Phylogenetic versus convergent relationship between piscivorous cichlid fishes from Lakes Malawi and Tanganyika

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Synopsis

The anatomy and phylogenetic relationships of two genera of African cichlid fishes, *Rhamphochromis* from Lake Malawi and *Bathybates* from Lake Tanganyika, are investigated. In accordance with the current methods of cladistic analysis data from representatives of a wide range of cichlid taxa are included for outgroup comparison. Particular emphasis is placed upon the anatomy of the ethmovomerine region of the neurocranium, the cheek musculature, and the pharyngeal jaw apparatus.

Based upon a number of synapomorphic characters an hypothesis of a sistergroup relationship between the monophyletic genus, *Bathybates*, and a monophyletic assemblage consisting of the genera *Hemibates* and *Trematocara* is formulated. A similar resolution of the relationships of *Rhamphochromis* has not been achieved; the differential success of the study is discussed and additional data relevant to unravelling the status and relationships of *Rhamphochromis* are introduced.

Introduction

The similarities that exist between individual species and whole communities of cichlid fishes in Lakes Malawi and Tanganyika have often been remarked upon (eg. Pellegrin, 1903; Regan, 1921, 1922; Fryer, 1959; Fryer & Iles, 1972; Galis & Barel, 1980). Regan (1921) felt that the majority of the Malawian genera were phyletically distinct from any found elsewhere and that they formed a 'natural group'. Since that time, because it has been assumed that the cichlid flock of each lake has had a separate ancestry, their similarities have been interpreted as examples of convergent evolution (Fryer, 1969; Fryer & Iles, 1972).

The recent papers of Greenwood (1978, 1979, 1980) cast considerable doubt upon existing ideas about the phylogeny and interrelationships of the lacustrine Cichlidae. With reference

to the Lake Malawi haplochromine species group Greenwood (1979) suggests that the prevalent idea of the Malawi group being entirely derived from one or a few anatomically generalized fluviatile haplochromine cichlids (see Regan, 1921; Trewavas, 1935, 1949; Greenwood, 1974) is an oversimplification. He now suspects that lineages related to *Thoracochromis, Astatotilapia,* and even to *Serranochromis* and *Chetia* may have contributed to the flock. Clearly there is a need to reconsider the phyletic relationships of these lacustrine Cichlidae.

Apart from the large number of species the problem of determining the interrelationships of the lacustrine Cichlidae is intensified by the fact that few characters have been found to be of use in phylogenetic analyses. The common occurrence of a range of morphological features confers a rather characteristic 'facies' upon many trophic groups (Greenwood, 1974). The problem of determining monophyletic assemblages, on the basis of shared derived characters, in the face of an apparent 'web of parallelisms' (Liem, 1978) is therefore particularly acute amongst these lacustrine Cichlidae. The two genera that form the subject of the present investigation, *Bathybates* Boulenger, 1898 from Lake Tanganyika and *Rhamphochromis* Regan, 1921 from Lake Malawi, have been selected for a number of reasons. Superficially, at least, *Bathybates* and *Rhamphochromis* are rather similar in external appearance, and Boulenger (1898) suggested that *Bathybates ferox* and *Paratilapia longiceps* (=*Rhamphochromis longiceps*) were closely related. Later, because Regan (1921) felt that the Malawian flock was a natural group, *Rhamphochromis* and *Bathybates* were considered to be an example of convergent evolution (Fryer & Iles, 1972; Lowe-McConnell, 1975).

Although data on the habits and ecology of these fishes are sparse it would appear that both occupy broadly similar biological positions in their respective lakes (Poll, 1956; Coulter, 1966, 1967; Fryer & Iles, 1972; Lowe-McConnell, 1975). Both are essentially off-shore, open-water predators feeding upon cichlid as well as non-cichlid members of the pelagic communities. Species in both genera are also known to frequent the benthic zone where they are able to adapt to the prevailing near anoxic conditions (Coulter, 1967; Lowe-McConnell, 1975).

The fact that both *Bathybates* and *Rhamphochromis* are exclusively piscivorous has also been a factor contributing to their selection for a comparative study. Amongst the trophic groups represented in the lacustrine flocks the piscivorous predatores comprise one of the largest groups (c.30–40% of total species number). The large number of piscivorous species seems to be attributable both to the large biomass of other cichlid species (Fryer & Iles, 1972; Witte, in press) and to the apparently minor anatomical modification necessary to facilitate the capture and ingestion of this food source (Fryer & Iles, 1972; Liem, 1978).

Methods, nomenclature and materials

Methods

In order to determine the phylogenetic relationships of *Bathybates* and *Rhamphochromis* a cladistic approach has been adopted. Monophyletic groups are defined on the basis of shared derived characters (synapomorphies), and in estimating the relative plesiomorph (primitive) or apomorph (derived) nature of various character states the 'commonality principle' (Schaeffer, Hecht and Eldredge, 1972) is applied.

A number of problems arise when cladistic principles are applied to an analysis of cichlid interrelationships (see Greenwood, 1979: 270). Apart from the phylogenetic breakdowns provided by Greenwood (1979, 1980), Liem and Stewart (1976) and Liem (1979) little guidance is available to aid the selection of appropriate cichlid outgroup taxa. Highly tentative and noncladistic phylogenies for members of the Lake Malawi and Lake Tanganyika flocks are to be found in Fryer & Iles (1972) (see also Regan, 1920, 1921, 1922; Trewavas, 1949). In the course of this investigation those taxa which have been thought by these authors to be 'close to' or 'implicated in the ancestry' of *Bathybates* or *Rhamphochromis*

have received particular attention. I have also placed an emphasis upon the examination of other lacustrine taxa although some riverine forms have been included. Otherwise my selection of cichlid outgroup taxa has been somewhat arbitrary.

The following review is a partial account of the anatomy of selected cichlid taxa. Only those structures found to yield characters suitable for phylogenetic analysis at the level of universality under consideration have been selected for description here. Characteristics of the ethmovomerine region of the neurocranium, the cheek musculature and the pharyngeal jaw apparatus (PJA *sensu* Hoogerhoud & Barel, 1978) receive particular attention.

Descriptions are based upon the type species, *Rhamphochromis longiceps* and *Bathybates ferox*, of the two major genera and where possible also of the type species of outgroup genera.

For more detailed and comprehensive accounts of cichlid anatomy see Goedel (1974*a*, *b*) and Anker (1978) for myology, and Barel *et al.* (1976) for osteology.

Nomenclature

The nomenclature of muscles follows that of Winterbottom (1974) and Anker (1978). Topographical and skeletal nomenclature is based upon that of Nelson (1969), Rosen (1973), Patterson (1975) and Barel *et al.* (1976).

To investigate myological structures specimens were dissected under a Wild M-7 stereo-microscope. Osteological study specimens were cleared in buffered trypsin solution and double stained following the procedure of Dingerkus & Uhler (1977). This material was supplemented by reference to the extensive osteological collections in the British Museum (Natural History).

Taxonomic nomenclature

Greenwood (1979) divides the polyphyletic genus *Haplochromis* into a number of monophyletic lineages (=genera) restricting *Haplochromis* to five species. Difficulties arise when reference is made either to species formerly included within the genus but have yet to be assigned to other genera, or to the former concept of the genus *Haplochromis*. To avoid confusion Greenwood (1979) suggests adopting a convention proposed by Patterson & Rosen (1977). Thus the specific names of species formerly placed in the genus *Haplochromis* and not allocated to other genera will be prefixed with the name *Haplochromis* cited between quotation marks. When referred to collectively all cichlid fishes with an *Haplochromis* type of pharyngeal apophysis (Greenwood, 1978) are termed haplochromine cichlids.

Taxonomic note on Bathybates and Rhamphochromis

The genus *Bathybates* is entirely restricted to Lake Tanganyika and was originally described by Boulenger (1898; type species *Bathybates ferox* Boulenger, 1898). Boulenger (1898) believed that *Bathybates* was closely related to *Paratilapia* with which it was connected by *Paratilapia longiceps* Günther (=*Rhamphochromis longiceps*) of Lake Malawi. He believed that the more formidable dentition coupled with characters of the body scales warranted the establishment of a new genus.

Since that time six more *Bathybates* species have been described; *Bathybates fasciatus* Boulenger, 1901; *Bathybates vittatus* Boulenger, 1914; *Bathybates minor* Boulenger, 1906; *Bathybates graueri* Steindachner, 1911; *Bathybates horni* Steindachner, 1911; *Bathybates leo* Poll, 1956. A key to the species of *Bathybates* can be found in Poll (1956).

In 1915 Boulenger brought together *Paratilapia caerulea* Boulenger, 1908, *Paratilapia esox* Boulenger, 1908 and *Hemichromis longiceps* Günther, 1864 into a new genus, *Champsochromis*. Regan (1921) was of the opinion that the type species of that genus, *Champsochromis caeruleus*, was not generically distinct from *Haplochromis* as then defined and therefore placed *caeruleus* in *Haplochromis*. For the remaining species he established the genus *Rhamphochromis,* and designated *Rhamphochromis longiceps* the type species. He added four additional species to his genus: *Rhamphochromis macrophthalmus* Regan, 1921;

Rhamphochromis ferox Regan, 1921; *Rhamphochromis woodi* Regan, 1921, and *Rhampho-chromis leptosoma* Regan, 1921. Since that time two more species have been described: *Rhamphochromis lucius* Ahl, 1926 and *Rhamphochromis brevis* Trewavas, 1935. A key to the species of *Rhamphochromis* can be found in Trewavas (1935). Unlike *Bathybates, Rhamphochromis* is not exclusively lacustrine and specimens have been collected in the Upper Shiré River (Boulenger, 1915; Ricardo-Bertram *et al.*, 1946; pers. obs.). More species of *Rhamphochromis* from Lake Malawi, particularly from the Nkata Bay region, have yet to be described (pers. obs.).

Materials

Material representative of the following cichlid genera has been examined. A complete list of specimens used in this study is deposited in the fish section of the British Museum (Natural History). The number in brackets following each generic name indicates the number of species examined.

South American genera:

Acaronia (1)	*Astatotilapia* (5)	*Lichnochromis* (1)
Aequidens (1)	*Aulonocara* (2)	*Limnochromis* (2)
Apistogramma (1)	*Aulonocranus* (1)	*Limnotilapia* (1)
Cichla (1)	*Bathybates* (7)	*Neotilapia* (1)
Cichlasoma (4)	*Boulengerochromis* (1)	*Orthochromis* (1)
Crenicichla (3)	*Callochromis* (1)	*Perissodus* (3)
Geophagus (3)	*Chetia* (1)	*Pharyngochromis* (1)
Petenia (1)	*Ctenochromis* (1)	*Prognathochromis* (3)
	Diplotaxodon (1)	*Rhamphochromis* (8)
Asian genera:	*Ectodus* (1)	*Sarotherodon* (1)
Etroplus (2)	*Haplochromis* (1)	*Serranochromis* (5)
	'Haplochromis' (25)	*Teleogramma* (1)
Madagascan genera:	*Haplotaxodon* (1)	*Telmatochromis* (2)
Paratilapia (1)	*Hemibates* (1)	*Tilapia* (1)
Paretroplus (1)	*Hemichromis* (1)	*Trematocara* (8)
Ptychochromis (1)	*Hemitilapia* (1)	*Trematocranus* (1)
	Lamprologus (10)	*Tylochromis* (2)
African genera:	*Lethrinops* (2)	*Xenotilapia* (2)
Aristochromis (1)		

Abbreviations used in the text figures

A_1, A_2, A_3, A_w	parts of the adductor man-dibulae muscle
aa	anguloarticular
aap	adductor arcus palatini muscle
ad5	5th adductor muscle
ad-fos	adductor fossa
art.fc-pb3	articulatory facet of pharyn-gobranchial 3
asp-aa	ascending process of the anguloarticular
asp-aa.f	flange on ascending process of the anguloarticular
ca	central aponeurosis
cart.ext.ep2	cartilaginous extension of epibranchial 2

cc	cranial condyle
con.tiss.tract	connective tissue tract
cp	coronoid process of the dentary
d-bb	dorsal bony bridge
dent	dentary
dl-f	dorsolateral fenestra
do	dilatator operculi muscle
ect	ectopterygoid
end	endopterygoid
ep1–4	epibranchials 1–4
ex.hd-ep4	expanded head of epibranchial 4
exs	extrascapula
fr	frontal
h-lpe	horn of lower pharyngeal element
hym	hyomandibula
im	intermandibularis muscle
intorb-s	interorbital septum
lac	lachrymal
l.ang-dent	angulodentale ligament
lap	levator arcus palatini muscle
le	lateral ethmoid
le-b	body of lateral ethmoid
le-e	anterior extension of lateral ethmoid
le-p	lateral ethmoid process
lev-ext 1–4	levatores externi muscles 1–4
lev-int 1–2	levatores interni muscles 1–2
lev-post	levator posterior muscle
l-fos	lateral fossa
lo	levator operculi muscle
l.pal-le	palatine-lateral ethmoid ligament
l.pal-mes	palatine-mesethmoid ligament
lpe	lower pharyngeal element
mc	Meckel's cartilage
m.c-p2	musculus cranio-pharyngobranchialis 2
mes	mesethmoid
mes-a	arm of mesethmoid
mes-p	plate of mesethmoid
mes-w	wing of mesethmoid
met	metapterygoid
m.t-e2	musculus transversus epibranchialis 2
m.t-p2	musculus transversus pharyn-gobranchialis 2
mx-f	maxillary flange

nlf 0–5	neurocranial lateral line foramina 0–5
nip-pr	nipple process
od-a	obliquus dorsalis anterior muscle
od-p	obliquus dorsalis posterior muscle
oes	oesophagus
op	operculum
ov-f	ovoid fenestra
pal	palatine
pal-fc	palatine facet
pb 1–3	pharyngobranchials 1–3
pmx-art	articular process of the premaxilla
pmx-asp	ascending process of the premaxilla
pop	preoperculum
postorb	postorbital process
preorb	preorbital process
psh	parasphenoid
pt	posttemporal
quad	quadrate
r-d	retractor dorsalis muscle
r-f	rostral fenestra
rost-cart	rostral cartilage
sc	supracleithrum
shank-s	shank spine
spin.oes	sphincter oesophagi
sym	symplectic
tA_{1a-c}	tendons of A_1
tA_2	tendon of A_2
tA_3	tendon of A_3
tA_w	tendon of A_w
td-p	transversus dorsalis posterior muscle
t.lev-ext3	tendon of levator externus 3 muscle
t.lev-int 1	tendon of levator internus 1 muscle
up-4	fourth upper tooth-plate
V	ramus mandibularis V
vl-f	ventrolateral fenestra
vl-bb	ventrolateral bony bridge
vo-fc	vomerine facet
vo-fos	vomerine fossa
vo-h	head of the vomer
v-s	stalk of the vomer
vo-wing	wing of the vomer

Note on the figures
The scale on all figures indicates 5 mm

Anatomical description

The ethmovomerine region of the neurocranium

Because of the position of the ethmovomer it acts as a base upon which the premaxillae move and are supported (Alexander, 1967; Rosen & Patterson, 1969). It is thus of importance in feeding and hence trophic adaptation, one of the key elements in the ecological success of lacustrine Cichlidae (Fryer & Iles, 1972; Greenwood, 1974).

