Anatomy, relationships and classification of the families Citharinidae and Distichodontidae (Pisces, Characoidea)

Richard Peter Vari

NATO Postdoctoral Fellow, Department of Zoology, British Museum (Natural History), Cromwell Road, London, SW7 5BD[1]

Contents

Synopsis . . . 261
Introduction . . . 262
Methods . . . 264
Materials . . . 264
Abbreviations used in text figures . . . 265
Nomenclatural comments . . . 265
Phylogenetic analysis . . . 266
  Jaws . . . 266
  Dentition . . . 275
  Supraethmoid . . . 277
  Anterior orbital region . . . 279
  Posterior orbital and anterior otic regions . . . 283
  Occipital region . . . 289
  Cranial fontanelle . . . 290
  Suspensorium . . . 290
  Opercle . . . 295
  Dermosphenotic, pterotic and suprapreopercle . . . 296
  Supraorbital and infraorbitals . . . 301
  Branchial apparatus . . . 303
  Weberian apparatus . . . 305
  Postcleithra . . . 310
  Pelvic bone . . . 311
  Caudal skeleton . . . 311
  Scale form . . . 313
  Myology . . . 315
  Swimbladder, intestinal and epibranchial organ forms . . . 321
  Olfactory bulbs . . . 322
Phylogenetic reconstruction . . . 324
  Families Citharinidae and Distichodontidae . . . 324
  Family Citharinidae . . . 326
  Family Distichodontidae . . . 327
Conclusions . . . 339
Comparisons with previous classifications . . . 340
Comments on the African Characidae . . . 341
Acknowledgements . . . 342
References . . . 342

Synopsis

Various osteological and soft anatomical systems in the families Citharinidae and Distichodontidae were examined to test: the hypothesized monophyly of the unit formed by citharinids and distichodontids

---

[1]Present address: Division of Fishes, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington D.C.

Bull. Br. Mus. nat. Hist. (Zool.) **36** (2) : 261–344 Issued 29 November 1979

within characoids; the interrelationships of the nominal genera within these families; and the monophyly of the nominal genera and suprageneric taxa.

The evidence of this study is congruent with the hypothesis that citharinids and distichodontids form a monophyletic subunit of characoids definable by a series of derived characters. However, the arrived at hypothesis of generic interrelationships necessitates several modifications of the previous generic and suprageneric taxonomy of these families. The retention of the previously recognized family Ichthyboridae was found to result in a non-monophyletic family Distichodontidae. Consequently, the Ichthyboridae of earlier workers is sunk into the Distichodontidae. At the generic level, *Congocharax* and *Dundocharax* are placed into synonymy of *Neolebias*, and *Gavialocharax* and *Phagoborus* are synonymized into *Ichthyborus*. These changes resolve the previously non-monophyletic natures of *Neolebias* and *Phagoborus* respectively. The conclusions of this study contraindicate the monophyly of the genus *Distichodus* as presently defined, and cast doubt on the monophyletic nature of *Hemigrammocharax* and *Nannocharax*. These three genera are, nonetheless, tentatively retained until such time as an analysis of the phylogeny of their contained species can be undertaken.

Finally, information uncovered during this study supports the concept of the monophyletic nature of the subunit of characoids formed by the African Characidae. However, the available evidence also indicates that as presently constituted the genus *Alestes* is non-monophyletic. This taxon is, however, retained until an indepth analysis of African characids permits its redefinition on the basis of derived characters. The subdivision of the African Characidae into the subfamilies Hydrocyninae and Alestiinae results in the latter taxon being non-monophyletic. Consequently the Hydrocyninae is sunk into the Alestiinae, which in this broader sense now constitutes a monophyletic unit.

Introduction

The superfamily Characoidea (Rosen & Greenwood, 1970) is one of the largest groups in the ichthyofauna of the Neotropical region and Africa, and one of the major freshwater fish assemblages. Although the classification of the superfamily has undergone extensive revision during the last century, questions on the interrelationships of characoids at all taxonomic levels remain largely unresolved. This paper deals with the relationships between and to a lesser extent within the genera which constitute the African endemic characoid families Citharinidae and Distichodontidae.

