is much narrower (Fig. 16J); as in *Semiplotus*, the anguloarticular covers a substantial area of the medial face of the dentary coronoid process. In all *Cyprinion* species, the anguloarticular extends posteriorly only marginally beyond the dentary.

The lower lip of *Cyprinion* is of the same layered type found in *Semiplotus* (Fig. 14D), with that of *C. macrostoma* having the greatest resemblance in terms of dimensions of the labial shelf, tissue layering, and tendinous connections with the *protractor hyoideus* muscles. The degree of keratinization is interspecifically variable but reaches its greatest development in *C. macrostomum*.

Onychostoma, *Varicorhinus* and *Capoeta* all lack the *Semiplotus* features of a synarthritic mandibular joint, medial anguloarticular processes, lateral quadrate facet, aponeurotic connection of the *adductor mandibulae* and *protractor hyoideus* muscles, interhyal connection of the *protractor hyoideus*, and complexity of lower lip structure. *Onychostoma* shares with *Semiplotus* a lateral dentary ridge and posteroventral process, but the nature of the coronoid process and the lack of the apomorphies cited above favour the hypothesis that the derived jaw characters held in common have been independently acquired. Likewise, the sector type of mouth morphology of *Varicorhinus* and *Capoeta* is believed to be a convergent feature.

The phyletic relationships of *Onychostoma*, *Varicorhinus* and *Capoeta* have yet to be determined, but other apomorphies (absent in *Semiplotus* and *Cyprinion*) suggest the following affinities: *Onychostoma* is related to *Ageniogarra* and possibly to a group of Chinese 'Schizothorax'; *Varicorhinus* forms a close relationship with certain African *Barbus* (Banister, in preparation); *Capoeta* is the likely sister-group to *Cyprinus* and *Carassius* (see Howes, 1981).

As noted above all *Cyprinion* species possess a synarthritic mandibular joint, aponeurotic connection of the *adductor mandibulae* and *protractor hyoideus* muscles and similarly developed lower lip structure. Synapomorphies other than those of the jaws also suggest a close relationship between *Semiplotus* and *Cyprinion*.

Other apomorph characters of *Semiplotus*

In addition to the jaws, *Semiplotus* species are characterized by other and presumed apomorphic features.

1. *Condylar articulation of the interhyal with the symplectic*. The usual condition in cyprinids is for the symplectic to be an elongate bone. It is rarely short and deep, and

only in a minority of taxa is the posterior face concave and in articulation with the interhyal. The common condition of the interhyal is a lamellate bone, sometimes incompletely ossified.

In *Semiplotus* the symplectic is short and buttress-like (Figs 6 & 17A), its posterior surface is concave and articulates directly with the interhyal, thereby forming part of the ball and socket joint between the two elements. The interhyal is short and cylindrical, and articulates with the dorsal surface of the posterohyal *via* a cartilaginous meniscus.

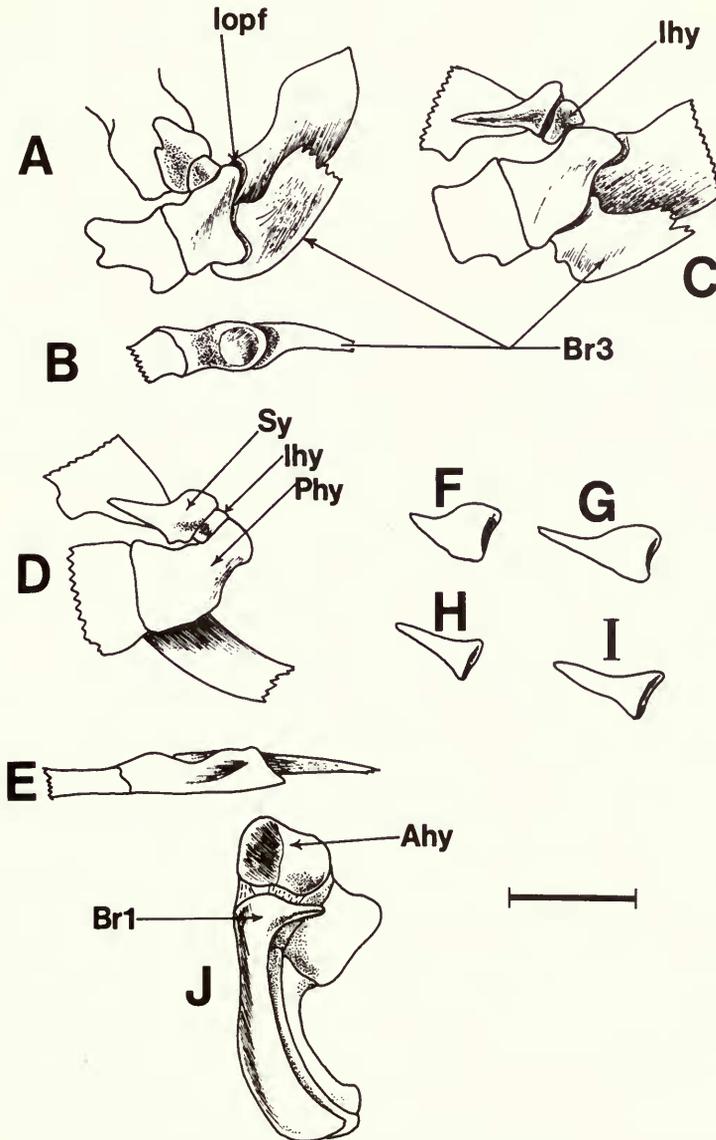


Fig. 17 Hyoid and suspensorial elements of A & B, *Semiplotus semiplotus*, medial and dorsal views of posterior hyoid bar; C, *Cyprinion macrostomum*, medial view of posterior hyoid bar; D & E, *Varicorhinus beso*, medial and dorsal views of posterior hyoid bar; F-I, symplectic bones of F, *Cyprinion microphthlamum*; G, *C. kais*; H, *C. acinaces*; I, *C. watsoni*; J, *Cyprinion kais*, anterior view of 1st branchiostegal ray and hyoid bar. Scale = 3 mm.

Amongst the taxa considered here, only in *Onychostoma* and some species of *Cyprinion* does the symplectic approach that of *Semiplotus* in size and shape. In *Onychostoma*, the condylar surface of the bone faces ventrally whereas in *Semiplotus* and *Cyprinion* it is angled postero-ventrally. The interhyal in all these genera, and in *Varicorhinus*, is hypertrophied and articulates with the dorsal aspect of the postero-hyal, but since there are no other synapomorphies of the hyoid elements shared by *Onychostoma*, *Varicorhinus* and *Semiplotus*, these are considered to be independently derived features (see p. 320).

2. *Ventral and lateral articulation of the 3rd branchiostegal ray with the posterohyal* (Figs 17A & B). Plesiomorphically the 3rd branchiostegal is attached ligamentously to the lateral face of the posterohyal. In *Semiplotus*, the posterohyal is short and thick, and the branchiostegal ray expanded medially so as to form a shelf underlying the ventral border of the posterohyal with whose posterior portion it articulates. The anterior part of the branchiostegal shelf is attached ligamentously to the medial face of the posterohyal whilst the proximal lamellate area of the branchiostegal ray is attached to the lateral face of the hyal.