As in most higher teleosts, the ethmovomer of the Cichlidae is composed of four bones: the paired lateral ethmoids, the mesethmoid and the vomer. Both the mesethmoid and the vomer are compound elements incorporating a number of dermal components (Patterson, 1975). The modal arrangement of these bones and associated cartilage in the African Cichlidae is illustrated in Fig. 1.
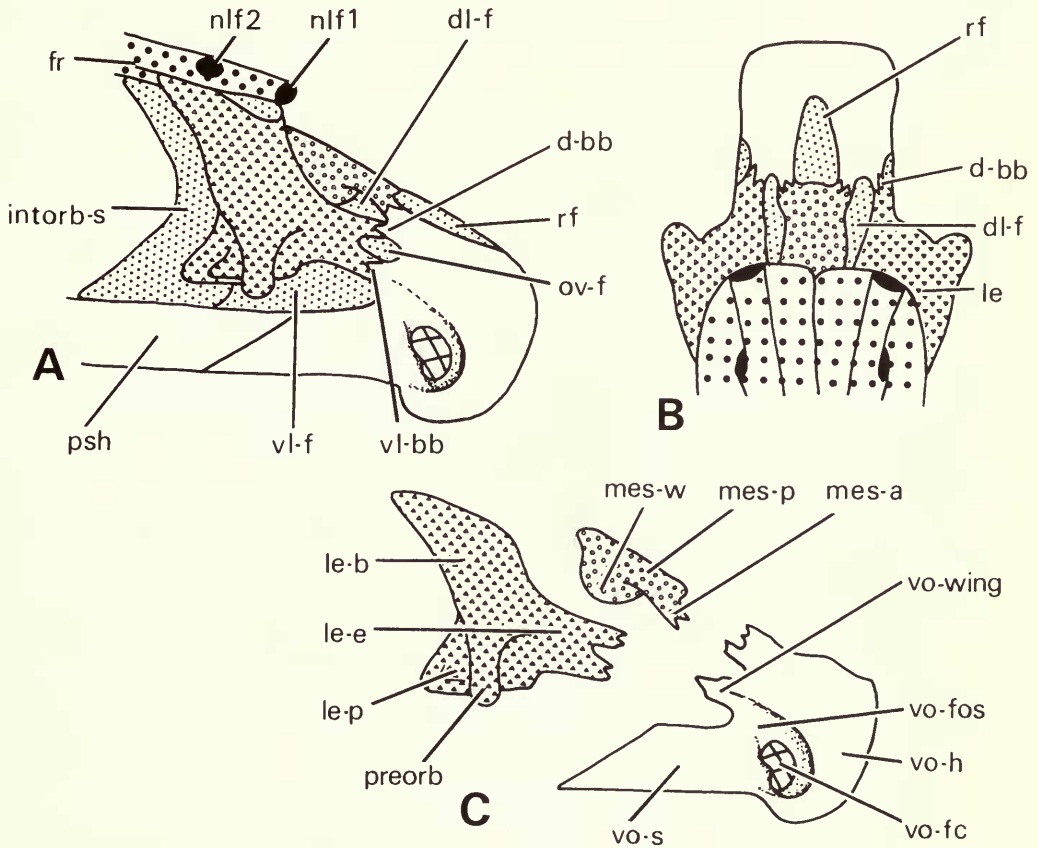

Fig. 1 Semidiagrammatic drawing of the modal arrangement of the bones of the ethmovomer in African cichlids. A. Lateral view. B. Dorsal view. C. Lateral view (exploded).

Regan (1920) was the first to attribute any phylogenetic significance to the particular associations of the bones in this region of the skull in cichlid fishes. He divided the genus *Tilapia* into a number of subgenera using the presence or absence of a sutural connection between the mesethmoid (=ethmoid of Regan, 1920) and the vomer as one of the characters for so doing. Trewavas (1973), Liem & Stewart (1976) and Liem (1979) also utilize ethmovomer characteristics in phylogenetic analyses of cichlid fishes. None of these authors has discussed the relationship of the lateral ethmoid bones to the other bones of that region.

Rhamphochromis

The lateral ethmoid bones (Figs 2 & 13A)

The elongate lateral ethmoids form the posterolateral part of the ethmovomer. The two bones are separated posteromedially by a cartilaginous interorbital septum and antero-medially by the mesethmoid and the ethmovomerine cartilage. Each bone may be described in two parts; the body and the anterior extension.

Dorsally the body contacts the frontal and ventrally it forms the floor, anterior wall and side of the anterior myodrome. Medially it bears a large well developed process (the lateral ethmoid process) which abuts against the ethmovomerine cartilage.

The anterior extension of the lateral ethmoid is suturally united with the vomer at two separate points. The dorsal sutural contact (the dorsal bony bridge) is separated from the lateroventral contact (the lateroventral bony bridge) so that the ethmovomerine cartilage is bridged dorsally and ventrally to expose an ovoid region of cartilage (the mesethmoid palatinad articulation facet of Barel et al., 1976).

A broad strap-like ligament, the palatine-lateral ethmoid ligament, originates from the ventral face of the anterior extension of the lateral ethmoid and attaches to the laterodorsal ridge on the palatine.
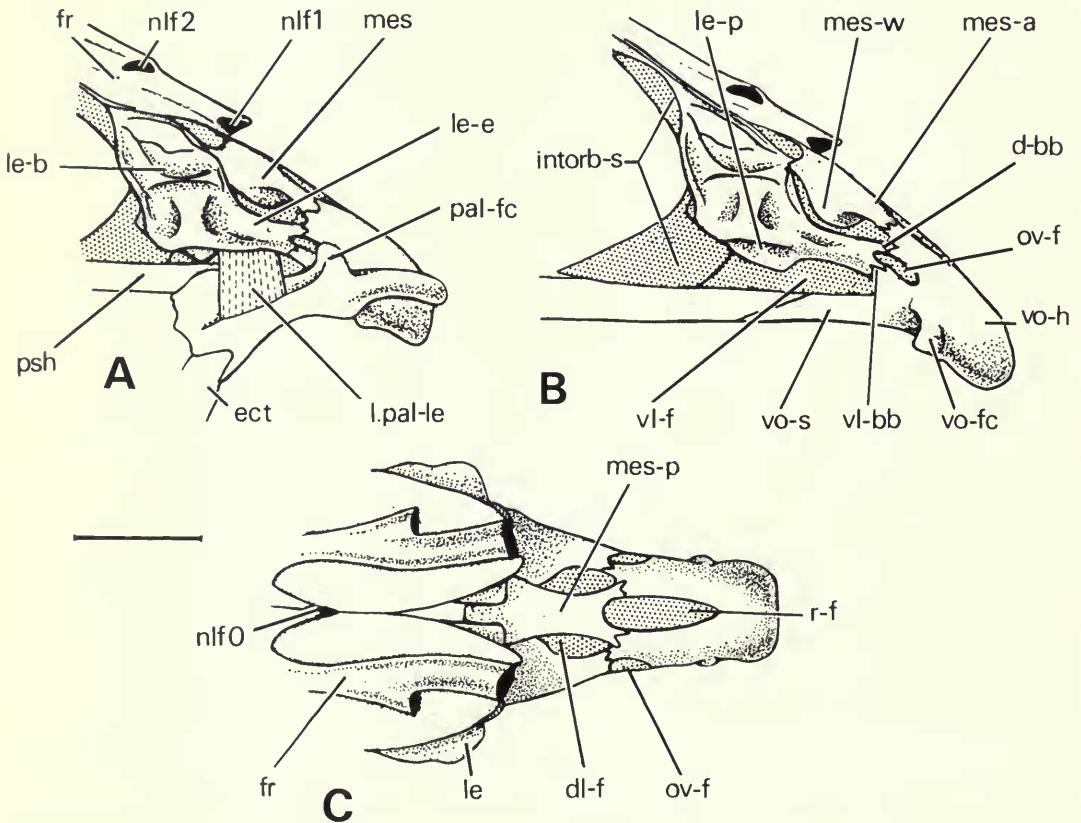

Fig. 2 *Rhamphochromis longiceps*, ethmovomerine region. A. Lateral view. B. Lateral view (suspensorium removed). C. Dorsal view.

The mesethmoid (Figs 2 & 13A)

The mesethmoid is a single, elongate bone situated medially and forming the posterodorsal part of the ethmovomer. The dorsal plate of the mesethmoid underlies the frontal bones forming the floor of the large frontal fossa. Anteriorly the dorsal plate is bifurcated and each

arm of bone is suturally united with the vomer medial to its dorsal suture with the lateral ethmoid. Between the two arms of the mesethmoid the ethmovomerine cartilage is exposed; the anterior margin of the mesethmoid forms the posterior margin of the rostral fenestra. A pair of medial wings are borne on the ventrolateral face of the dorsal plate of the mesethmoid. In lateral view the mesethmoid wings are hemispherical and are separated medially by the ethmovomerine cartilage.

The vomer (Figs 2 & 13A)

The vomer is a large strongly ossified element that forms the anterodorsal and ventral parts of the ethmovomer. It is most conveniently described in two parts: the head and ventral stalk.

The stalk of the vomer is slender and its posterior extremity is enclosed within a channel in the parasphenoid. Dorsally a wing of the stalk is produced above the lateral fossa and becomes suturally united with the lateral ethmoid (the lateroventral bony bridge).

Above the lateroventral bony bridge the head of the vomer is suturally united with the dorsal part of the lateral ethmoid anterior extension (the dorsal bony bridge) and medial to this it is suturally united with the mesethmoid. Dorsomedially the head of the vomer is divided by the rostral fenestra.

The vomer bears a pair of well developed facets for articulation with the palatine.
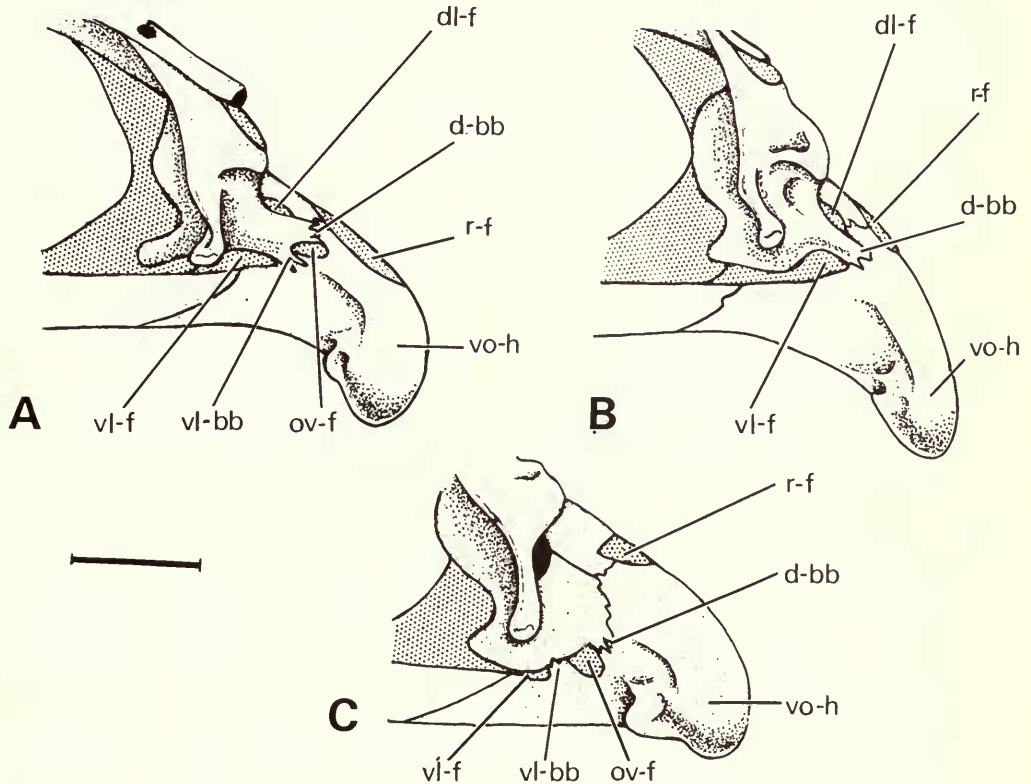

Fig. 3 Ethmovomer (lateral view). A. *Tylochromis lateralis*. B. *Geophagus brasiliensis*. C. *Petenia splendida*.

Bathybates and other cichlid taxa

Outgroup comparisons amongst other cichlid taxa indicate that the arrangement of the bones of the ethmovomer of *Rhamphochromis* represents the modal (ie. plesiomorphic) type found in the majority of African Cichlidae.

Interestingly, in the majority of South American taxa examined the anterior extension of the lateral ethmoid only contacts the vomer dorsally; the ventrolateral bony bridge is absent (compare Fig. 3B of the South American *Geophagus* and Fig. 3A of the African *Tylochromis*). However, in the South American *Petenia* (Fig. 3C) a ventrolateral bony bridge is present, but unlike the 'African' arrangement, in *Petenia* it is the vomer, rather than the vomer and the lateral ethmoid, that is produced to form the bridge.

The ethmovomerine region of *Bathybates* differs from that of *Rhamphochromis* in two salient features:

(i) the absence of a palatine-lateral ethmoid ligament (Figs 4A & 13B),

(ii) the reduction or loss of a dorsal bony bridge (Figs 4 & 13B).

The palatine-lateral ethmoid ligament is present in all the other cichlid taxa examined with the notable exceptions of *Hemibates* and *Trematocara* (Figs 5 & 14). Because of the widespread intrafamilial occurrence of this ligament its absence is interpreted as a synapomorphy uniting *Bathybates*, *Hemibates* and *Trematocara*.

A well developed dorsal bony bridge, formed by the sutural union of the anterior extension of the lateral ethmoid and the head of the vomer, is also present in all other taxa except *Bathybates*, *Hemibates* and *Trematocara*. In a few specimens of *Bathybates* and *Hemibates* a narrow splinter of bone has been found linking the lateral ethmoid and the vomer, but in no instance was a well developed dorsal sutural union found. The reduction or loss of the dorsal bony bridge is interpreted as a further synapomorphy uniting the genera *Bathybates*, *Hemibates* and *Trematocara*.

Hemibates and *Trematocara* share a further synapomorphy of the ethmovomerine region; the presence of a palatine-mesethmoid ligament (Fig. 5).