A series of workers including Boulenger (1909), Regan (1911) and Gregory & Conrad (1938) have suggested that citharinids and distichodontids form a closely related subunit of characoids, with Regan (1911, p. 22) terming them 'a very natural group of African Fish'. Although Greenwood *et al.* (1966) did not deal with interfamilial relationships within the Characoidea, they do list these families sequentially, a procedure meant to indicate close relationship (Weitzman, pers. commun., in Roberts, 1969, p. 399). Despite this broad consensus, the basis for the hypothesized close relationship of these families has remained obscure. Furthermore, as shown in Table 1 the number and limits of the suprageneric taxa recognized within the families Citharinidae and Distichodontidae have been subject to considerable differences of opinion. The conflicting nature of these classifications is reflected in the history of the group recognized as the subfamily Distichodontinae by Boulenger (1909) and more recently as the family Distichodontidae by Greenwood *et al.* (1966) (both of these concepts differ from the Distichodontidae of this work, see p. 265). This assemblage was subdivided into two subfamilies with different limits by Eigenmann (1909) and Regan (1911). Subsequently, Gregory & Conrad (1938) removed the distichodontid genera *Xenocharax*, *Neolebias*, *Hemistichodus* and *Nannaethiops* to their subfamily Citharininae. More recently Poll (1973) carried this trend further by placing all distichodontids (*sensu* Greenwood *et al.*, 1966) into his family Citharinidae. Monod (1950), in turn, defined the suprageneric taxa among citharinids and distichodontids in such a manner as to exclude the distichodontid genera *Xenocharax*, *Neolebias*, *Nannaethiops* and *Paradistichodus* from all of his subfamilies. To the extent that these authors used their classifications as a mode of conveying concepts on the relationships between taxa, such differing classifications reflect the uncertainty that exists concerning the phylogenetic history of citharinids and distichodontids.

This uncertainty was a consequence of a series of factors, three of which appear to have been of paramount importance. Firstly, earlier classifications were based on a limited number of

Table 1 Previous classifications of the families Citharinidae and Distichodontidae with members of the suprageneric units listed where originally specified

Boulenger, 1909	Citharininae	*Citharinus*, *Citharidium*
	Distichodontinae	*Nannaethiops*, *Neolebias*, *Distichodus*, *Nannocharax*, *Xenocharax*
	Ichthyborinae	*Ichthyborus*, *Neoborus* (=*Phagoborus*), *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago*
Eigenmann, 1909	Citharininae	
	Neolebiinae	
	Distichodontinae	
	Phaginae	
	Ichthyborinae	
Regan, 1911	Citharininae	*Citharinus*, *Citharidium*
	Xenocharacinae	*Xenocharax*, *Nannaethiops*, *Neolebias*
	Distichodontinae	*Distichodus*, *Nannocharax*
	Hemistichodinae	*Hemistichodus*
	Ichthyborinae	*Ichthyborus*, *Neoborus* (=*Phagoborus*), *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago*
Gregory & Conrad, 1938	Citharininae	*Citharinus*, *Citharidium*, *Xenocharax*, *Nannaethiops*, *Neolebias*, *Hemistichodus*
	Distichodontinae	*Distichodus*, *Nannocharax*, *Ichthyborus*, *Mesoborus*, *Phagoborus*, *Eugnatichthys*, *Paraphago*, *Phago*
Greenwood *et al.*, 1966	Citharinidae	
	Distichodontidae	
	Ichthyboridae	
Poll, 1973	Citharinidae	*Citharinus*, *Citharidium*, *Xenocharax*, *Neolebias*, *Nannaethiops*, *Dundocharax*, *Congocharax* ?, *Paradistichodus*, *Distichodus*, *Nannocharax*, *Hemigrammocharax*
	Ichthyboridae	*Ichthyborus*, *Phagoborus*, *Gavialocharax*, *Hemistichodus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago*, *Belonophago*

primarily external characters. The utility of the limited information available from these systems was, however, reduced by several misinterpretations of characters and character states. Secondly, the small size of many distichodontid species resulted in a series of errors in character state determination. These errors were especially prevalent in the description of tooth form and distribution; characters which, nonetheless, were weighed heavily by many workers. Finally, and perhaps most importantly, generic and suprageneric taxa were defined on the basis of primitive or combinations of primitive and derived characters, a procedure which often failed to define monophyletic groups.