A slight medial shelf is present on the 3rd branchiostegal rays of *Varicorhinus* and *Capoeta*. It is, however, barely developed in these taxa and the posterohyal is not distally expanded as in *Semiplotus* (Fig. 17). Such an expansion of the branchiostegal is lacking in *Onychostoma*. Only in *Cyprinion* is there a substantial 3rd branchiostegal shelf, which in *C. macrostomum* is developed much as in *Semiplotus* (Fig. 17).

3. *Ventrally directed supraethmoid and hypertrophied vomer* (Figs 18A–C). Although the rostral curvature of the ethmoid bloc is variable in the Cyprinidae (see Howes, 1980) nowhere is it more extreme than in *Semiplotus* where the supraethmoid is almost vertically aligned. An apparent correlate of this condition is the hypertrophied vomer, whose enlargement also results in a steep angle forming between it and the parasphenoid (Fig. 18A).

In both *Onychostoma* and *Varicorhinus* the ethmoid is strongly curved ventrally and there is a corresponding hypertrophy of the vomer. In these genera the ventrally directed part of the supraethmoid is confined to the lower part of the bone. In *Cyprinion macrostomum* the curvature of the supraethmoid more closely resembles the condition in *Semiplotus* where the entire bone slopes ventrally.

4. *Frontal-supraethmoid foramen* (Figs 18B–C). Synapomorphic for *Semiplotus semiplotus* and *S. burmanicus* is a foramen between the frontals and the supraethmoid (see p. 304). The posterior border of the foramen indents each frontal to form a notch in much the same way as the antero-medial supraethmoid notch occurs in other cyprinids. Likewise, the frontal notch of *Semiplotus* performs a similar function, namely in providing a hold-fast for the kinethmoid ligaments. Attachment of kinethmoid ligaments to the frontal instead of the supraethmoid is unknown in any other cyprinid.
5. *Elliptical subtemporal fossa with major contribution from the pterotic* (Fig. 18D). The plesiomorph subtemporal fossa is shallow with a round or oval outline (see Howes, 1981). In *Semiplotus* the fossa is deep and markedly ellipsoidal, its long axis transverse. Only in *Onychostoma* does the subtemporal fossa approach the shape of that in *S. semiplotus* and *S. burmanicus*, but it lacks the extreme depth of those species.

Typically the posterior wall of the subtemporal fossa in cyprinids is formed principally by the exoccipital, with a minor contribution from the pterotic (see, for example, Howes, 1978, Figs 6 & 33; 1980, Fig. 13). In *Semiplotus* the greater part of the posterior wall is formed by the pterotic (Fig. 18D); only in *Cyprinion* is there a similarly substantial contribution of the pterotic.

6. *Proximal part of supraoccipital crest formed by the parietals* (Fig. 19A). *Semiplotus* species have a high supraoccipital crest; the parietals are short and slope upwards, their medial portions extending posteriorly and embracing the base of the supraoccipital crest. With the exception of *Cyprinion*, in no other cyprinid taxon, even

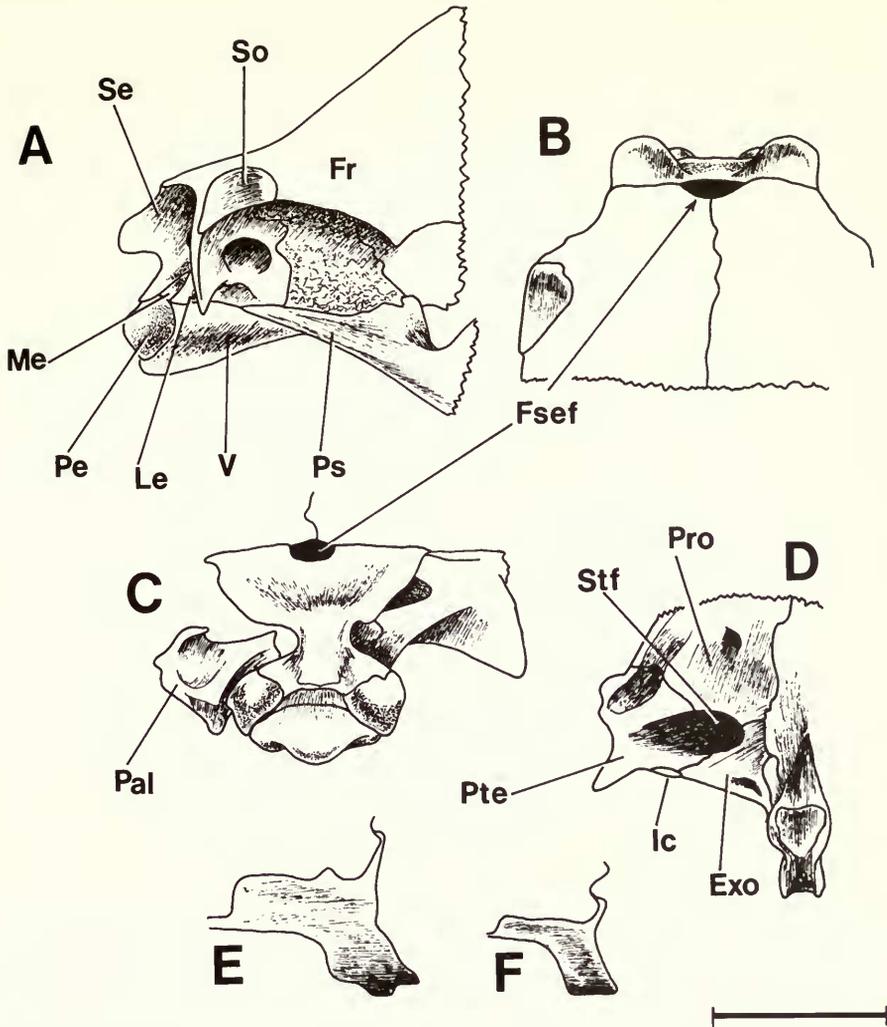


Fig. 18 *Semiplotus semiplotus*, cranium. A, lateral view of ethmo-vomerine and orbital areas; B, dorsal & C, anterior views of ethmoid region; D, ventral view of posterior cranial area; E & F, basioccipital process in lateral view of E, *S. semiplotus* and F, *S. burmanicus*. Scale = 10 mm.

those with a relatively high supraoccipital crest, does the parietal extend postero-medially. In *Cyprinion* there is some variability in the length of the parietal, but in all species it extends postero-medially to form part of the supraoccipital crest (Figs 19B–C).

7. *Reduced basioccipital process and masticatory plate* (Figs 18E & F).