In all of the cichlids examined, the dorsal articulatory facet of the palatine (the mesethmoidad process of Barel *et al.*, 1976) abuts against the lateral aspect of the ethmovomer.
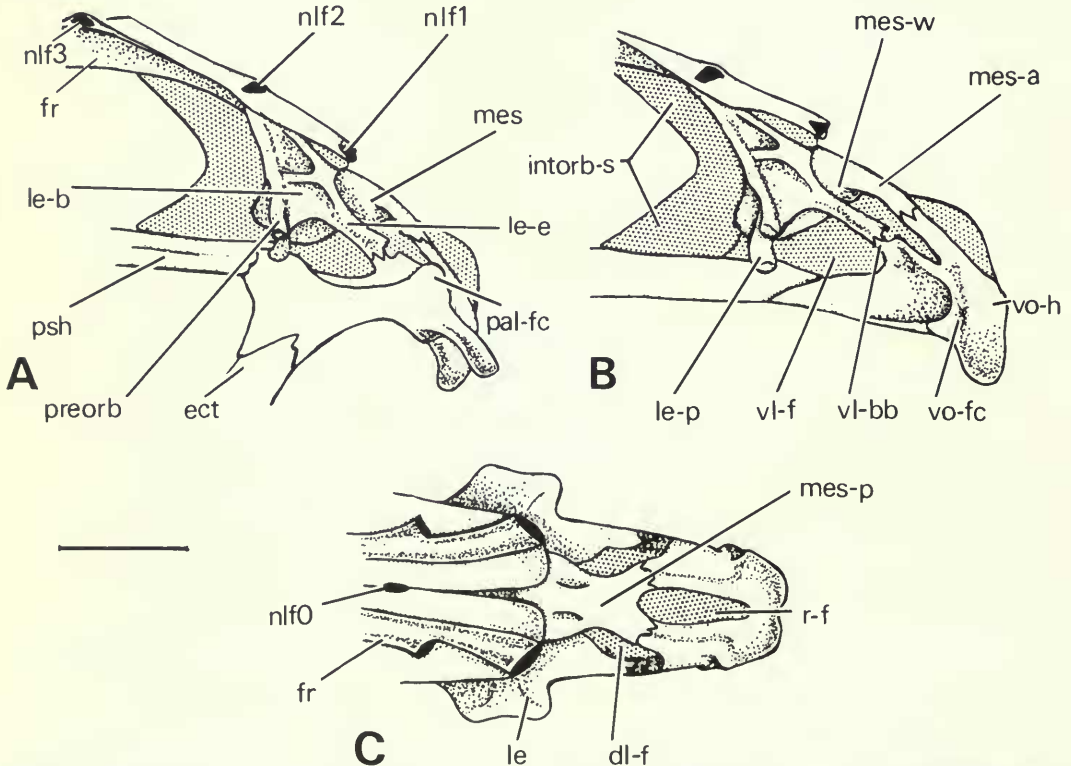

Fig. 4 *Bathybates ferox*, ethmovomerine region. A. Lateral view. B. Lateral view (suspensorium removed). C. Dorsal view.

Whilst in other taxa the facet of the palatine is attached to the ethmovomer by a few strands of connective tissue, in *Hemibates* and *Trematocara* the facet is also attached to the mesethmoid by a palatine-mesethmoid ligament. This ligament arises from the dorsal aspect of the palatine facet and passes posterodorsally to the dorsal face of the mesethmoid. Since it has only been found in *Hemibates* and *Trematocara* it is interpreted as a synapomorphy indicative of a sistergroup relationship between the two genera.

Further evidence of a sistergroup relationship between these two genera is found in the form of the rostral cartilage. In the majority of cichlids each premaxilla has ascending and articular processes and the two ascending processes are closely apposed and firmly bound by connective tissue. The rostral cartilage is a small nubble of cartilage situated on the posterodorsal face of the ascending processes, just above the articular processes. In *Trematocara* and *Hemibates* (Fig. 6C, D), although well developed articular and ascending processes are present, the rostral cartilage is not restricted by them and extends about halfway along the long ascending process. A similar elongation of the rostral cartilage has not been found in any other cichlid taxa.

The premaxillae of *Bathybates* is exceptional since there are no distinct articular processes (Fig. 6B).

The Cephalic muscles

On the basis of their shared innervation the muscles of the cheek may be divided into two groups. The first (group one muscles) includes the adductor mandibulae, the levator arcus palatini, and the dilatator operculi muscles. All are innervated by branches of the fifth
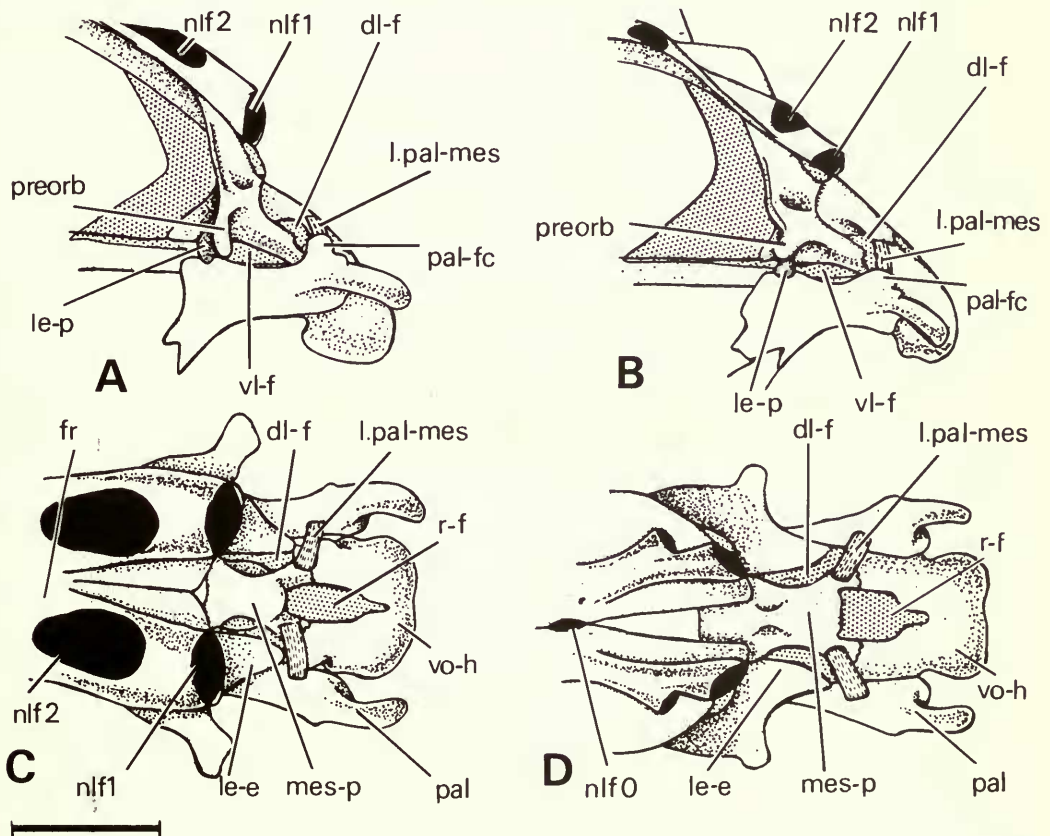

Fig. 5 Ethmovomerine region. Left, *Trematocara marginatum* A. Lateral view. C. Dorsal view. Right, *Hemibates stenosoma* B. Lateral view. D. Dorsal view.

cranial nerve. Group two muscles include the adductor arcus palatini, the adductor operculi and the levator operculi muscles; this group is innervated by branches of the seventh cranial nerve.
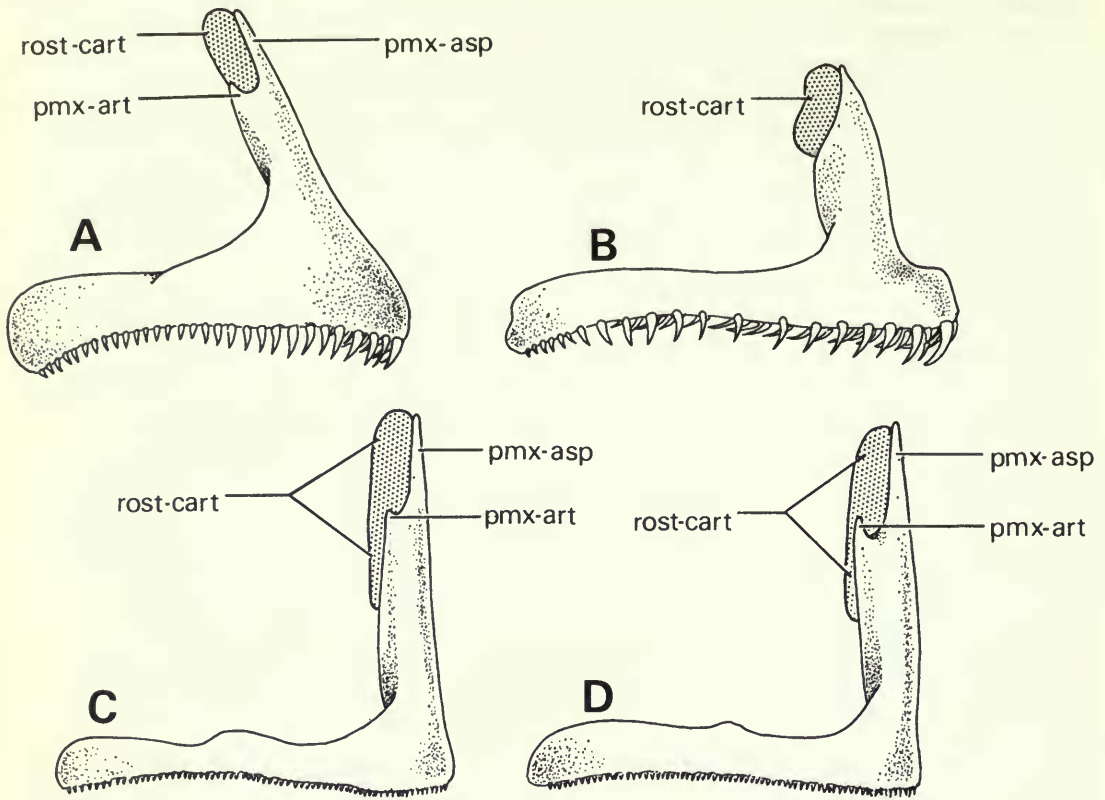

Fig. 6 Right premaxilla (lateral view). A. *Rhamphochromis longiceps*. B. *Bathybates ferox*. C. *Trematocara marginatum*. D. *Hemibates stenosoma*.

Group one muscles

These develop from the masticatory muscle plate which divides early in ontogeny into a dorsal and ventral section. The former gives rise to the constrictor dorsalis and the latter develops into the adductor mandibulae (Edgeworth, 1935).

The adductor mandibulae muscles. This is the largest muscle complex of the head; it occupies the lateral face of the suspensorium and inserts onto both upper and lower buccal jaws. In the Cichlidae four subdivisions are recognized. Following Anker (1978) a distinction is made between a part and a section of a muscle. A part is a subdivision having no, or hardly any, anatomical connection with other subdivisions of the same muscle. A section remains anatomically continuous with the rest of the muscle but may be distinguished from it on the basis of some other criterion such as fibre direction.

Hardly any connection exists between the four subdivisions of the adductor in cichlid fishes. Each part is well defined and easily separable from the others, and each is inserted via a separate tendon.

Although, as compared with some other families, the range of morphological variation of the adductor within the Cichlidae is narrow, numerous small differences are detectable.
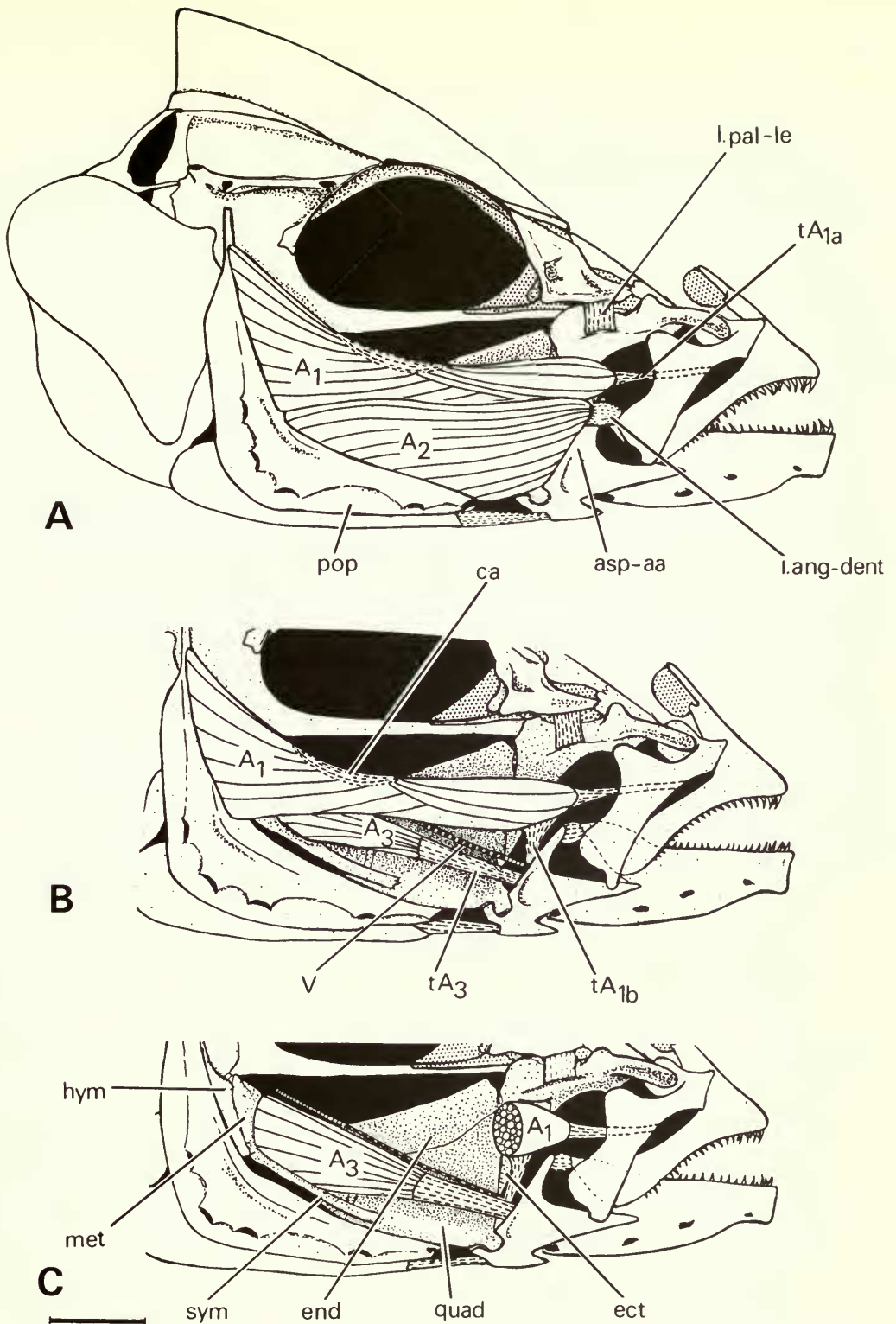
Fig. 7 *Rhamphochromis longiceps*. A. Lateral view of the adductor mandibulae muscle complex after removal of the lachrymal and circumorbital bones and the eyeball. B. After removal of A_2 to expose A_3. C. After the removal of A_2, and with A_1 cut away.