The present study attempts to determine the phylogenetic relationships, both at the generic and suprageneric levels, within the subunit of characoids formed by the families Citharinidae and Distichodontidae. The phylogenetic reconstruction is based primarily on osteological characters, although myological and other soft anatomical systems are also utilized. The three main objectives of this study are: (1) to test the hypothesis of the monophyletic nature of the unit formed by citharinids and distichodontids within characoids; (2) to determine the interrelationships of the genera within these families; and (3) to define the various generic and suprageneric taxa on the basis of shared derived characters.

Methods

Relationships between and within the families Citharinidae and Distichodontidae are evaluated using the methods of phylogenetic analysis first described in detail by Hennig (1966). These methods along with the two predominant alternative methodologies (numerical taxonomy and evolutionary biological classification) have been and continue to be a source of controversy with respect to their relative merits. However, the author feels that the Hennigian methodology best suits the aims of this study – the erection of an hypothesis of the evolutionary relationships of the groups in question.

In using the Hennigian or cladistic methodology, certain principles are followed: recognized taxa must be monophyletic in that they include all descendants of a hypothesized common ancestor (the concept of monophyly advanced by the evolutionary biological school, in contrast, does not require the inclusion in a taxon of all descendants of a common ancestor). Monophyletic groups are defined on the basis of shared derived (synapomorphic) characters which are considered to be the only type of characters valid for the erection of a hypothesis of common ancestry. In contrast, shared primitive (symplesiomorphic) characters and estimated degrees of similarity or difference are not utilized for the analysis of interrelationships. Species or species groups (two or more species forming a monophyletic unit) hypothesized to have had a common ancestor are termed sister species or sister groups. A derived (apomorphic) character used for the definition of a sister group relationship cannot serve for the definition of the contained taxa in either of the sister groups since it is primitive (plesiomorphic) at the level of the included subtaxa.

As discussed by Nelson (1973*a* & *b*), the apomorphic or plesiomorphic nature of characters can be evaluated by two methods. The first of these, outgroup comparisons, involves the examination of the state of the character in a variety of other groups in order to determine which of the relevant character states is probably primitive. For the purposes of this study, outgroup comparisons were carried out on representatives of other characoid families and selected non-characoid ostariophysans. The second method of character polarity determination involves information available from ontogenetic transitions. If in two sister groups X and Y, the species of group X undergo an ontogenetic transition in character A from state A to state A′, a transition that does not occur in the species of group Y, then two explanations exist for the distribution of the transition: (1) that the transition (state A to A′) was not present in the common ancestor of X and Y, but rather arose in lineage X; or (2) that the transition was present in the common ancestor of X and Y, but was secondarily lost in lineage Y. Comparing these hypotheses, we find that the first makes a single assumption; that of the acquisition of the transition in group X. The second in contrast, makes two assumptions, that of the presence of the transition in the common ancestor of groups X and Y, and a second assumption of its subsequent loss in lineage Y. If we accept a parsimony criterion for the evaluation of the preferability of alternative hypotheses, then the first, more parsimonious, hypothesis is preferable. Consequently, in this study, ontogenetic transitions (ontogenetic shifts from state A to state A′) are considered to indicate phylogenetic polarity (state A′ is considered apomorphic with respect to state A).

In the following discussion, osteological terminology follows Weitzman (1962) with several exceptions. As noted by Roberts (1969) vomer is substituted for prevomer and intercalar for opisthotic. Furthermore, I follow Patterson (1975) in using epioccipital rather than epiotic, and supraethmoid rather than ethmoid, and follow Nelson (1973*c*) in substituting angulo-articular for articular, and retroarticular for angular. Myological terminology is that of Winterbottom (1974).

All drawings were made using a Wild M5 drawing tube. Details were added freehand under higher magnification. Myological drawings are based on dissections of the right side of the specimen and are reversed into conventional orientation.