Although a reduction of the basioccipital process and masticatory plate occurs in several groups of cyprinids (see Howes, 1981), in none is the reduction so extreme as in *Semiplotus*. In *S. burmanicus*, the basioccipital (masticatory) plate is entirely absent and the ventral (aortic) ossification is transversely convex. Only in some *Cyprinion* species (*C. kais* and *C. microphthalmum*) is a truncated basioccipital process associated with marked reduction of the ventral plate.

8. *Interoperculum-preoperculum articulation* (Figs. 6B–C).

In *Semiplotus* the anterior tip of the preoperculum is formed into a condyle and is curved medially so as to overlies the anterodorsal part of the interoperculum; the

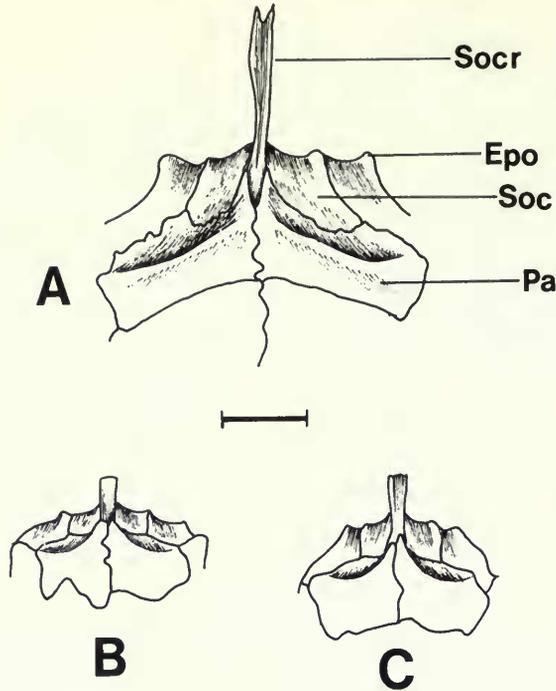


Fig. 19 Dorsal posterior cranium of A, *Semiplotus semiplotus*; B, *Cyprinion macrostomum*; C, *Cyprinion kais*. Scale = 5 mm.

anterior tip of the interoperculum is formed into a facet. The two elements are firmly articulated and the medial curvature of the preoperculum beneath the quadrate appears to reinforce the rigidity of the quadrate-lower jaw articulation. The interoperculum also bears a medial facet with which the rounded tip of the posterohyal articulates.

In *Varicorhinus* there is a similar development of the terminal point of the interoperculum, but only in *Cyprinion* do both elements articulate as in *Semiplotus* (Fig. 16I). A medial interopercular facet is variously developed in the Cyprinidae, but in *Cyprinion* alone is it of similar depth and position.

9. *Development of the supraneurals and articulation with 1st dorsal pterygiophore* (Fig. 20).

The supraneurals of *Semiplotus* are hypertrophied and each is in contact with its respective neural spine. The 'neural complex' of the Weberian apparatus is upright and has an almost straight anterior edge; dorsally it contacts the posteriorly directed supra-occipital process. This is contrary to the usual cyprinid condition where the anterior border of the neural complex is concave, giving it an axe-shaped appearance. In *Semiplotus semiplotus* there are 5 or 6 supraneurals, each articulating with its neighbour; the posterior element is bifurcated and overlaps the anterior margin of the 1st dorsal pterygiophore. *Semiplotus burmanicus* has 7 supraneurals, all somewhat thinner than in *S. semiplotus* but similarly and sequentially joined, each bearing a vertical ridge laterally. The 1st supraneural is narrowly separated from the neural complex.

Although enlarged supraneurals occur in other cyprinid taxa they are never so tall as those in *Semiplotus semiplotus*. Apart from *S. burmanicus*, interlocking of the last supraneural with the 1st pterygiophore occurs only in *Cyprinion macrostomum*, and a straight-edged neural complex is shared only with *Cyprinion microphthalmum*.

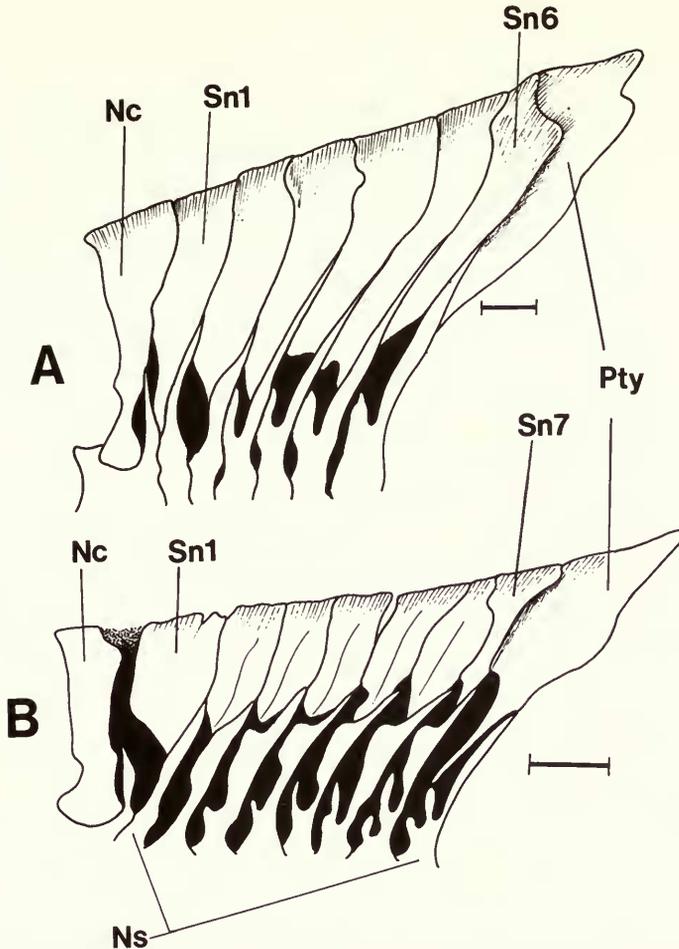


Fig. 20 Anterior vertebral column of A, *Semiplotus semiplotus*; B, *S. burmanicus*. Scale = 5 mm.

The relationship between *Semiplotus* and *Cyprinion*

In addition to the jaw synapomorphies (p. 320), *Semiplotus* shares with *Cyprinion* species a series of derived hyoid, cranial and vertebral features (enumerated above as 1–9), some of which are present in all *Cyprinion* (1, 2, 5, 6, 8), others in only some species of that genus (3, 7, 9).

At present, the genus *Cyprinion* cannot be defined on the basis of even a single autapomorphy. Derived characters such as the expansion of the proximal portion of the pelvic fin rays, interpelvic papillate flaps (see Banister & Clarke, 1977) and a naked pre-dorsal ridge (see Mirza, 1969) although synapomorphic for some species do not occur in all members of the genus. If, however, the concept of *Cyprinion* is expanded so as to include *Semiplotus*, then the taxon so formed is recognisable as a monophyletic unit on the basis of several synapomorphies (the principal one being the presence of a synarthritic dentary joint), and the problem posed by those apomorphies shared by *Semiplotus* and some *Cyprinion* species is also overcome. Thus (following Heckel, 1843; see p. 331), *Semiplotus* is regarded as a junior synonym of *Cyprinion* and any references to *Cyprinion* from here onwards must be taken to include *Semiplotus semiplotus* and *S. burmanicus*. (A synopsis of included taxa is given on p. 331.)