Rhamphochromis

INNERVATION. The path of the ramus mandibularis V is constant. It passes internal to A_1, external and dorsal to A_3, and divides, medial to A_2, sending a minor branch to the anteromedial surface of A_2. The main trunk enters the lower jaw dorsal to the tendon of A_3. On the medial face of the lower jaw the nerve branches, innervating A_w. For a precise description of the course of the ramus mandibularis see Goedel (1974*a, b*) and Anker (1978).

PART A_1 (Figs 7 & 8). This is the dorsal, superficial part of the adductor defined by its dorsal position and insertion onto the maxilla (Vetter, 1874). Part A_1 is a complex elongate muscle which connects the suspensorium with the maxilla and mandible. Origin is from the dorsal face of the vertical limb of the preoperculum and from the hyomandibular transverse zone. Dorsal muscle fibres pass anteroventrally and converge upon a well developed sheet-like aponeurosis situated beneath the eye. The fibres which originate from the middle section of the vertical limb of the preoperculum pass forward, bypassing the dorsal aponeurotic sheet, and intercalate with fibres that have originated from the anterior region of the aponeurosis. Together these fibres converge upon an anteroventral aponeurosis from which two tendons arise. The dorsal tendon, tA_{1a}, passes forward, medial to the maxillary shaft, and inserts on the anterior border of that bone just below the cranial condyle of the maxillary head. The second tendon, tA_{1b}, passes ventrally, medial to tA_3 and the ramus mandibularis V. On the inner aspect of the lower jaw a portion of tA_{1b} intergrades with tA_w, the remainder passes lateral to A_w and inserts onto the nipple process on the anteromedial face of the anguloarticular.

PART A_2 (Fig. 7A). This is the largest component of the adductor. Part A_2 is a parallel-fibred muscle occupying the ventrolateral region of the cheek, connecting the ventral elements of the suspensorium with the lower jaw.

Dorsally A_2 overlies A_1 and it conceals the anteroventral aponeurosis of the latter. Origin is from the crescentic zone and horizontal limb of the preoperculum, the symplectic, and the ventrolateral ridge of the quadrate. Part A_2 is composed of two sections distinguished by their differing sites of insertion. The dorsal section ($A_{2\alpha}$) is composed of fibres originating from the crescentic zone of the preoperculum and inserting onto the coronoid process of the dentary. The fibres contact the coronoid process on its lateral face via an association with the angulodentale ligament and, on its medial face, via a strap-like tendon, tA_2. In the ventral section ($A_{2\beta}$) the fibres originating from the horizontal limb of the preoperculum, the
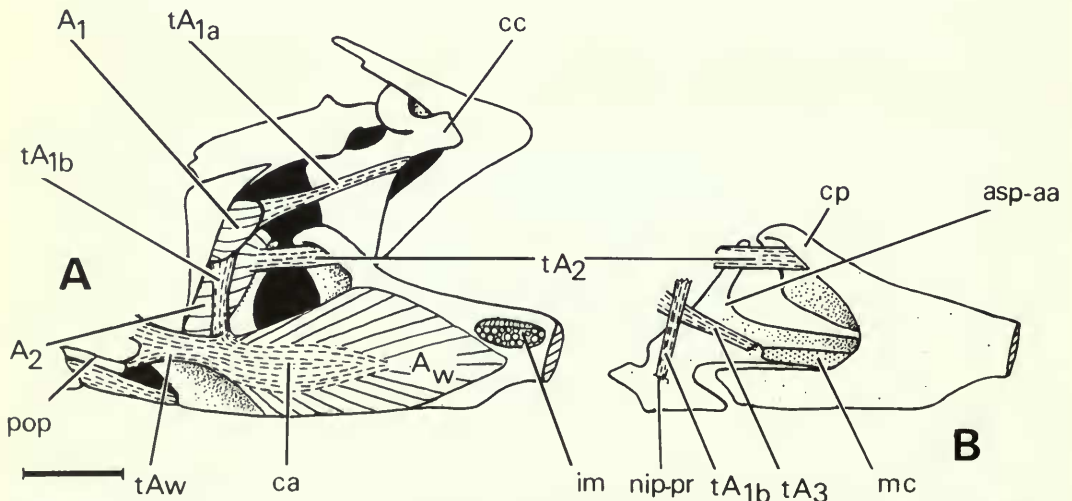

Fig. 8 *Rhamphochromis longiceps*. A. Buccal jaws and anterior suspensorial elements (medial view). B. Dentary, A_2 and A_w removed (medial view).

symplectic, and the quadrate insert musculously onto the posterior border of the ascending process of the anguloarticular. Part A_2 has no connection with part A_w.

PART A_3 (Fig. 7C). This is the medial part of the adductor complex and it underlies both A_1 and A_2. Part A_3 is a small, flat muscle which is roughly triangular in outline with the apex directed rostroventrally. Origin is from the lateral face of the metapterygoid and the dorsal border of the symplectic. Fibres converge upon a well developed strap-like tendon, tA_3 which runs anteroventrally and enters the lower jaw lateral to tA_{1b}. On the inner aspect of the lower jaw tA_3 passes lateral to A_w and inserts onto a small sesamoid ossification (the coronomeckelian ridge of Barel *et al.*, 1976).

PART A_w (Fig. 8A). Part A_w lies on the medial face of the mandible and connects it with the medial face of the suspensorium.

Fibres fan out from a central sheet-like aponeurosis, and attach musculously to the medial face of the coronoid process, the inner and outer walls of the Meckelian fossa and the ventral face of the anguloarticular. Towards the quadrato-mandibular articulation the aponeurosis becomes consolidated into a tendon, tA_w, which is firmly inserted onto the medial face of the quadrate and preoperculum.

THE INTERMANDIBULARIS (Fig. 8A). According to Edgeworth (1935) the mandibular muscle plate, in the early stages of its development, extends from the Gasserian ganglion to the anterior edge of the pericardium or to the midventral line. With the development of Meckel's cartilage the mandibular muscle plate separates into a masticatory muscle plate and the intermandibularis. The latter is innervated by either the ramus mandibularis V (Kesteven, 1943) or it may also receive innervation from the VII cranial nerve.

In the Cichlidae a single intermandibularis is present just caudal to the symphyseal facets of the dentaries. The intermandibularis passes transversely between left and right rami, attaching musculously to their medial faces.

Bathybates

The adductor in *Bathybates* is essentially similar to that of *Rhamphochromis* and a separate description is not warranted. However, certain differences in detail do exist and these are described and illustrated:

(i) The tA_{1a} is considerably reduced in length. The anterior muscle fibres of A_1 have apparently encroached upon the tendon so that the anterior portion of A_1 comes to lie medial to the maxillary shaft (Fig. 9A).

(ii) The short tA_{1a} inserts onto a distinct flange developed on the anterior border of the maxilla, just below the cranial condyle of the maxillary head (Fig. 9A, B).
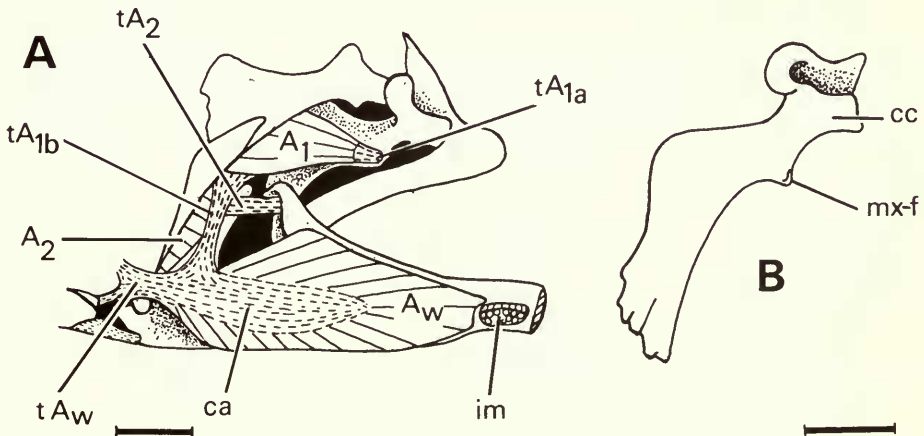

Fig. 9 *Bathybates ferox*. A. Buccal jaws and anterior suspensorial elements (medial view). B. Left maxilla (medial view).

(iii) The posterior face of the ascending process of the anguloarticular is expanded laterally to accommodate a large insertion of section $A_{2\beta}$ (Fig. 10A).

(iv) Part A_3 is large and well developed.

Other cichlid taxa

In the majority of cichlid taxa examined the mode of A_1 insertion is as described in *Rhamphochromis*. The presence of an elongate tA_{1a} is therefore interpreted as a plesiomorphic character of cichlid fishes. The reduction of the length of tA_{1a} in *Bathybates* is, on the basis of its limited distribution, interpreted as a derived character.

Liem (1978: Fig. 6) illustrates the medial aspect of the mandible, maxilla, and the anterior portion of the suspensorium and associated muscles, tendons, and ligaments of *Hemibates stenosoma*. He represents tA_{1a} (tam_1) as a short tendon of the *Bathybates*-type. This contradicts my own observations of tA_{1a} in a range of *H. stenosoma* specimens in which I found tA_{1a} to be of the standard *Rhamphochromis* (i.e. modal) type.

One species of *Lamprologus* (a large genus, most of whose species are endemic to Lake Tanganyika, see Poll, 1978) has a tA_{1a} approaching the *Bathybates* type. This species, *Lamprologus elongatus*, is united with the other *Lamprologus*, none of which has a short tA_{1a}, by the possession of a suite of characters that on the basis of their restricted distribution, are assessed to be apomorphic. For example all *Lamprologus* possess a hyomandibula in which the head is deeply notched, widely spaced extrascapular bones, a prominent flange on the prootic, and the infraorbital bones reduced or absent. All these characters are restricted to *Lamprologus*, or, in the case of infraorbital reduction, also occur in *Telmatochromis, Julidochromis, Chalinochromis,* and *Teleogramma.* In view of the number of synapomorphies uniting *L. elongatus* with the remaining *Lamprologus* species, the presence of a reduced tA_{1a} in *L. elongatus* is interpreted as a convergent development rather than a synapomorphy shared with *Bathybates*.

In all species of *Bathybates* the maxilla bears a distinct flange on its anterior border just below the cranial condyle of the maxillary head. This maxillary flange forms a platform onto which tA_{1a} is firmly inserted. An incipient flange is sometimes present in individual specimens of *Trematocara* and *Hemibates*. The presence of a well developed maxillary flange is interpreted as an apomorphic character within the Cichlidae.
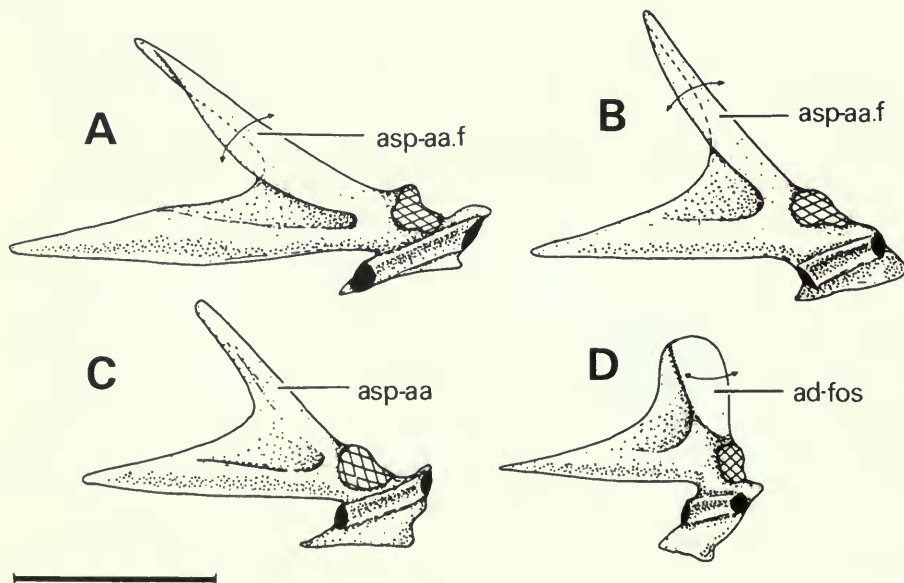

Fig. 10 Left anguloarticular bone. A. *Bathybates ferox.* B. *Trematocara marginatum.* C. *Rhamphochromis longiceps.* D. *Callochromis melanostigma.*

In all species of *Bathybates* (Fig. 10A), *Trematocara* (Fig. 10B), and *Hemibates* the ascending process of the anguloarticular has the posterior border laterally expanded into a ledge on which $A_{2\beta}$ inserts. The presence of this expansion of the anguloarticular is interpreted as a synapomorphy uniting these three genera.

Liem and Osse (1975) describe an adductor fossa in a number of Lake Tanganyika genera. This fossa is an indentation on the lateral face of the anguloarticular (Fig. 10D) which also serves to increase the insertion area of $A_{2\beta}$, and it is of a form quite distinct from that of *Bathybates*, *Trematocara* and *Hemibates*; it therefore is assessed as an independent character state.

The relatively large A_3 of *Bathybates* is difficult to interpret phylogenetically as there is considerable variation in A_3 development throughout the family.

The A_1 of all *Trematocara* species displays a novel tendinous connection with the lachrymal bone (Fig. 11). In *Trematocara* a third tendon (tA_{1c}) arises from the anteroventral aponeurosis of A_1 and passes forward to insert on the medial face of the large lachrymal bone. A similar connection between the lachrymal and A_1 was not found in any other cichlid taxon examined, and its presence in *Trematocara* is interpreted as a synapomorphy uniting the species of that genus.
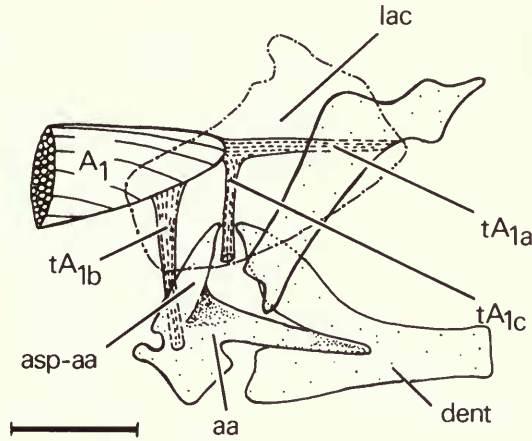

Fig. 11 *Trematocara marginatum*, buccal jaws, lachrymal bone and anterior portion of A_1 (lateral view). The outline of the lachrymal bone is indicated with a broken line.