Materials

Osteological and soft anatomical systems were examined on alcohol preserved material, dry skeletons, and cleared, alizarin-stained specimens of representative species of the citharinid genera

Citharinus and *Citharidium* and the distichodontid genera *Xenocharax*, *Neolebias*, *Nannaethiops*, *Paradistichodus*, *Distichodus*, *Nannocharax*, *Hemigrammocharax*, *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Phago* and *Belonophago*. In the case of the monotypic distichodontid genus *Paraphago*, known only from the syntypic series, only osteological characters revealed by radiographs and external anatomy could be examined. Comparative studies were carried out on representatives of all other African and Neotropical characoid families and for certain characters on examples of the major non-characoid ostariophysan groups, both otophysan and anotophysan. A detailed listing of this extensive material would add little to the paper. Rather, a list of material examined, both skeletal and whole, quoting museum catalogue numbers, is deposited in the Fish Section and General Library of the British Museum (Natural History).

Abbreviations used in text figures

A_1	A_1 division of the *adductor mandibulae* muscle
A_{2-l}	lateral portion of the A_2 division of the *adductor mandibulae*
A_{2-m}	medial portion of the A_2 division of the *adductor mandibulae*
A_3	A_3 division of the *adductor mandibulae*
A_w	intramandibular (A_w) division of the *adductor mandibulae*
aa	angulo-articular
ac	anterior chamber of swimbladder
ant	antorbital
bo	basioccipital
cca	canal for coeliac artery
cl	cleithrum
cts	connective tissue sheath
den	dentary
DOP	*Dilatator operculi* muscle
dph	dorsal process of hyomandibula
ds	dermosphenotic
e	epibranchial
ep	epural
epi	epioccipital
ex	exoccipital
fr	frontal
h	hypural
hyf	hyomandibular fossa
hyo	hyomandibula
io	infraorbital
ico	independent coeliac ossification
ip	ischiac process
LAP	*levator arcus palatini* muscle
le	lateral ethmoid
les	lateral ethmoid strut
LP	*ligamentum primordiale*
max	maxilla
o	opercle
ops	opercular spine
orb	orbitosphenoid
os	os suspensorium
par	parietal
para	parasphenoid
pb	pharyngobranchial
pc	posterior chamber of swimbladder
pcl	postcleithrum
pdg	posterolateral dentary groove
pel	pelvic bone
ph	parhypural
plp	posterolateral preopercular process
pmp	posteromedial preopercular process
pmx	premaxilla
pop	preopercle
pro	prootic
psc	pterotic sensory canal
ptf	posttemporal fossa
pto	pterotic
pts	pterosphenoid
q	quadrate
ra	retroarticular
rt	replacement teeth
soc	supraoccipital
sor	supraorbital
sph	sphenotic
spo	suprapreopercle
T	tendon
ti	terminal section of intestine
up	upper pharyngeal tooth plate
ur	uroneural
vpv	ventral process of vertebra

Nomenclatural comments

The conclusions of this study necessitate several changes in the previous generic and suprageneric classifications within the family Distichodontidae. In so far as the modified terminology is used throughout the following discussion, these changes are briefly summarized at this point.

Within recent years, most workers have recognized two subfamilies (Distichodontinae and Ichthyborinae) or families (Distichodontidae and Ichthyboridae) for the unit termed the family

Distichodontidae in this work. However, the retention of both taxa as previously defined was found to be untenable under the taxonomic procedures adopted as a basis for this study. Rather only a single suprageneric taxon, the family Distichodontidae, is recognized to contain the species previously divided between the Distichodontidae and Ichthyboridae of Greenwood *et al.* (1966) and the subfamilies Distichodontinae and Ichthyborinae of many other recent workers. Similarly, the genera *Dundocharax* and *Congocharax* are placed as synonyms of *Neolebias*, with *Dundocharax bidentatus*, *Congocharax gossei*, *C. spilotaenia* and *C. olbrechtsi* hereafter termed *Neolebias bidentatus*, *N. gossei*, *N. spilotaenia* and *N. olbrechtsi* respectively. Finally, both *Gavialocharax* and *Phagoborus* are placed as synonyms of *Ichthyborus*, with *Gavialocharax monodi*, *Phagoborus ornatus* and *P. quadrilineatus* hereafter referred to as *Ichthyborus monodi*, *I. ornatus* and *I. quadrilineatus* respectively.