Discussion

Apomorph character distribution in *Cyprinion* species

If the jaws of *Cyprinion semiplotum* are seen as the terminal stage of increasing complexity, then there is a possibility that an evolutionary or 'transitional sequence' of jaw types might reflect the pattern of interspecific relationships within the genus *Cyprinion*. However, such an arrangement of increasingly derived jaw morphology (in terms of hypertrophy or reduction of various elements) is not congruent with polarized morphoclines in other characters amongst *Cyprinion* species.

Jaw synapomorphies possessed by *C. semiplotum* and *C. burmanica* unite them with other *Cyprinion* species in the following patterns:

- (i) A greatly increased complexity of the mandibular synarthritic joint, a broad angulo-articular with a medial process and a cleft between the lateral and medial faces of the bone. Shared with *C. macrostomum*, *C. microphthalmum* and *C. watsoni*.
- (ii) A lateral quadrate facet and a medial A₂ tendon. Shared with *C. macrostomum* and *C. microphthalmum*.
- (iii) A medial maxillary notch. Shared with *C. watsoni*.
- (iv) A divided insertion of *adductor mandibulae* A₁ muscle. Shared with *C. microphthalmum*.

Any 'transitional series' present amongst this character complex is interrupted by the distribution of characters (iii) and (iv). The following synapomorphies uniting *C. semiplotum* and *C. burmanica* among other *Cyprinion* species display incongruent patterns when set against those of the jaw:

- (v) A deep symplectic and a truncated basioccipital process with a reduced masticatory plate. Shared with *C. kais* and *C. microphthalmum*.
- (vi) A straight-edged neural complex. Shared with *C. microphthalmum*.
- (vii) Articulation of the last supraneural with the 1st pterygiophore.
Shared with *C. macrostomum*.

Synapomorphies which are not present in *C. semiplotum* and *C. burmanica* unite the following species:

- (viii) 1st branchiostegal ray articulating ventrally with the ceratohyal through a long medial process (Fig. 17). Shared only by *C. macrostomum* and *C. kais*. (*Cyprinion kais*, it should be remembered has neither of the derived jaw characters (i) nor (ii) which *C. macrostomum* shares with other species).
- (ix) Pelvic flaps and papillate interpelvic region. Shared by *C. watsoni*, *C. acinaces* and *C. milesi*. The two latter species are conservative in their cranial and jaw morphologies (see p. 320) and are thought to comprise the plesiomorph lineage within the genus. Thus, unlike *C. watsoni*, *C. acinaces* and *C. milesi* share none of those characters that distinguish the more derived lineage (see (i) and (ii) above).

In virtually all monophyletic assemblages of cyprinid fishes so far identified there are sets of incongruent apomorphies, a state of affairs which makes it impossible to apply a rigidly dichotomous system of relationships. Such incongruencies usually can be ascribed to some form of homoplasy, particularly when the characters in question occur in outgroups, as for example the medial maxillary notch present in *Cyprinion semiplotum*, *C. burmanica*, *C. watsoni* and also in *Capoeta*. Here the most likely explanation for its presence in *Capoeta* and *Cyprinion* is one of parallelism as no other synapomorphies unite *Capoeta* with *Cyprinion*; see p. 320. However, its distribution within the three *Cyprinion* species can only be accounted for most parsimoniously by assuming its loss in two other species (*C. microphthalmum* and *C. macrostomum*).

Other character sets also reveal incongruency when treated dichotomously. For example, in *Cyprinion kais* one must postulate the loss of all jaw synapomorphies plus the parallel evolution in this species and in *C. semiplotum*, *C. burmanica* and *C. microphthalmum* of similarly derived symplectic and basioccipital characters. Furthermore, the loss of a