The dilatator operculi.

Rhamphochromis (Fig. 12A)

The muscle lies behind and above the levator arcus palatini but there is no intercalation of their fibres and the two muscles are distinct. The main muscle mass of the dilatator occupies the well developed dilatator fossa, which is formed anteriorly by the sphenotic and posteriorly by the pterotic bones. The fossa lies between the crest bearing neurocranial lateral line foramina 4, 5 and 6 (Barel *et al.*, 1976) and the hyomandibular articulation sockets. Anteriorly the dilatator is bounded by the postorbital process of the sphenotic bone.

The dilatator origin is extensive, occupying the entire surface of the fossa. Fibres converge ventrocaudally and merge into a tendon-like aponeurosis inserting firmly on the dorsal surface of the dilatator process of the operculum (the dorsal process of Winterbottom, 1974).

Bathybates (Fig. 12B)

The dilatator of *Bathybates* differs from that of *Rhamphochromis* in being expanded anteriorly so that it covers the border of the postorbital process of the sphenotic.

Other cichlid taxa

In all the other cichlid taxa examined, the dilatator operculi is as described for *Rhampho-*

chromis. The anterior expansion of the dilatator in *Bathybates* species is interpreted as a synapomorphy uniting the species of that genus.

The levator arcus palatini. The position and structure of the levator arcus palatini is constant in the taxa examined in this study, although variations were observed in its size and shape. The following brief description of the levator in *Rhamphochromis* is representative of the modal cichlid arrangement.
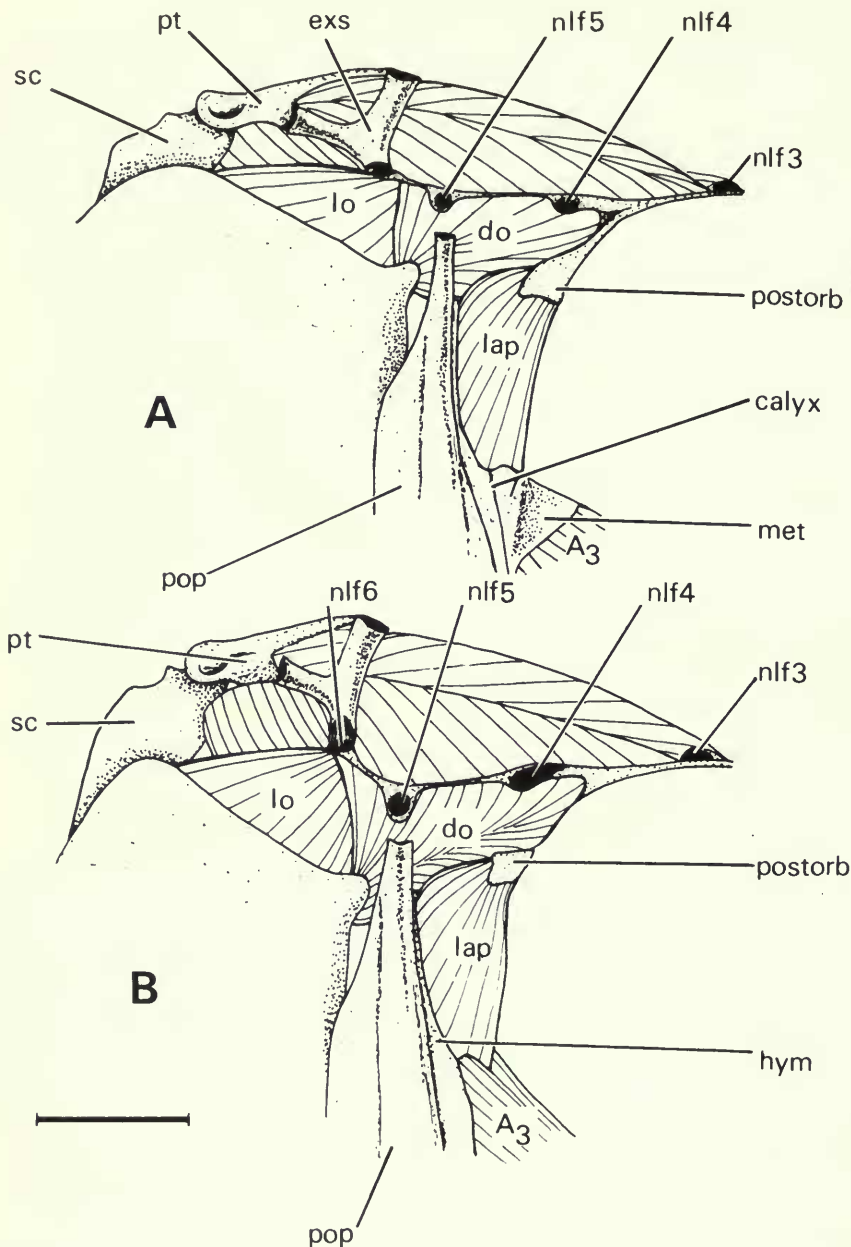

Fig. 12 Superficial postorbital musculature (lateral view) of A. *Rhamphochromis longiceps*. B. *Bathybates ferox*.

Rhamphochromis (Fig. 12A)

The levator is approximately conical in shape with its apex situated dorsally. Origin is from the ventral face of the postorbital process of the sphenotic. The fibres fan out from here and pass ventrally to insert musculously onto the hyomandibular transverse zone and flange, and into the calyx (Barel *et al.*, 1976).

No trenchant differences in the form of the levator in *Bathybates* were recognized.

Group two muscles

All group two muscles are derived from the constrictor hyoideus dorsalis and are innervated by the ramus hyomandibularis of the VIIth cranial nerve (Edgeworth, 1935).

The adductor arcus palatini. The adductor is well developed in the Cichlidae; it extends anteriorly to fill the fissura infraorbitalis and forms the floor of the orbit between the neurocranium and the suspensorium.
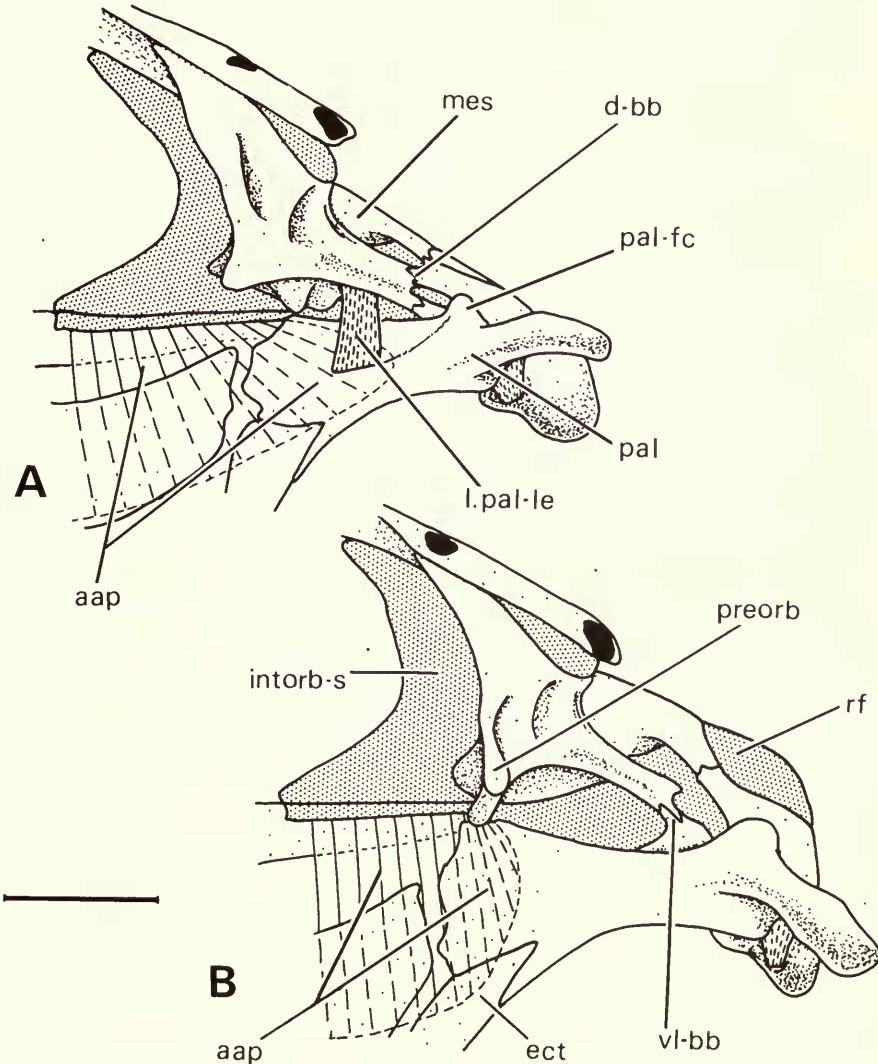

Fig. 13 Ethmovomerine region of A. *Rhamphochromis longiceps.* B. *Bathybates ferox.* The insertion area of the adductor arcus palatini muscle is indicated by broken lines.

Rhamphochromis (Fig. 13A)

The adductor originates musculously from the parasphenoid ventral crest and wing, and from the prootic anteroventral to the lateral commissure. The posterior border of the adductor is demarcated by the prootic-parasphenoid crest.

Fibres originate from the length of the dorsoventral crest of the parasphenoid, and the rostral margin of the muscle lies below the transverse level of the preorbital process. The fibres insert musculously on the medial face of the suspensorium. A sheet of connective tissue originates from the ventromedial face of the lateral ethmoid bones and fans out ventrally to cover the dorsal surface of the adductor.

The posterior fibres pass caudoventrally and insert musculously on the medial face of the hyomandibular flange and the dorsomedial face of the metapterygoid. Anteriorly the muscle fibres slope sharply forward and insert on the medial face of the palatine fossa and the ectopterygoid. The adductor is considerably thicker posteriorly although a slight thickening of the section inserting onto the palatine is discernible.
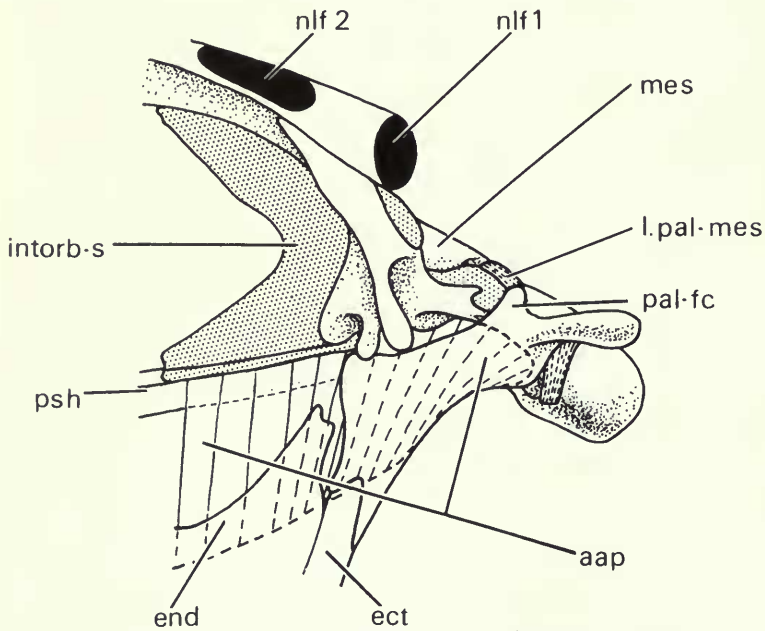

Fig. 14 Ethmovomerine region of *Trematocara unimaculatum*. The insertion area of the adductor arcus palatini muscle is indicated by broken lines.

Bathybates and other cichlid taxa (Figs 13B & 14)

The adductor of *Bathybates* is essentially similar to that of *Rhamphochromis* although as can be seen from the accompanying figure (Fig. 13B) the angle of orientation of the fibres inserting onto the palatine fossa is not as acute and the fibres pass ventrally. This seems to be a result of the position of the lateral ethmoid-palatine articulation facet which is situated more anteriorly in *Rhamphochromis*.

An arrangement similar to that of *Rhamphochromis* is present in other elongate piscivores of Lake Malawi e.g. '*Haplochromis*' *caeruleus* and '*Haplochromis*' *spilorhynchus*, and those of Lake Victoria e.g. *Prognathochromis macrognathus*, whilst one similar to that of *Bathybates* is present in other Lake Tanganyika genera e.g. *Haplotaxodon, Callochromis, Hemibates, Ectodus,* and *Aulonocranus*. Unfortunately insufficient outgroup data are available to enable the polarity of this character complex to be determined.

In *Trematocara marginatum* the arrangement is as in *Bathybates* but in the remaining species of *Trematocara* the adductor has apparently migrated anteriorly along the parasphenoid and onto the ventrolateral face of the vomer from where the fibres pass posteroventrally to insert into the palatine fossa (Fig. 14).

In common with Chichoki's (1976) observations, I have found that the adductor in all of the South American, Madagascan, and Asian species examined does not contact the medial face of the palatine and extends only as far rostrally as the medial face of the endopterygoid bone.

The levator operculi. The levator passes between the lateral neurocranial wall and the operculum, caudal to the dilatator operculi.

The levator is constant in form and position throughout the Cichlidae. It is an approximately triangular muscle with the apex situated dorsally. Origin is from the ventrocaudal region of the pterotic facet of the neurocranium, and the fibres fan out ventrally to insert on the medial face of the operculum, caudal to the site of insertion of the adductor operculi and the adductor hyomandibulae muscles. The anterior portion of the muscle inserts musculously onto the levator ledge on the medial face of the operculum, whilst the posterior fibres merge into a connective tissue sheet situated near the posterior margin of the operculum.

The adductor operculi. This cylindrical muscle connects the neurocranium with the medial face of the operculum, at a point adjacent to its articulation with the hyomandibula.

Rhamphochromis

The adductor originates musculously from the lateral region of the lateral awning (Barel *et al.*, 1976), its fibres passing laterally to insert on the adductor process which lies just behind the suspensoriad articulation socket on the levator ledge of the operculum.

No trenchant differences in the form of the adductor in *Bathybates* were recognized.

The adductor hyomandibulae. In the Cichlidae a small adductor hyomandibulae usually is present. It has apparently developed from the anterior fibres of the adductor operculi. The muscle slip originates, with the adductor operculi, from the prootic and inserts onto the medial face of the hyomandibular head adjacent to the opercular condyle of that bone.

The pharyngeal jaw apparatus (PJA)

It appears that throughout the cichlid radiation the full complement of perciform branchial muscles and bony elements of the PJA is retained and that no major changes occur in their spatial relationships to one another. However, within this configuration a seemingly endless spectrum of minor morphological variation is expressed. This is realized through differences in the relative size and robustness of the pharyngeal bones, the shape and distribution of their teeth, and through proportional changes in the various muscles coupled with slight differences in their sites of origin and insertion.