Phylogenetic analysis

The analysis of the phylogenetic relationships of the genera and suprageneric units within the complex formed by the families Citharinidae and Distichodontidae is divided into two sections. The first part of the analysis deals with the relevant characters in the various anatomical systems examined, along with a discussion of the basis for their hypothesized polarity within characoids. In the second portion of the analysis the evidence from these characters is incorporated into a reconstruction of the hypothesized most parsimonious phylogeny of the genera within these families. It should be emphasized that it is not the purpose of this study to provide detailed anatomical descriptions of the osteology and soft anatomy of all citharinid and distichodontid genera. Rather, only those characters used in the phylogenetic reconstruction are discussed.

Jaws

A series of modifications of the upper and lower jaws distinguish the unit formed by the Citharinidae and Distichodontidae within characoids and unite groups of varying levels of universality within this complex. The following discussion will deal firstly with the hypothesized derived characters common to the upper and lower jaws; secondly, with those limited to the lower jaw; and finally, with those of the upper jaw. Dental characters of phylogenetic interest are discussed separately in the following section.

Replacement tooth trenches

The form of the dentary and premaxillary replacement tooth trenches exhibits several character states among citharinids and distichodontids. In *Xenocharax* (Fig. 1a) the dentary and premaxilla are solid basally, with the replacement tooth trenches having the form of relatively shallow grooves, not or only slightly open to their partners across the symphyses. Such a trench form is close to the generalized and probably plesiomorphous characoid condition and is thus considered to represent the least derived state of this character within citharinids and distichodontids. Two major modifications of the *Xenocharax* form of replacement tooth trench occur in these families, one shared by most distichodontids and the other unique to citharinids.

The distichodontid genera *Nannaethiops* and *Neolebias* share with *Xenocharax* the plesiomorphous condition of shallow premaxillary and dentary replacement tooth trenches. In all other distichodontids, in contrast, the trenches are expanded, bulbous cavities, broadly open to their partners across the symphysis (Fig. 1b.) The expansion of the trenches into the primitively solid centres of the premaxilla and dentary both provides an increased surface for the attachment of the pleurodont dentition common to these genera, and space for their multiple rows of replacement teeth. Such a greatly expanded replacement tooth trench would appear to be unique to and apomorphous for these genera among characoids. In contrast, the greatly expanded trenches of the Neotropical characoid family Parodontidae differ from the above in being limited to the premaxilla, in not being open to each other across the symphyses, and in having the replacement tooth series separated by bony partitions. Similarly, the broad replacement tooth trenches of the Anostomidae fail to open to their partners symphyseally.

A second mode of expanded replacement tooth trench characterizes the family Citharinidae. In *Citharinus* and *Citharidium* the trenches are widened along the primitively horizontal plane of the dentaries and premaxillae to form broad shallow grooves. More significantly, the replacement tooth trenches of both jaws are rotated outwards relative to the *Xenocharax* condition. This reorientation is especially pronounced in the lower jaw where it has resulted in the shift of the primitively distal, anterior ridge of the trench to the outer surface of the dentary, and the formation of the distal edge of the lower jaw by the posterior ridge of the replacement tooth trench. Such a reorientation and broadening of the trenches appears to be unique to and autapomorphous for the Citharinidae among Characoids.

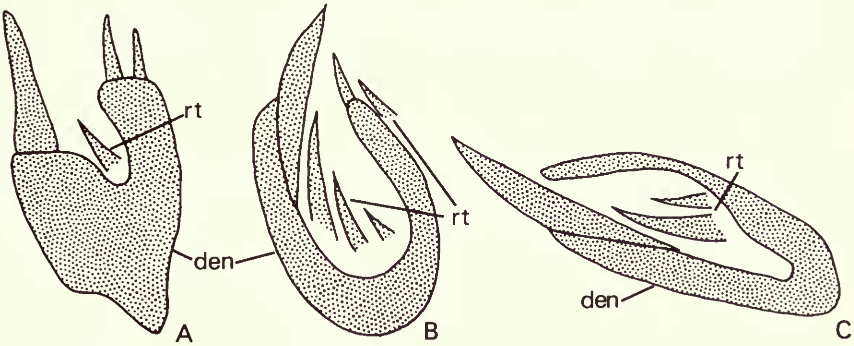

Fig. 1 Sagittal section through the dentary symphysis of A. *Xenocharax spilurus*, B. *Distichodus brevipinnis*, C. *Ichthyborus quadrilineatus*.