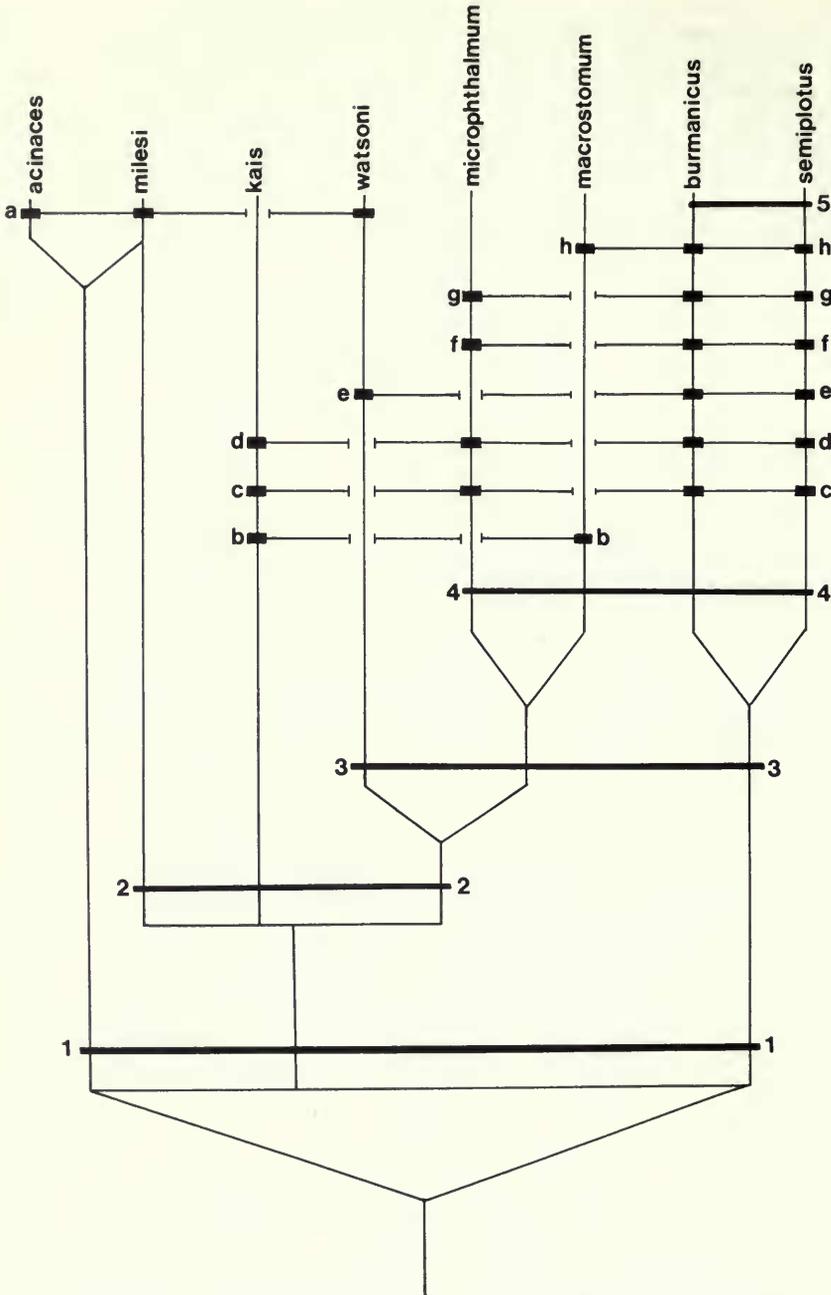


Fig. 22 Reticulate synapomorphy scheme for *Cyprinion* characters Level 1, *Cyprinion* synapomorphies (see text, p. 325); 2, expanded pelvic fin rays; 3, increased complexity of synarthritic joint, broadened anguloarticular with medial process A_3 ; 4, lateral quadrate facet, medial A_2 tendon, interopercular-preopercular articulation; 5, jaw and cranial synapomorphies (see text, p. 312). *Conflicting synapomorphies*: (a) interpelvic papillate flaps; (b) articulation of 1st branchiostegal ray; (c) upright neural complex; (d) divided *adductor mandibulae* A_1 ; (e) medial maxillary notch; (h) supraneural-ptyerygiophore articulation. Black boxes indicate the presence of that character on a particular lineage, a break in the horizontal indicates its absence.

the greatest number of synapomorphies as an assessment of relationship is avoided (Tarsitano & Hecht, 1980: 178). Likewise, the alternative approach, using unresolved polychotomies, serves only to indicate that there is an absence of characters rather than the presence of conflicting ones.

It may be argued that the choice of character sets employed here is itself a weighting procedure, and that the use of other sets would reveal dichotomous sister-group relationships. The counterclaim to these arguments is that the characters employed are those whose intraspecific variability is known, and indeed are the only definitive characters recognizable at this level of investigation. Cyprinids are 'notorious' for their conservative characters (see for example Regan, 1911). Banister (1980) held that this conservatism '... coupled with the occasional small saltatory morphological changes ... has the effect of making it difficult, if not impossible to distinguish between parallelism and the sharing of characters derived through common ancestry'. In each of the cyprinid groups so far identified as monophyletic (the aspinines, chelines, bariliines and abramines) one lineage appears as the bearer of a large number of autapomorphies and thus leaves a considerable 'morphological gap' between it and the more conservative corpus of lineages comprising that particular group. Examples are *Macrochirichthys* + other chelines and *Hypophthalmichthys* + other abramines (see Howes, 1979; 1981). Such also appears to be the case within *Cyprinion* where *C. semiplotum* and *C. burmanica* represent a highly derived lineage characterized by many jaw synapomorphies. Presumably the accumulation of synapomorphies in one such lineage is the result of a cumulative series of speciation events, lacking in the other, more generalized lineages (i.e. 'the occasional small saltatory changes' of Banister, 1980).

Whether the reticulate pattern of relationships is an artifact resulting from incomplete character analysis or a reflection of polymorphic descent through populations of the intra-group lineages is a problem as yet unresolved.

Evolution of the *Cyprinion* jaw and the 'sector mouth'

Even though no 'transitional series' of jaw types emerges from the reticulate pattern presented (Fig. 22), particular synapomorphies indicate a possible evolutionary course leading to the specialized morphology of the *Cyprinion semiplotum*-*C. burmanica* lineage. Comparison of these apomorphies with similar but independently derived characters in other cyprinid lineages indicates those features which are prerequisites for the development of a sector mouth.

In the upper jaw a decisive step towards a sector mouth appears to have been taken with the reduction of the premaxillary ascending process. Matthes (1963) remarks that reduction of this process probably occurred independently in several genera and is not therefore indicative of close relationship. Matthes was referring particularly to similarities between *Varicorhinus*, *Labeo* and *Garra*. Whilst this study endorses Matthes' view that this particular feature is not necessarily a synapomorphy for all three genera, it does not refute its possible synapomorphic status in *Labeo* and *Garra*, which share other derived characters (Reid, unpublished thesis).

At first sight it would seem that reduction of the premaxillary processes should lead to restricted protrusibility of the upper jaw. However, this may be compensated for by a pronounced downward curvature of the ethmoid bloc as seen in *Cyprinion* and *Onychostoma* and, to a lesser extent, in *Varicorhinus* and *Capoeta*. The depressed ethmoid region in *Labeo* and *Garra* possibly fulfills the same function.

The reduced and medially curved mid-lateral ascending maxillary process of *Cyprinion semiplotum* appears otherwise only in *Onychostoma*. In both taxa this feature is apparently correlated with an extensive area of connective and tendinous tissue attaching to the inner face of the 1st infraorbital (see p. 305). The medial notch on the posterior arm of the maxilla in some *Cyprinion* species and in *Capoeta* performs a similar function as a hold-fast for the thick tissue connecting the maxilla with the coronoid process of the dentary (see p. 305).

Concerning the *Cyprinion* lower jaw, the most important evolutionary innovation appears

to have been the development of a synarthritic mandibular joint. Such a joint usually suggests some degree of lateral movement, as in the 'knuckle joint' of cynodontine characoids (Howes, 1976), but in the case of *Cyprinion* it may act as a compensatory device to the torque induced by the contraction of the thickly ligamentous *protractor hyoideus* muscle. The absence of any lateral jaw movement is also suggested by the strongly produced lateral and medial anguloarticular processes which provide a rigid coupling with the quadrate.

Changes associated with increased medial curvature of the dentary appear to be manifest in the outward slope of the coronoid process so that the axis and insertion angle of the *adductor mandibulae* A_2 and A_3 muscles remain unchanged. This is contrary to the condition in *Capoeta* where the coronoid process and muscle fibres are set at an angle to the body axis. In *Cyprinion* there is a noticeable change in the relative position of the coronoid process from its mid-lateral point in the plesiomorph *C. acinaces* to a posterior position in *C. semiplotum*. This apparent positional shift is due to morphological changes in the surrounding elements, i.e. broadening and posterior shortening of the anguloarticular and the medial curvature of the dentary (Fig. 16A-E, G-K).

The rigid articulation of the lower jaw in *Cyprinion semiplotum* and *C. burmanica* appears to restrict its vertical movement and it seems merely to act as a firm platform for the highly mobile lip.

The lower lip of *Cyprinion* differs from that in other taxa in being a mobile structure; the epidermis is so loosely attached to the underlying labial shelf that it is free to move antero-posteriorly, and its mobility appears to be controlled by the action of the *protractor hyoideus* complex via dorsal and ventral tendinous linkages. This additional function of the *protractor hyoideus* is also indicated by a multi-directional joint between the hyoid and the suspensorium.

Thus, in the more derived *Cyprinion* species, increased complexity of the jaw-quadrate articulatory surfaces and of the lower lip is correlated with increased mobility of the hyoid bar and hypertrophy of the *protractor hyoideus*.