Osteological features of the PJA

The lower pharyngeal element. The lower pharyngeal element in cichlid fishes is composed of the suturally united ceratobranchials of the fifth branchial arch and their associated tooth plates. The size and shape of the resultant element, as well as the form and distribution of the pharyngeal teeth, shows considerable interspecific variation. Indeed, tooth form varies not only between taxa but also in different fields of the element in one individual. An anteroposterior gradient of increasing tooth specialization is considered as being the standard cichlid arrangement (Liem, 1978). Typically the lower pharyngeal element, which is the

largest element of the PJA, is shaped somewhat like an indented triangle with the apex lying rostrally. Posterolaterally the bone terminates, on either side, in a posteriorly directed horn (=muscular process of Liem, 1973) and a ventral keel is developed.

Liem (1973, 1978) and Liem & Osse (1975) have drawn attention to convergence in pharyngeal tooth form in trophically related groups. Amongst piscivores Liem (1978) illustrates the pharyngeal teeth of *Lamprologus compressiceps* and '*Haplochromis*' *compressiceps*, fishes which belong to distinct phyletic lineages, but which have an almost identical pharyngeal dentition.
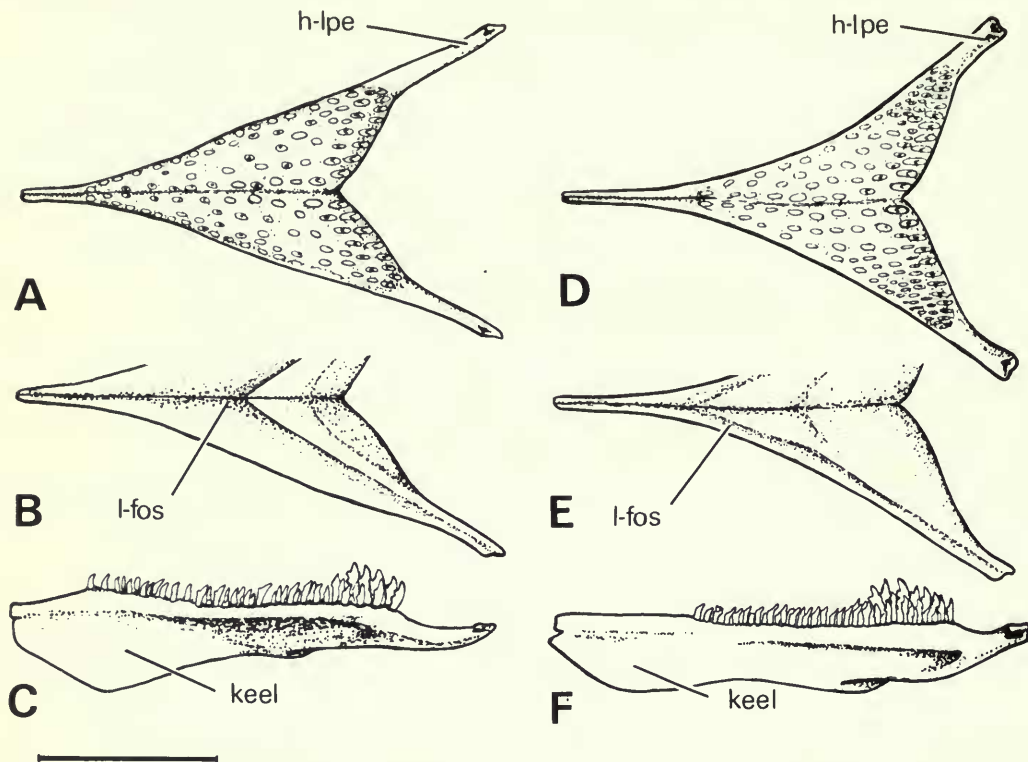

Fig. 15 Lower pharyngeal element. Left, *Bathybates ferox*. A. Dorsal view. B. Ventral view (right half). C. Lateral view. Right, *Rhamphochromis longiceps*. D. Dorsal view. E. Ventral view (right half). F. Lateral view.

Rhamphochromis

The lower pharyngeal element of *Rhamphochromis* is illustrated in Fig. 15D, E, F and as can be seen the bone is relatively elongate and is of a form commonly encountered amongst piscivorous cichlids (Poll, 1956; Greenwood, 1962, 1974; Barel, van Oijen, Witte & Witte-Maas, 1977; Hoogerhoud & Barel, 1978; Liem, 1978).

Seen ventrally, the medial region of the bone is rounded and convex and the lateral fossae are narrow. The dentigerous surface is roughly triangular in outline and the teeth are relatively fine. As in most cichlids the pharyngeal teeth located in the posterior field of the bone are the larger ones. In the anterior field the teeth are slender unicuspids in which the acutely pointed cusp is frequently directed caudally. The teeth become increasingly bevelled and the final two rows of somewhat enlarged teeth bear slightly hooked major cusps below which are a series of two to four accessory cusps. On the lower pharyngeal element these cusps are borne on the anterior edge of the teeth. It is this series of accessory cusps that gives these teeth their serrated appearance. The pharyngeal teeth are 'crowded' caudolaterally but uniformly distributed over the rest of the dentigerous surface.

Bathybates

The lower pharyngeal element is elongate and the tooth form and gradation are similar to those described for *Rhamphochromis*. A caudolateral 'crowding' of the teeth also occurs in *Bathybates* although the remaining teeth are sparsely and less uniformly arranged over the rest of the dentigerous surface. As can be seen from the accompanying illustration (Fig. 15A, B, C) the dentigerous area is enlarged and covers most of the pharyngo-buccal face of the lower pharyngeal element. In ventral view the lateral fossae are expanded and the bone is usually flattened but in some individuals it is concave.

Of the *Bathybates* species examined, *Bathybates ferox* displays the most extreme modification of the lower pharyngeal element, but all the species share an enlargement of the dentigerous area, a dorsoventral flattening of the caudal region of the bone, and an increased fossa width.

Both the enlargement of the dentigerous surface and the dorsoventral flattening of the caudal region of the pharyngeal element in *Bathybates* species are, on the basis of their limited distribution, interpreted as derived characters. The lower pharyngeal element of *Rhamphochromis* is rather typical of that found in the majority of piscivorous, elongate cichlids and no trenchant differences are recognized.

The pharyngeal dentition is similar in all of the piscivorous cichlids examined. The occurrence of this specialized tooth form amongst the piscivorous lineages in Lake Victoria (Greenwood, 1974), in *Lamprologus compressiceps* and other distantly related piscivores (Liem & Osse, 1975; Liem, 1978) seems to indicate that an independent evolution of this type of pharyngeal dentition is not uncommon amongst piscivorous cichlids. For this reason the extreme similarity in tooth form and gradation between *Bathybates* and *Rhamphochromis* is interpreted as convergence.

The upper pharyngeal jaws. As with the lower pharyngeal element, the size and shape of the constituent elements of the upper pharyngeal jaws as well as the form of their dentition, show considerable interspecific variation. Less consideration has, however, been given to the upper pharyngeal elements as a potential source of taxonomically useful characters. This is partly because of their relative inaccessability but also, since both upper and lower elements operate as a functional unit, adaptational changes in the lower element are reflected in concomitant changes in the upper elements.

Rhamphochromis (Fig. 16A)

The principal bony elements constituting the upper pharyngeal jaw in *Rhamphochromis*, in common with all cichlids, are the paired second and third* pharyngobranchials (and their associated tooth plates) and the fourth upper tooth-plate.

A pair of first pharyngobranchials (Pb1) serve to suspend the jaws from the neurocranium. Each is a stick-like ossified element connecting the anterior arm of the first epibranchial with the prootic just below the lateral commissure. The first pharyngobranchials lack associated tooth plates.

Each second pharyngobranchial (Pb2) is situated anterior to the third and is linked to the dorsomedial face of that element by a tract of connective tissue so that it lies with its caudal border closely apposed to the third pharyngobranchial (Pb3). Fused to the ventral surface of each Pb2 is a narrow, relatively elongate tooth plate with five or six teeth arranged in a single row. Each tooth bears a hooked major cusp with two accessory cusps above it. These cusps are borne on the lateral side of the teeth.

The third pharyngobranchials are the largest elements of the upper jaws. On the dorsal

*The term pharyngobranchial as used in this study refers to the infrapharyngobranchial. Amongst recent teleosts, ossified suprapharyngobranchials only occur in the first arch of elopids and alepocephalids and are thus not considered.

The problem of the correct homology of the element with which the third and fourth epibranchials articulate is discussed by Ismail (1979) and Ismail & Verraes (in prep.). Throughout the present study it is assumed that this element represents the third pharyngobranchial alone.
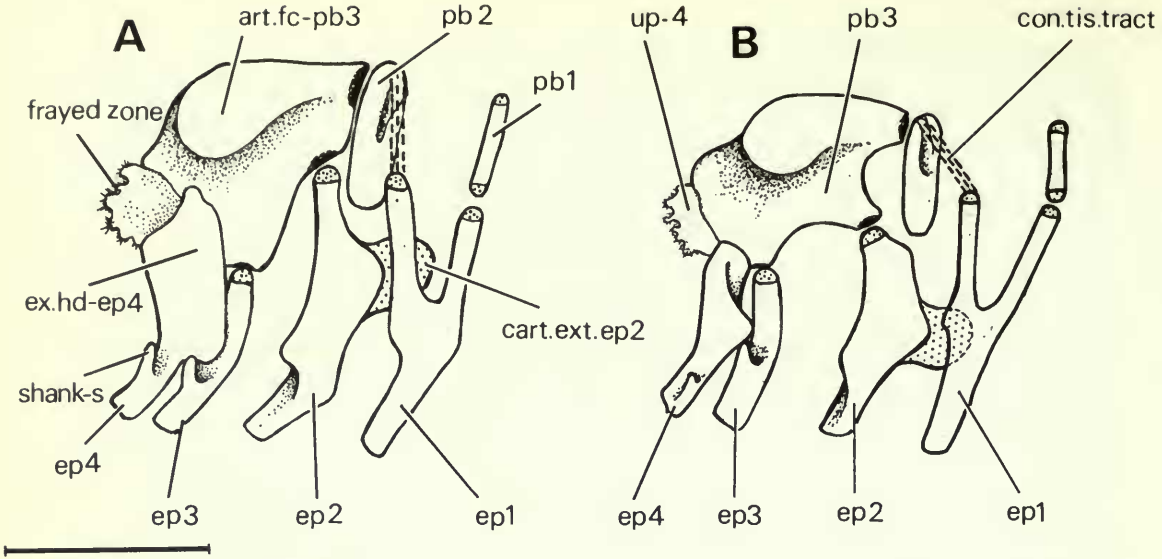
Fig. 16 Right upper pharyngeal jaw (dorsal view) in A. *Rhamphochromis longiceps* B. *Tremato-cara marginatum.*

surface of each bone there is a prominent raised facet which articulates with a corresponding process, the pharyngeal apophysis, on the base of the neurocranium (see Greenwood, 1978). Fused to the ventral surface of each Pb3 is a large tooth plate in which all the teeth have a hooked major cusp with two or three accessory cusps below it. In the caudal region the teeth become progressively smaller and more numerous.

The fourth upper tooth-plates (UP4) are well ossified and each is closely apposed to the caudal border of the corresponding Pb3. Each tooth plate bears numerous small hooked teeth also with tiny accessory cusps. Along the caudal margin of these bones there is a 'frayed zone' (the crista pharyngobranchialis of Goedel, 1974b) composed of numerous, very small, irregularly scattered unicuspid teeth. A strong connective tissue link exists between the Pb3 and UP4 of either side of the pharynx so that the whole complex apparently functions as a single unit.

Bathybates

As in *Rhamphochromis* the upper pharyngeal jaw complex as a whole is not robust and it is relatively elongate. The form and arrangement of the teeth are similar to those described in *Rhamphochromis* (see Liem, 1978 for other piscivorous cichlids).

In the course of this investigation, no trenchant differences were recognized in the form and composition of the upper pharyngeal jaws of *Rhamphochromis* and *Bathybates*. Both genera possess the typical piscivorous cichlid configuration (Hoogerhoud & Barel, 1978; Liem, 1978).

Other cichlid taxa

Of the outgroup taxa examined, all the *Trematocara* species share a characteristic feature of the third pharyngobranchial bones, *viz* the anterior margin of Pb3 is deeply indented, giving the margin a 'U'-shaped outline (Fig. 16B). This feature of Pb3 is not found in any other taxa and is assumed to be a synapomorphy uniting the species of the genus.

The epibranchial skeleton. Because of the intimacy of their association with the pharyngo-branchials, both in terms of structure and function, the epibranchials are considered as part of the upper pharyngeal jaw complex.

Barel *et al.* (1976) have produced an admirable description of the epibranchial series in

Astatotilapia elegans, and since the form of these bones in *Bathybates* and *Rhamphochromis* differ little from those of *A. elegans*, the following description will only highlight those features which are of presumed phylogenetic significance.

Rhamphochromis (Fig. 16A)

The first epibranchials (Ep1) are 'Y'-shaped elements. In each the rostral arm contacts the medial face of its respective Pb2 via a thin tract of connective tissue. An interarcual cartilage (Rosen & Greenwood, 1976) is completely absent in the majority of specimens examined. One specimen did retain a small nubble of cartilage suspended in this connective tissue tract, but the cartilage did not contact either Ep1 or Pb2.

Each second epibranchial (Ep2) contacts the dorsolateral face of Pb2 and the uncinate process contacts the anterior margin of Pb3 on its dorsolateral face. The main body of each Ep2 is rostrally expanded and the anterior margin projects medial to the uncinate process of Ep1. This expanded margin is capped with a flange of cartilage.

The third epibranchials (Ep3) are the smallest of the series. The main shaft of each contacts Pb3, and a well developed caudolateral process articulates with a corresponding facet on the fourth epibranchial.

Each forth epibranchial (Ep4) has a rostrally expanded head (the quadrangular region of Barel *et al.*, 1976). This enlarged head is slightly incurved and forms a large, posteriorly directed cupped area that overlies the dorsal face of UP4. The dorsal tip of the head of Ep4 articulates with a dorsal eminence formed at the junction of Pb3 and UP4. The rostral margin of each Ep4 bears an articulatory facet for the caudolateral process of Ep3; just below this facet the shank of Ep4 is produced into a well developed shank spine.

Bathybates

No trenchant differences in the form or arrangement of the epibranchials of *Bathybates* and *Rhamphochromis* were recognized

Other cichlid taxa

In the great majority of taxa examined the epibranchials are of the form described above. However, amongst the Lake Tanganyika genera all species of *Trematocara* possess a characteristically shaped Ep4 (Fig. 16B). In these fishes the head of Ep4 is not expanded or cupped, and the shank spine is reduced in size. The absence of this expanded head in *Trematocara* is interpreted as a secondary loss within the family rather than as the retention of the plesiomorphic perciform condition. It has been suggested elsewhere (page 77) that *Trematocara* is the sistergroup of *Hemibates* and that together these two form the sistergroup of *Bathybates*. A typical cichlid expansion of the head of Ep4 is present in both *Hemibates* and *Bathybates*. It must be assumed therefore that the ancestor of the whole group possessed an Ep4 with an expanded head. If this was the case then the expansion must have been secondarily lost in *Trematocara* species.