Lower jaw

A series of modifications of the dentary and of the articulation between the dentary and anguloarticular characterize various assemblages among citharinids and distichodontids. One of the distinctive characters in the lower jaws of these families is their common lack of the bony interdigitating symphyseal processes that interconnect the dentaries of most characoids. Such dentary interdigitations form a hinge permitting horizontal pivoting of the dentaries about the symphysis but reducing or eliminating twisting of the bones with respect to each other. This symphyseal dentary hinge ranges in complexity from the rather simple processes common to many tetragonopterines, to the massive interlocking systems in *Hydrocynus* (Gregory & Conrad, 1936) and the Cynodontini (Nelson, 1949). An interdigitating symphyseal dentary hinge is widespread among characoids and is found in the Hepsetidae, the family that has been considered to be the most 'primitive' living member of the Characoidea (Roberts, 1969, p. 442). If *Hepsetus* is indeed the sister group to other characoids, its possession of the dentary hinge along with the widespread distribution of this character within the Characoidea would indicate that an interdigitating symphyseal dentary hinge is plesiomorphous for characoids. The lack of such a joint would then be a apomorphous secondary loss. It should be emphasized, however, that the phylogenetic placement of hepsetids has not been satisfactorily resolved. Furthermore, an interdigitating dentary symphyseal joint is also lacking in the Neotropical characoid families Curimatidae, Hemiodontidae, Prochilodontidae, Anostomidae, Chilodontidae and Parodontidae. Be that as it may, at the least, the common lack of the interdigitating symphyseal dentary hinge in citharinids and distichodontids is consistent with the hypothesized monophyletic nature of the unit that they form within characoids.

Although the lack of an interdigitating dentary symphyseal hinge is common to all citharinids and distichodontids, the exact form of the interdentary articulation varies within these families. Citharinids and the distichodontid genera *Xenocharax*, *Neolebias*, *Nannaethiops*, *Paradistichodus*, *Distichodus*, *Nannocharax*, *Hemigrammocharax* and *Hemistichodus* have a solely syndesmotic articulation between the dentaries. Within this assemblage, in *Citharinus*, *Citharidium*, *Xenocharax*, *Nannaethiops* and *Neolebias* the combination of the relatively limited contact of the dentaries across the symphysis and the syndesmotic joint permits a slight mobility of the dentaries relative to each other. In contrast, *Paradistichodus*, *Distichodus*, *Nannocharax*, *Hemigrammocharax* and *Hemistichodus* have an immobile though syndesmotic interdentary joint as a consequence of their expanded replacement tooth trenches and the resultant greater cross-sectional contact across the symphysis. This union of the dentaries is further developed in some larger individuals of *Distichodus lussso* and *D. brevipinnis* which have irregular interdigitations between the dentaries (see Daget, 1959, Fig. 5).

The dentaries in the distichodontid genera *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* are synarthritically immovably interconnected in either of two ways. In *Ichthyborus* this union takes the form of a symphyseal fusion of the dentaries, an adaptation which provides a firm implantation for the enlarged median canine that characterizes this genus. *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Belonophago*, *Paraphago* and *Phago*, alternately, have a series of bony interdigitations uniting the dentaries. These interdigitations differ, however, from those forming the symphyseal dentary hinge of most characoids both in their location at the rear of the dentary symphysis and in rendering the dentaries totally immobile relative to each other. Both this synarthritic dentary articulation and the fused dentaries of *Ichthyborus* appear to be unique to their possessors among characoids and indicative of the monophyletic nature of each of these assemblages.

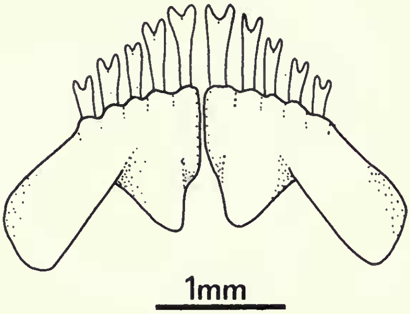

Fig. 2 *Nannocharax niloticus*, dentaries, ventral view.