Where it occurs, a sector mouth appears to have the same basic function i.e. for scraping or ploughing epilithic material (see Matthes, 1963). Certainly, there are some 'necessary design components' common to all lineages of taxa with a sector mouth, viz. marked medial curvature of the anterior portion of the dentary; a broadened anguloarticular and barely extending beyond the posterior border of the dentary; greater mobility of the hyoid-suspensorial joint; 3rd branchiostegal ray shifting ventrally to the posterohyal, and an hypertrophy of the *protractor hyoideus* musculature.

Apart from *Cyprinion* such specializations can be found among *Barbus-Varicorhinus* species. Doubtless, cranial and vertebral apomorphies (deepening of the posterior cranial region and increased rigidity of the anterior vertebral column) form a functional unity contributing to epilithic feeding activity. Just how these components interact functionally with those of the jaws, the hyoid and branchial arches, are problems to be solved.

An earlier remark (Howes, 1981) that the '... morphology of the lower jaw is possibly the most variable unit in Cyprinidae ...' is borne out by this study. That the cyprinid jaw appears to be so adaptable suggests that, as in cichlids, the pharyngeal bones perform a dominant functional role of food manipulation and mastication, so freeing the jaws for specialized food gathering. No comparative experimental functional data are available for cyprinid taxa and it is not known whether the pharyngeal apparatus is as versatile as that of cichlids and whether it exerts a primary dominant influence on jaw modification. Liem (1980) has pointed out that in cichlids epilithic feeding patterns are of a kind requiring specializations that exceed those of simple inertial suction feeding. Certainly this appears to be true for sector-mouthed cyprinids as well, where (in the more derived forms) upper jaw protrusion is minimal and the manipulative function of the jaw in food gathering has been transferred, in part, to the hyoid arch.

Synopsis of *Cyprinion* species

The synonymies include only the original citation of the species.

CYPRINION Heckel, 1843

Semiplotus Bleeker, 1863

Scaphiodonichthys Vinciguerra, 1889

Scaphiodontopsis Fowler, 1934

The reasons for synonymising *Semiplotus* with *Cyprinion* have been explained in this paper (p. 299).

Scaphiodonichthys was separated from '*Semiplotus*' on the differences in the number of branched dorsal fin rays (9–12 in *Scaphiodonichthys*, 20–25 in '*Semiplotus*'). Smith (1945 : 206) quotes from a letter he received from Dr S. L. Hora who suggested that intermediate forms were '. . . yet to be discovered with a number of branched rays intermediate between 12 and 20. When such forms are found *Semiplotus* and *Scaphiodonichthys* will have to be regarded as congeneric . . .' To my knowledge no such 'intermediate' forms have been found. The existence of synapomorphic osteological and myological characters in species of both '*Scaphiodonichthys*' and *Cyprinion* indicates their generic unity (see p. 312 for a list of characters). When viewed as species of *Cyprinion*, then 'intermediate forms' linking '*Semiplotus*' and '*Scaphiodonichthys*' are in fact present, and indeed the number of branched dorsal fin rays does range from 10–25.

Species occurring east of the Himalayas

Cyprinion semiplotum McClelland, 1839

Cyprinus semiplotus McClelland, 1839 *Asiat. Reschs.* **19** : 374

Cyprinion semiplotus Heckel, 1843 in Russeger's *Reisen* **1** : 1015

Semiplotus semiplotus Bleeker, 1863 *Atlas Ichth.* **3** : 25

Semiplotus maclellandi Bleeker, 1863 *Atlas Ichth.* **3** : 25

Semiplotus cirrhosus Chaudhuri, 1919 *Rec. Ind. Mus.* **16** : 280

DISTRIBUTION. Nepal, north Bengal (see Hora, 1937; Hora & Gupta, 1940).

Cyprinion modestum Day, 1870

Semiplotus modestus Day, 1870 *Proc. Zool. Soc. Lond.* : 101

Day (1870) considered this species as '. . . intermediate between the genera *Semiplotus* and *Cyprinion*'. Unlike *C. semiplotum* but in common with other *Cyprinion* species, *C. modestum* has a serrated dorsal fin spine. No specimens have been examined in the course of this study (the presumed types are in Calcutta) but according to Hora (1937 : 46) Day's species is 'quite distinct'.

DISTRIBUTION. Akyab Hills, Upper Burma.

Cyprinion burmanica Vinciguerra, 1889

Scaphiodonichthys burmanicus Vinciguerra, 1889 *Ann. Mus. Civ. Storia Nat. Genova* (2) **9** : 285

Scaphiodontopsis acanthopterus Fowler, 1934 *Proc. Acad. Nat. Sci. Philad.* **86** : 119

Onychostoma macroacanthus Pellegrin & Chevey, 1936 *Bull. Soc. Zool. France* **61** (1) : 18–27

Taki (1975) demonstrated an overlap of lateral line scale numbers between *C. burmanicus* and *C. acanthopterus* and stated that the two species were distinguishable only by the number of dorsal fin rays. I find that in a sample of 16 specimens identified as *C. burmanica* (28–65 mm SL uncat. Smithsonian Coll. Upper Thailand), there are nine specimens with 11 and seven with 10 branched dorsal rays. There are thus no meristic differences separating the two 'species'. Since I can find no morphological differences between the syntypes of *C. burmanica* and the series of *C. acanthopterus* studied by Smith (1945), I consider the species to be synonymous.

DISTRIBUTION. Burma, Thailand, Laos, Vietnam.

Species west of the Himalayas

Despite the revision of Berg (1949) and the work of Mirza (1969), many taxonomic problems remain concerning the species in this area. As yet, no author has examined all the nominal types. Also, too few specimens have been examined to judge the degree of intraspecific variability in certain characters.

Cyprinion acinaces Banister & Clarke, 1977

Cyprinion acinaces Banister & Clarke, 1977 *J. Oman Studies* : 123–126

DISTRIBUTION. Saudi Arabia

Cyprinion macrostomum Heckel, 1843; type species of the genus

Cyprinion macrostomum Heckel, 1843 *Ichthyologie* in Russegger's Reisen 1 : 1065

?*Cyprinion neglectum* Heckel, 1846 *Die Fische Persiens* in Russegger's Reisen 2 (3) : 223

?*Cyprinion tenuiradius* Heckel, 1846 *Die Fische Persiens* in Russegger's Reisen 2 (3) : 261

Berg (1949) included *C. neglectum* in synonymy without having seen the type and regarded *C. tenuiradius* as a valid species. However, from Heckel's figure *C. tenuiradius* would seem to be simply a 'variant' of *C. macrostomum*.

DISTRIBUTION. Tigris-Euphrates (see Banister, 1980).

Cyprinion kais Heckel, 1843

Cyprinion kais Heckel, 1843 *Ichthyologie* in Russegger's Reisen 1 : 1066

?*Cyprinion cypris* Heckel, 1843 *Ichthyologie* in Russegger's Reisen 1 : 1067

Berg (1949) included *C. kais* in the synonymy of *C. macrostomum* on the grounds of minor variation in position of the dorsal fin with respect to the pelvic fin insertion (the character Heckel had used to separate the species). Although Berg (1949) recognised differences in mouth shape between the taxa, he obviously considered them to be of little taxonomic worth. I have seen the types of neither *C. macrostomum* nor *C. kais*, and the recognition of these species is based on a comparison of Heckel's (1843) figures with two recognisably distinct taxa represented in the BMNH collections. In *C. kais* the mouth is small, with the keratinized lip of the lower jaw prominent and more upwardly directed than in *C. macrostomum*. Other differences involving the morphology of the jaws and hyoid elements are given elsewhere in this paper.