Myological features of the PJA

The dorsal branchial muscles develop from the muscle plates which are formed in each of the branchial segments, and may be grouped according to their developmental origin and innervation (Edgeworth, 1935).

Group one muscles

The levatores externi muscles. The four pairs of levator externus muscles connect the neuro-cranium with the four pairs of epibranchials and the lower pharyngeal element. They originate, together with the levatores interni, as a single muscle mass from the hyomandibulad shell of the neurocranium.
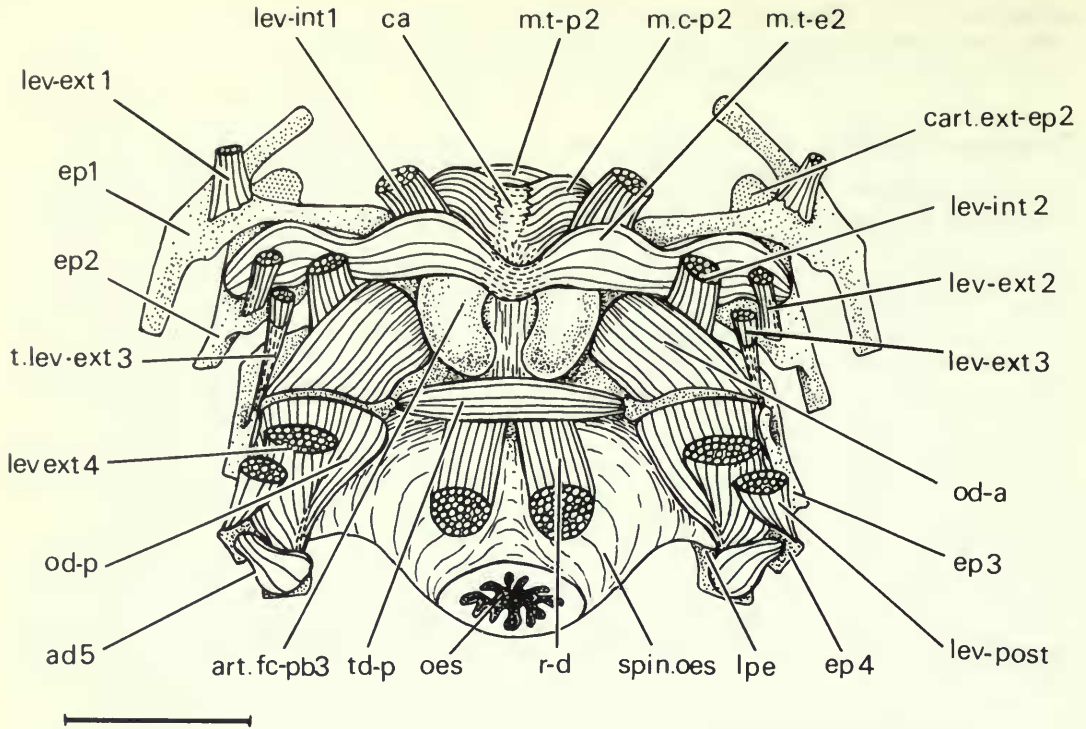
Fig. 17 *Rhamphochromis longiceps,* dorsal view of isolated pharyngeal jaw apparatus.

Rhamphochromis (Fig. 17)

FIRST LEVATOR EXTERNUS. This rostral levator passes caudoventrally from the hyomandibulad shell to insert musculously onto the dorsal face of Ep1. The insertion site is quite extensive and is situated on the dorsomedial face of Ep1 at the junction of its rostral and caudal arms.

SECOND LEVATOR EXTERNUS. This muscle originates, with the first levator, from the rostral part of the lateral rim of the hyomandibulad shell. It inserts onto the dorsolateral face of Ep2 at a point just above the triangular edge of the caudal border of that bone. The anterolateral fibres are tendinously associated with Ep2; the remaining fibres insert musculously.

THIRD LEVATOR EXTERNUS. This is the smallest of the series and is closely apposed to the rostrolateral side of the fourth levator for its entire length. It terminates in a long tendon which inserts onto the tip of the caudolateral process of Ep3.

FOURTH LEVATOR EXTERNUS. This is the largest of the levator series. The lateral section originates from the lateral rim of the hyomandibulad shell, the remaining section originating behind the levatores interni from the medial part of the shell. The two sections merge ventrally to form a single muscle mass. A small slip of lateral fibres inserts, via a short tendon, onto the well developed shank spine. The mass of the levator bypasses the shank spine, passing medial to it, and tapers onto a tendon which inserts on the horn of the lower pharyngeal element medial to the insertion of the fifth adductor muscle.

Bathybates (Fig. 18)

The levatores externi series of *Bathybates* is similar to that of *Rhamphochromis*. However, in *Bathybates* the third levator inserts onto a small aponeurosis and a long tendon is not developed.

Other cichlid taxa

In other cichlids the mode of insertion of the first three levatores externi is as described for

Rhamphochromis. The elongation of the tendon of the third levator externus in *Rhamphochromis longiceps* (and to a lesser extent that of the other *Rhamphochromis* species) is unusual although the length of this tendon in some other species, for example *Prognathochromis prognathus* from Lake Victoria, does approach the *Rhamphochromis* condition.

In the majority of taxa examined the third levator externus inserts onto Ep3 via a well developed, but not elongate, tendon. The reduction of this tendon, like that in *Bathybates*, is also found in other Lake Tanganyika genera, for example *Hemibates, Trematocara, Lamprologus, Limnochromis, Aulonocranus,* and *Ctenochromis.* Insufficient data on the distribution of various character states of the third levator insertion are available to permit interpretation of polarity in the character at an intergeneric level.

According to Liem & Osse (1975) and Liem (1978) the fourth levator externus in all cichlid fishes is composed of a small strap-like lateral head inserting onto the shank spine of Ep4, and a large medial head which passes medial to the spine to insert tendinously onto the posterior horn of the lower pharyngeal element. It was this shift in the major insertion site of the fourth levators (from the fourth epibranchials to the lower pharyngeal element) that Liem (1973) considered to be part of the 'key innovation' of the Cichlidae.

In *Trematocara* the fourth levator externus does not retain an attachment on Ep4 and the entire muscle passes over the head of Ep4 to insert tendinously on the horn of the lower pharyngeal element. The loss of a lateral section inserting onto Ep4 is interpreted as a synapomorphy uniting the species of the genus.

The levator posterior muscle. According to Edgeworth (1935) the levator posterior represents a fifth levator externus that has migrated caudally to originate from the ventrolateral face of the pterotic region of the neurocranium.

The levator posterior is separated from the rostral levators by a hiatus within which the adductor operculi muscle is situated.

Rhamphochromis (Fig. 17)

The fibres of this large muscle pass ventrocaudally from their origin on the ventral face of the pterotic and intercalar bones to insert musculously on the dorsolateral margin of Ep4 and the dorsal border of the shank spine. Some ventromedial fibres intercalate with the dorsal fibres of the medial section of the fourth levator externus.

Bathybates (Fig. 18)

The origin of the levator posterior is situated further medially in *Bathybates* than in *Rhamphochromis,* and is restricted to the intercalar bone.

Other cichlid taxa

In the majority of cichlid taxa examined the levator posterior originates from the ventro-lateral region of the lateral awning, usually from the pterotic and intercalar bones (see Hoogerhoud & Barel, 1978).

In *Hemibates* the origin of the levator has migrated medially onto the exoccipital bone at a site just anterior to the vagus foramen. This shift in origin does not appear to be correlated with the presence of an inflated otic bulla since in *Aulonocranus*, another genus with an inflated bulla, the origin of the levator is in the usual position. Similarly in *Trematocara* although the origin of the levator is more medially situated than in *Rhamphochromis* it is still restricted to the lateral awning.

The medial migration of the levator posterior in *Hemibates* is interpreted as the derived condition and it represents the end point of a trend visible in both *Bathybates* and *Trematocara.*

The levatores interni muscles. The two pairs of levatores interni muscles originate, together
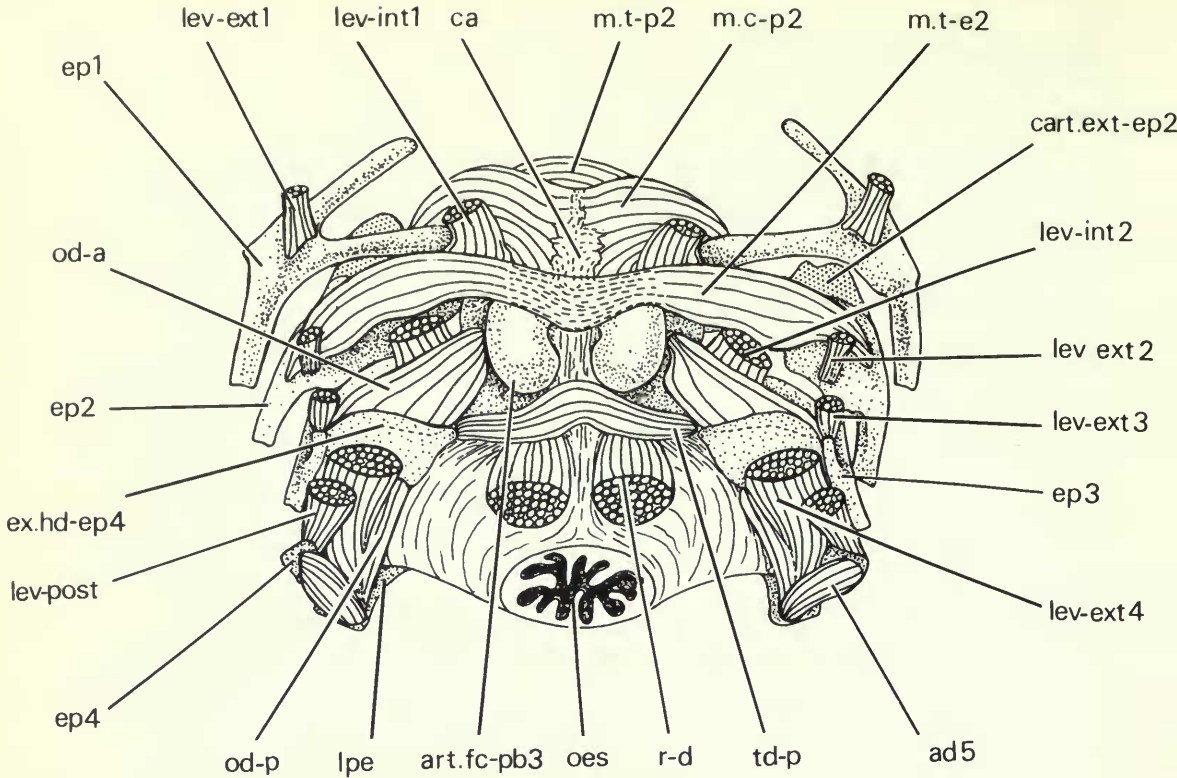
Fig. 18 *Bathybates ferox*, dorsal view of isolated pharyngeal jaw apparatus.

with the levatores externi 1–3, from the hyomandibulad shell between the lateral and medial sections of the fourth levator externus.

Rhamphochromis (Fig. 17)

FIRST LEVATOR INTERNUS. This rostral levator originates on the hyomandibulad shell medial to the second levator internus. It is a relatively large muscle that passes ventrally (and slightly caudally) and tapers into a short aponeurosis that inserts on the dorsomedial junction of Pb2 and Pb3 just caudal to the uncinate process of Ep1.

SECOND LEVATOR INTERNUS. The second levator is slightly pinnate and originates lateral to the first levator internus. Fibres pass ventrocaudally to insert via a short aponeurosis onto the ventrolateral face of Pb3 just anterior to the head of Ep3.

Bathybates (Fig. 18)

The levatores interni have similar sites of origin and insertion to those described above for *Rhamphochromis*. The first levator inserts musculously and is slightly expanded at its base.

Other cichlid taxa

The size of the levatores interni varies considerably amongst cichlid fishes (see Liem & Stewart, 1976). Hoogerhoud & Barel (1978) interpret the relatively large levatores interni of piscivorous species to be part of a complex of adaptations associated with the trituration of prey.

Insufficient outgroup data render ambiguous any phylogenetic interpretation of the differences between the insertion of the first levator internus in *Rhamphochromis* (via a short aponeurosis) and that in *Bathybates* (musculously).
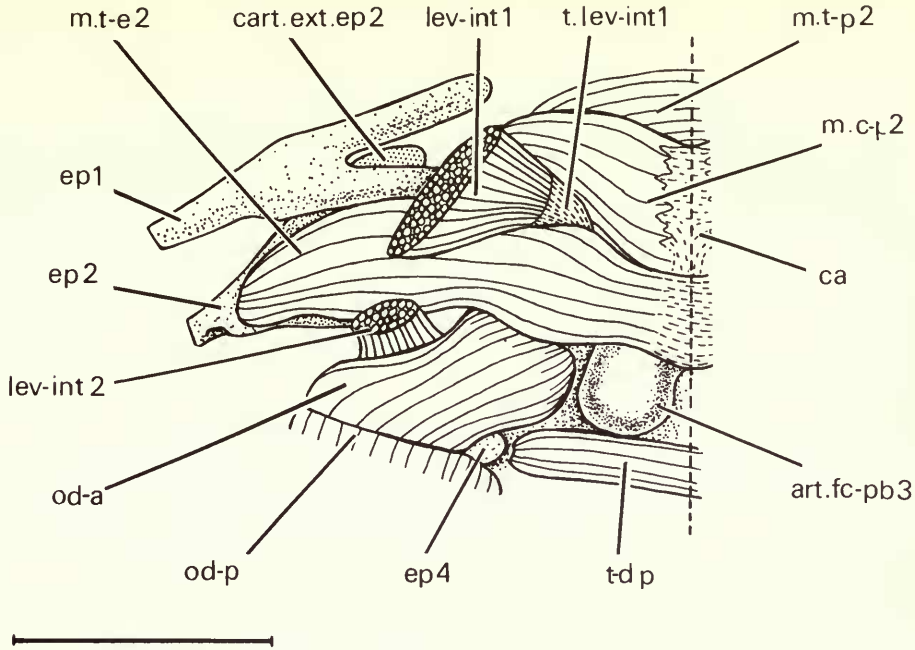
Fig. 19 *Trematocara marginatum*, dorsal view of anterior region of isolated pharyngeal jaw apparatus (left side).