From Heckel's (1843) figure (Fig. 3, pl. 7) it seems likely that *C. cypris* is synonymous with *C. kais* rather than with *C. macrostomum* as indicated by Berg (1949), and that it represents a juvenile specimen in which the keratinization of the jaw is still incomplete.

DISTRIBUTION. Tigris-Euphrates.

Cyprinion microphthalmum Day, 1880

Scaphiodon microphthalmum Day, 1880 *Proc. Zool. Soc. Lond.* : 227

?*Scaphiodon muscatensis* Boulenger, 1887 *Proc. Zool. Soc. Lond.* : 665

Cirrhina afghana Gunther, 1889 *Trans. Linn. Soc. Zool.* 5 : 106

Cirrhina afghana nikolskii Berg, 1905 *Ann. Mus. Zool. Acad. Sci.* 10 : 106

Scaphiodon baluchiorum Jenkins, 1910 *Rec. Ind. Mus.* 5 : 124

This synonymy is that of Berg (1949) but appears suspect. The type specimens of *Scaphiodon microphthalmum* are possibly lost (see Banister & Clarke, 1977) and until such time as they reappear certain identification of this species is not possible. However, Mirza's (1969) description based on specimens from Quetta, the type locality, appears to represent the species Day (1880) described. Specimens I have examined from Baluchistan (BMNH

1883.8.2 : 20–26) and the syntypes of *Cirrhina afghana* (BMNH 1886.9.12 : 155–159; 21) conform to Mirza's description and that given by Jenkins (1910) for *Scaphiodon baluchiorum*.

Banister & Clarke (1977) followed Berg (1949) in regarding *Cyprinion muscatensis* as synonymous with *C. microphthalmum*.

DISTRIBUTION. Baluchistan, Afghanistan, the Indus Plain and Saudi Arabia.

Cyprinion milesi Day, 1880

Barbus milesi Day, 1880 *Proc. Zool. Soc. Lond* : 228

Barbus bampurensis Nikolsky (1899) 1900 *Ann. Mus. St. Petersb.* 4 : 410

Scaphiodon daukesi Zugmayer, 1912 *Ann. Mag. nat. Hist.* 8 : 596

Barbus baschakirdi Holly, 1929 *Anz. Akad. Wiss. Wien* 7 : 1

Cyprinion milesi Berg, 1949 *Trudy zool. Inst. Leningr.* 8 (4) : 821

DISTRIBUTION. West Pakistan and Iran (see Mirza, 1969); BMNH specimens from Afghanistan (1889.2.1 : 263–4) and Dizak, Baluchistan (1883.8.2 : 2–3).

Cyprinion watsoni Day, 1872

Scaphiodon watsoni Day, 1872 *J. Asiatic Soc. Bengal* 41 : 324

Scaphiodon irregularis Day, 1872 *J. Asiatic Soc. Bengal* 41 : 321

?*Cyprinion kirmanse* Nikolski, 1899 *Ann. Mus. St. Petersb.* 4 : 412

Scaphiodon macmahoni Regan, 1906 *J. Asiatic Soc. Bengal* 2 : 8

Scaphiodon watsoni var. *belensis* Zugmayer, 1912 *Ann. Mag. nat. Hist.* (8) 10 : 596

Scaphiodon readingi Hora, 1923 *Rec. Ind. Mus.* 25 : 379–382

Cyprinion watsoni Berg, 1949 *Trudy zool. Inst. Leningr.* 8 (4) : 814

The above synonymy mainly follows that of Mirza (1969) who found a complex overlap of morphometric and meristic characters between *C. watsoni* and *Scaphiodon irregularis*. Certainly, there appear to be no osteological or myological differences between these 'species'.

Scaphiodon macmahoni was included by both Berg (1949) and Mirza (1969) in the synonymy of *Cyprinion microphthalmum*. However, I find that *S. macmahoni* possesses the same mouth morphology and degree of dorsal fin spine serration as does *Cyprinion watsoni* and thus it is included in the synonymy of that species.

DISTRIBUTION. West Pakistan, Iran and Afghanistan, and the Helmand basin of Baluchistan.

The taxonomic status of *Semiplotus dayi* Fowler, 1958

Fowler (1958) considered that *Scaphiodon aculeatus* of Day (1880) was a misidentification and that the specimens concerned represented a new species of *Semiplotus* for which Fowler (1958) created the species *S. dayi*.

Although Day's specimens can no longer be traced, his description (1880) gives no cause to think that he was not describing *Scaphiodon aculeatus*. Since *Scaphiodon aculeatus* (Val. 1844) is a synonym of *Capoeta capoeta* (see Karaman, 1969) it follows that *Semiplotus dayi* must also become a synonym of that taxon.

Relationship of the genus *Cyprinion*

In this study the presence of a sector mouth in various cyprinid taxa is seen both as a character indicating relationship (synapomorphy) and as one independently evolved as a parallelism. Taki (1975) used mouth morphology, degree of dorsal fin spine serration and ossification, and the presence or absence of barbels as the criteria for determining relationships amongst 'semiplotine' genera. Taki considered *Onychostoma* closely related to 'Semiplotus', 'Scaphiodonichthys', *Scaphiodon* and *Scaphiognathops*. On the basis of these supposed relationships he recognised an *Onychostoma* group and constructed an elaborate dispersal hypothesis to explain the distribution of the included genera.

Taki (1975) supposed that the onychostomine genera were '... derived from *Barbus-Varicorhinus* stock'. As he indicated the group's 'origin' to have been in northern Asia, I take it that he was referring to Euroasiatic *Barbus* and that his '*Varicorhinus*' was in fact *Capoeta* (see Karaman, 1969). Taki further confuses the issue by referring both the middle Asian and western Indian species to *Scaphiodon* thereby implying their monophyly. In fact, Taki's middle Asian '*Scaphiodon*' are all *Cyprinion* species and those along the western Ghats of India are *Osteocheilus* (see Hora, 1942, for synonymies).

The remaining genus included in Taki's *Onychostoma* group is *Scaphiognathops*. Osteological data on this taxon are completely lacking; examination of the type specimen of *S. stejnegeri* (USNM 90303) reveals a quite different jaw morphology to that of any *Cyprinion* species (see figures in Smith, 1931 and Taki, 1974), or for that matter, from any *Onychostoma* species.

Taki's (1975) hypothesis of relationships and dispersal are falsified by the conclusions of this study, namely: 1. That *Semiplotus*, *Scaphiodonichthys* and *Scaphiodon* (part) are all synonymous with *Cyprinion*; 2. That there are no synapomorphies linking *Cyprinion* with *Onychostoma* or with *Capoeta*.

The relationships of *Cyprinion* are still in doubt and the sister-group remains unidentified. This is due to lack of comparative anatomical data for the corpus of species currently referred to the genus *Barbus*. Initial researches cast doubt on the assumed monophyly of *Barbus* and also indicate one group within the complex which could be the sister lineage to *Cyprinion*. The taxa involved are the north African species *B. luteus*, *B. paytoni*, *B. callensis*, *B. waldoi*, *B. rothschildi* and *B. sharpyei*. In particular '*Barbus*' *paytoni* possesses cranial and jaw features similar to those of *Cyprinion* viz. deep and ventrally curved ethmoid bloc, transverse dilatator fossa, an almost identical posterior neurocranial morphology, broad and deflected labial surface on the dentary, and a broad anguloarticular facet. The shape of the quadrate, the hypertrophy of the interhyal, and the inward curvature of the interoperculum appear to be further indications of relationship. More research is however, necessary to test the hypothesis that the north African '*Barbus*' species group is itself monophyletic.

Acknowledgements

I wish to express deep gratitude to Drs Humphry Greenwood and Keith Banister. To the former for his critical reading of the manuscript and the many helpful suggestions that have made for its improvement, and to the latter for spending so many hours in discussing the vagaries of the carps.

My thanks are due to my former colleague Margaret Clarke for her assistance in compiling the species synopsis, to Robert Travers for preparing alizarin specimens and Gina Sandford for typing the manuscript.

It is a pleasure also to thank Dr George Lauder for our many stimulating discussions on cyprinoid myology and functional anatomy.

Special thanks go to Dr Christine Karrer for translating, from the Russian, passages of L. S. Berg's '*Freshwater Fishes of Iran*'.

Finally, my thanks are due to Dr Richard Vari for his assistance in locating H. M. Smith's specimens in the Smithsonian Institution and for his hospitality during my visit there.

References

- Alexander, R. McN. 1966. The function and mechanism of the protrusile upper jaw in two species of cyprinid fish. *J. Zool., Lond.* **149**: 288-296.
- Ballantijn, C. M. 1969. Functional anatomy and movement co-ordination of the respiratory pump of the carp (*Cyprinus carpio* L.). *J. exp. Biol.* **50**: 547-567.
- Banister, K. E. & Bunni, M. K. 1980. A new blind cyprinid fish from Iraq. *Bull. Br. Mus. nat. Hist. (Zool.)* **38** (3): 151-158.

- & Clarke, M. A. 1977. The freshwater fishes of the Arabian Peninsula, In: The scientific results of the Oman flora and fauna survey 1975. *Jl. Oman Stud.* 1977 : 111–154.
- Berg, L. S. 1949. Freshwater fishes of Iran and of neighbouring countries. *Trudy zool. Inst. Leningr.*, 8 (4) : 783–858.
- Bremer, K. & Wanntorp, H. G. 1979. Hierarchy and reticulation in systematics. *Syst. Zool.* 28 (4) : 624–627.
- Day, F. 1980. On the fishes of Afghanistan. *Proc. zool. Soc. Lond.* : 224–232.
- 1889. *The fauna of British India, including Ceylon and Burma*. Fishes I London 548 pp.
- Fowler, H. W. 1958. Some new taxonomic names of fishlike vertebrates. *Notul. nat.* 310 : 1–16.
- Hora, S. L. 1937. Notes on fishes in the Indian Museum. XXIX. On a collection of fish from Nepal. *Rec. Ind. Mus.* 39 (1) : 43–46.
- 1942. Notes on fishes in the Indian Museum. XLII. On the systematic position of the Indian species of *Scaphiodon* Heckel. *Rec. Ind. Mus.* 54 (1) : 1–10.
- & Gupta, J. C. 1940. On a collection of fish from Kalimpong Duars and Siliguri Terai, Northern Bengal. *J. roy. Asiat. Soc. Bengal* 6 (2) : 77–83.
- Howes, G. J. 1976. The cranial musculature and taxonomy of characoid fishes of the tribes Cynodontini and Characini. *Bull. Br. Mus. nat. Hist. (Zool.)* 29 (4) : 201–248.
- 1978. The anatomy and relationships of the cyprinid fish *Luciobrama macrocephalus* (Lacepède). *Bull. Br. Mus. nat. Hist. (Zool.)* 34 (1) : 1–64.
- 1979. Notes on the anatomy of the cyprinid fish *Macrochirichthys macrochirus* with a review of the subfamily Cultrinae. *Bull. Br. Mus. nat. Hist. (Zool.)* 36 (3) : 147–200.
- 1980. The anatomy, phylogeny and classification of bariliine cyprinid fishes. *Bull. Br. Mus. nat. Hist. (Zool.)* 37 (3) : 129–198.
- 1981. Anatomy and phylogeny of the Chinese major carps *Ctenopharyngodon* Steind., 1866 and *Hypophthalmichthys* Blkr, 1860. *Bull. Br. Mus. nat. Hist. (Zool.)* 41 (1) : 1–52.
- Karaman, M. S. 1969. Süßwasserfische der Türkei 7. Revision der kleinasiatischen und vorderasiatischen Arten des Genus *Capoeta* (*Varicorhinus*, partim). *Mitt. Hamburg Zool. Mus. Inst.* 66 : 17–54.
- Liem, K. F. 1980. Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. *Amer. Zool.* 20 : 295–314.
- Matthes, H. 1963. A comparative study of the feeding mechanism of some African Cyprinidae (Pisces, Cypriniformes). *Bijdr. Dierk.* 33 : 3–35.
- Mirza, M. R. 1969. Fishes of the genus *Cyprinion* Heckel (Cyprinidae, Osteichthyes) from West Pakistan. *Pakistan J. Zool.* 1 (2) : 141–150.
- Regan, C. T. 1911. The classification of the teleostean fishes of the order Ostariophysi. 1. Cyprinoidea. *Ann. Mag. nat. Hist.* (8) 8 : 13–32.
- Smith, H. M. 1931. Description of new genera and species of Siamese fishes. *Proc. U.S. natn Mus.* 79 art 7 : 1–48.
- 1945. The fresh-water fishes of Siam or Thailand. *Bull. U.S. natn Mus.* 188 : 1–622.
- Takahasi, N. 1925. On the homology of the cranial muscles of the cypriniform fishes. *J. Morph.* 40 : 1–109.
- Taki, Y. 1974. New species of the genus *Scaphognathops*. Cyprinidae, from the Lao Mekong river system. *Jap. J. Ichthyol.* 21 (3) : 129–136.
- Cyprinid fishes of the genera *Onychostoma* and *Scaphiodonichthys* from upper Laos, with remarks on the dispersal of the genera and their allies. *Jap. J. Ichthyol.* 22 (3) : 143–150.
- Tarsitano, S. & Hecht, M. K. 1980. A reconsideration of the reptilian relationships of *Archaeopteryx*. *Zool. J. Linn. Soc.* 69 : 149–182.