In *Hemibates* and *Trematocara* (Fig. 19) the first levator internus muscles are rostrocaudally expanded and insert via well developed strap-like tendons. The rostrocaudal expansion of the first levator occurs in other species with inflated otic bullae eg. *Aulonocranus* and *Aulonocara* (cf. Hoogerhoud & Barel, 1978) but the presence of a well developed strap-like tendon is not so correlated. It is therefore assumed that this strap-like tendon is a synapomorphy shared by *Trematocara* and *Hemibates*.

The adductores muscles. *Rhamphochromis*

With the exception of the fifth muscle the adductores are situated in the angle between the dorsal part of the ceratobranchial and the shank of the epibranchial of each arch. The fifth adductor is the caudal representative of the series whose site of attachment has shifted onto Ep4 with the loss of Ep5. The fifth adductor is spindle shaped and it passes from the shaft of Ep4 at a point below the shank spine to insert onto the horn of the lower pharyngeal element. A few ventromedial fibres intercalate with those of the fourth levator externus.

No trenchant differences in the adductor series of *Bathybates* were recognized

Group two muscles

The remaining muscles of the dorsal gill arches are all derived from the sphincter oesophagi (Edgeworth, 1935) which is itself a derivative of the upgrowth around the oesophagus of the ventral ends of the muscle plates of the fifth branchial arch (Holstvoogd, 1965). All these muscles are innervated by branches of the vagus nerve (Edgeworth, 1935).

The sphincter oesophagi. The sphincter oesophagi forms a continuous muscle sheath around the oesophagus. No separate muscle bundle crosses the dorsal midline anterior to the entrance of the retractor dorsalis into the oesophageal tissues.

The transversi dorsales muscles
Rhamphochromis (Fig. 17)

As in all cichlids there are two distinct parts of this muscle, the transversus dorsalis anterior and posterior.

The transversus dorsalis anterior is a large tripartite muscle. The anterior part (the musculus transverus pharyngobranchialis 2 of Anker, 1978) is a relatively small, well defined muscle. It arises from the lateral part of the rostral face of Pb2 and its fibres pass medially across the midline to attach to the Pb2 of the opposite side.

The second part of this muscle complex (the musculus cranio-pharyngobranchialis 2 of Anker, 1978) connects the second pharyngobranchials with each other as well as with the neurocranium. The anterior fibres pass medially and insert on a complex median aponeurosis which in turn is attached to the parasphenoid bone at the base of the pharyngeal apophysis. The bulk of the muscle passes caudomedially to join the central aponeurosis of the third part of the muscle and the fibres of the opposite side.

The third part (the musculus transversus epibranchialis 2 of Anker, 1978) originates from the dorsal face of Ep2; its fibres pass medially to insert on a flat, strip-like aponeurosis which traverses the anterior face of the articulatory facets of the third pharyngobranchials.

The transversus dorsalis posterior (the musculus transversus epibranchialis 4 of Anker, 1978) is separated from the anterior muscle complex by a hiatus so that the articulatory facets of the third pharyngobranchials are exposed to form a diarthrosis with the pharyngeal apophysis. The strap-like transversus dorsalis posterior originates from the caudal eminence formed at the junction of Pb3 and UP4. The fibres pass medially and are not interrupted by a central aponeurosis.

Bathybates (Fig. 18)

The arrangement of this muscle complex is similar to that just described. However, the musculus cranio-pharyngobranchialis 2 is considerably larger in *Bathybates* than is its counterpart in *Rhamphochromis*. This is also the case in other Lake Tanganyika genera, whilst in other Lake Malawi genera and in the riverine *Serranochromis* the muscle proportions are as described in *Rhamphochromis*. Unfortunately too few outgroup data preclude any phylogenetic interpretation of these differences.

The obliqui dorsales muscles. Winterbottom (1974) discusses the nomenclatural confusion that has centred around the muscles connecting the posteromedial face of Ep4 and the dorsal tip of the fifth ceratobranchial. It is considered that, with the loss of the fifth pharyngo-branchial, the obliquus posterior represents a part of the obliquus dorsalis whose medial site of attachment has shifted to Ep4.

Rhamphochromis (Fig. 17)

The obliquus dorsalis anterior is a well developed muscle. It originates from the lateral wall of the articulatory facet of Pb3 and its fibres pass caudomedially to insert along the inner face of the expanded head of Ep4. Some fibres also insert along the caudolateral process of Ep3.

The obliquus dorsalis posterior is also well developed. It connects the expanded head of Ep4 with the horn of the lower pharyngeal element. The fibres of the obliquus posterior insert onto the tendon of the fourth levator externus, and together these two muscles insert tendinously on the horn.

Bathybates (Fig. 18)

The obliquus posterior is markedly reduced and is represented by a small strand of fibres originating from the dorsomedial face of the head of Ep4; as a result most of the head of that bone is exposed.

Other cichlid taxa

Liem (1978:346) states that '. . . the obliquus posterior is either weakly developed or absent in piscivorous cichlids.' Observations made during the course of this study contradict that assessment. For example in the *Rhamphochromis, Boulengerochromis, Serranochromis, Lamprologus,* and *Hemibates* species examined, as well as in '*Haplochromis*' *caeruleus*, '*Haplochromis*' *dimidiatus*, '*Haplochromis*' *woodi* and *Prognathochromis prognathus*, many

of which species were studied by Liem, an obliquus posterior is present and is not markedly reduced.

On the basis of these data, as well as the widespread occurrence of a well developed obliquus posterior in the majority of taxa from other trophic groups, the reduced area of origin and total size of the obliquus posterior in *Bathybates* is interpreted as a derived character.

The retractor dorsalis muscles. The bilaterally paired muscles connect the posterior pharyngobranchial elements with the vertebral column. The size of the retractor varies markedly within the Cichlidae (Hoogerhoud & Barel, 1978) and the site of origin is from the ventral face of the anterior vertebrae and includes the apophysis that is developed on the third, fourth or fifth abdominal vertebrae (Trewavas, 1964; Greenwood, 1979).

Rhamphochromis (Fig. 17)

The retractor originates from the ventrolateral face of the first, second, and third abdominal vertebrae and from the ventral apophysis on the third vertebra. Its fibres pass rostro-ventrally and insert musculously as two distinct bundles on the mediocaudal face of the third pharyngobranchials; a few fibres insert on the rostral region of UP4.

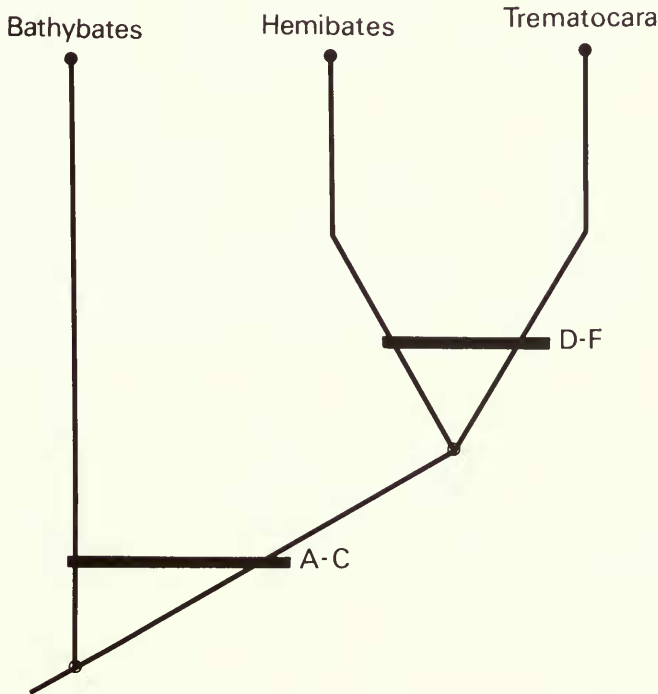No trenchant differences in the retractor of *Bathybates* were recognized.

Fig. 20 Cladogram illustrating the hypothesis of relationship for *Bathybates*. Apomorphic characters defining the genera *Bathybates, Hemibates* and *Trematocara* are discussed in the text (see Stiassny, 1980 for additional data). Synapomorphies: A. Laterally expanded ascending process of the anguloarticular. B. Palatine-lateral ethmoid ligament absent. C. The dorsal bony bridge reduced or absent. D. Tendon of the first levator internus broad and strap-like. E. Palatine-mesethmoid ligament present. F. Elongate rostral cartilage extending below the articular processes of the premaxillae.

Discussion

A number of apomorphic characters has been identified amongst the cichlid taxa studied and on the basis of these features it is possible to establish the monophyly of *Bathybates* and to generate an hypothesis of phylogenetic relationships for that genus (Fig. 20).

The relatively high degree of morphological differentiation exhibited by the Lake Tanganyika Cichlidae renders that flock a most suitable subject for cladistic analysis at the intergeneric level. This was not found to be the case with the Lake Malawi Cichlidae.

Although the range of morphological differentiation throughout the whole flock is greater in Lake Malawi than in Lake Victoria, with respect to the piscivorous species at least, a similar situation exists in the two lakes. The range of morphological variation amongst the various taxa is narrow and in most cases if structures are simply regarded in terms of presence or absence no character differences are distinguishable. In this respect Greenwood's (1974) conclusion that the different characteristics identified in the Lake Victoria 'Haplochromis' flock are but slight variants of a basic 'bauplan' developed and differentiated by ontogenetic reorganization, may be broadened to include the piscivorous grade of Lake Malawi. This is not to imply that a close phylogenetic relationship exists between the Lake Victoria and Lake Malawi haplochromines or that the Lake Malawi piscivores are necessarily a phylogenetic lineage.

None of the character complexes investigated in the preceding sections has revealed apomorphic character states in *Rhamphochromis*. Although all of the species currently included in this genus do have a highly distinctive 'facies' such an overall similarity does not, in itself, constitute evidence of monophyly.

Given the extreme appearance of these *Rhamphochromis* species it is surprising that very few apomorphic characters can be found to define the genus.

Regan (1921) was of the opinion that the beak-like expansion of the premaxillae (Fig. 6A) characterized the genus, but similar premaxillary expansion is also present in 'Haplochromis' *caeruleus*, 'Haplochromis' *strigatus*, and 'Haplochromis' *compressiceps* from Lake Malawi as well as in some Lake Victoria piscivores. Regan also noted that the anterior teeth of the second series in the upper jaw are enlarged in *Rhamphochromis* species. This feature does appear to characterize all the species of *Rhamphochromis*. In all *Rhamphochromis* species the urohyal bone lacks an anterodorsal process. In the great majority of other cichlid species the urohyal bears a distinct anterodorsal spine (Barel *et al.*, 1976) and thus its presence is interpreted as a plesiomorphic character within the Cichlidae. *Rhamphochromis* is unique amongst Lake Malawi Cichlidae in lacking this spine. The loss of the spine occurs mosaically amongst the Lake Tanganyika genera and therefore is assumed to have taken place independently a number of times within that lake. All of the Lake Victoria taxa examined have an anterodorsal spine on the urohyal.

All *Rhamphochromis* are large, elongate, streamlined fishes and similar features also characterize the piscivorous grade of Lake Victoria 'Haplochromis' (Greenwood, 1962, 1974). In Lake Victoria body elongation is not accompanied by a marked increase in the total number of vertebrae. The range of vertebral counts for these species is 30–32, whilst that of the more 'generalized' forms is 27–30 (Greenwood, 1962; Greenwood & Barel, 1978). This slight increase in total number involves an increase in the number of caudal, rather than abdominal vertebrae (Greenwood, 1979).

Amongst the piscivores of Lake Malawi an increase in size and elongation of the body is frequently accompanied by an increase in the total number of vertebrae, and many species have a higher total count than their Lake Victoria counterparts. For example; 'Haplochromis' *strigatus* 30–32 (13–14 + 17–18), 'Haplochromis' *dimidiatus* 32–33 (13–14 + 18–20), 'Haplochromis' *caeruleus* 34 (15 + 19), 'Haplochromis' *spilorhynchus*, 33–34 (15 + 17–18), 'Haplochromis' *lepturus* 33–35 (15–16 + 18–19), 'Haplochromis' *macrostoma* 31–32 (13–14 + 17–18), 'Haplochromis' *compressiceps* 31–32 (13–14 + 17–18), *Aristochromis christyi* 32 (14–15 + 17–18), *Diplotaxodon argenteus* 33 (16 + 17).

Rhamphochromis stands alone amongst the Lake Malawi Cichlidae in possessing a much

higher total number of vertebrae (as many as 39 in some specimens of *Rhamphochromis leptosoma*). Furthermore, *Rhamphochromis* is easily distinguished from the other Lake Malawi (and Lake Victoria and Lake Tanganyika) cichlids by the fact that the increase in the total number of vertebrae involves an increase in the number of abdominal vertebrae. In all species of *Rhamphochromis* the number of abdominal vertebrae is 17 or more.

This increase in the total number of vertebrae, and the increase in the number of abdominal vertebrae, are both interpreted as apomorphic characters which serve to distinguish *Rhamphochromis* from other Lake Malawi haplochromines. But as can be seen from the figures given above '*H.*' *caeruleus*, '*H.*' *spilorhynchus* '*H.*' *lepturus, Aristochromis* and *Diplotaxodon* display a slight increase in the number of abdominal vertebrae, and a similar, though more marked increase is found in the members of the *Serranochromis* lineage (Greenwood, 1979; Trewavas, 1964; Bell-Cross, 1975).

Greenwood (1979) has suggested that *Serranochromis* may have contributed to the Lake Malawi flock; the shared apomorphic character of an increased number of abdominal vertebrae found in *Serranochromis* and *Rhamphochromis,* and to a lesser extent, also in '*H.*' *caeruleus*, '*H.*' *spilorhynchus* '*H.*' *lepturus, Aristochromis* and *Diplotaxodon* may reflect a close relationship amongst these fishes.

In many ways *Rhamphochromis* represents an endpoint in an evolutionary trend towards the production of a highly specialized morphotype. Though often extreme, the characters involved in the production of this large mouthed, streamlined fish are linked through a gradal series to those found in the less modified piscivores of Lakes Malawi and Victoria. From a knowledge of intra- and interspecific variation in meristic characters, neurocranial and dental morphology, and from ecological and biological data for much of the Lake Victoria flock, Greenwood was later able to breakdown the piscivorous grade into two phyletic lineages (1980). Unfortunately, comprehensive data of this nature are not available for the majority of the Malawi Cichlidae and in their absence a similar breakdown of the Malawi piscivores cannot be achieved.

The level of discrimination provided by this purely anatomically based cladistic investigation has proven to be adequate when applied to an intergeneric analysis of the Lake Tanganyika cichlids but insufficient to detect salient character differences within the Lake Malawi flock. It seems that in the face of low morphological differentiation combined with a high level of species proliferation, a cladistic approach relying upon purely anatomical data is stretched to its limits. If the phylogenetic relationships of *Rhamphochromis* and the other Lake Malawi cichlids are to be resolved then ecological, ethological and possibly physiological characters must be employed within the same framework (see also Greenwood, 1980).

Acknowledgements

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