Various modifications of the dentary serve to distinguish subunits within the family Distichodontidae. The genera *Hemigrammocharax* and *Nannocharax* are characterized by a pronounced posteriorly-directed process arising from the posteroventral edge of the dentary slightly lateral to the dentary symphysis (Fig. 2). This process, which serves as the point of attachment for the *protractor hyoidei* muscles, is unique to these genera among the characoids examined and is thus hypothesized to be apomorphous. *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*, in turn, have a prominent dorsally-directed posterodorsal dentary ramus that is laterally overlapped by, and tightly joined to, the closely connected maxilla and premaxilla common to these genera. Such a posterodorsal ramus of the dentary (Figs 3c & d) contrasts with the hypothesized plesiomorphous dorsally straight-edged process common to most characoids (Fig. 3a). Outgroup comparisons have failed to reveal any other charcoid group with such a pronounced development of this process. Thus the prominent posterodorsal ramus of the dentary common to these distichodontids is considered derived.

Further adaptations of this dentary ramus characterize less universal subunits of the Distichodontidae. In *Hemistichodus* this posterodorsal dentary ramus is autapomorphically further enlarged into an elongate, inwardly curved process passing medial to the premaxilla (see Daget, 1968, Fig. 2). *Eugnatichthys*, *Paraphago*, *Phago* (Fig. 3d) and *Belonophago*, in turn, have the lateral face of the ramus restructured to form a shallow groove articulating with the rounded posteroventral portion of the maxilla characteristic of these genera. This alteration of the dentary in conjunction with a series of modifications of the maxilla forms a sliding joint between the upper and lower jaws during jaw movements.

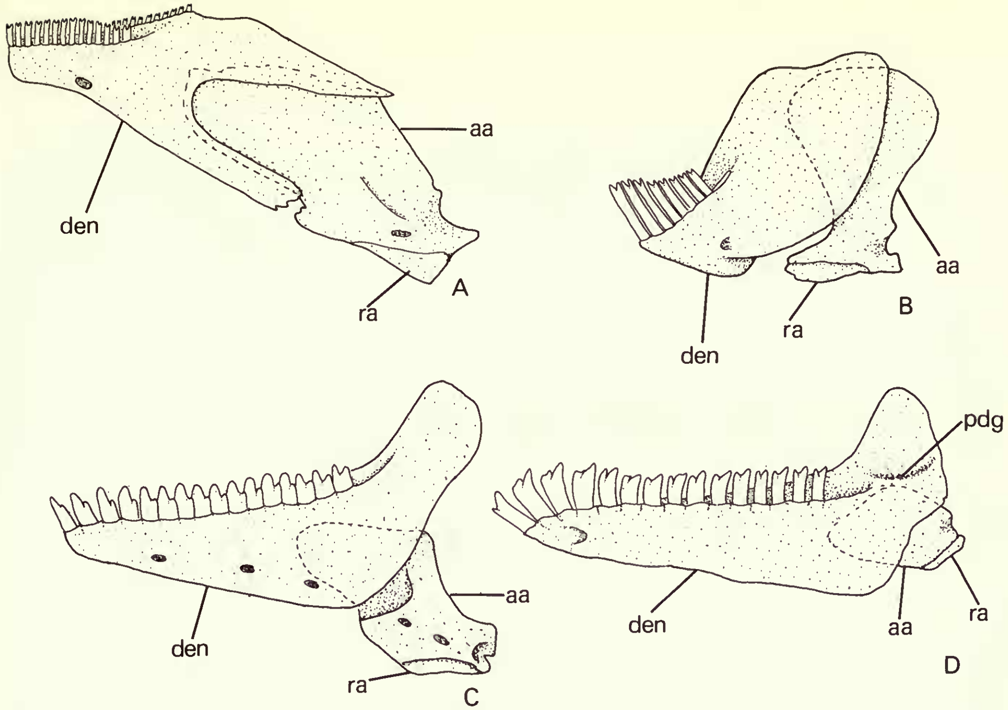

Fig. 3 Lower jaws of A. *Xenocharax spilurus*, B. *Distichodus notospilus*, C. *Ichthyborus quadrilineatus*, D. *Phago intermedius*, left lateral view.

The greatest morphological variation in the lower jaw of the families Citharinidae and Distichodontidae involves the form of the articulation of the dentary with the angulo-articular. In *Xenocharax* (Fig. 3a) the angulo-articular and dentary meet along an elongate triangular joint with the posteroventral process of the dentary bearing a lengthy mandibular sensory canal segment. The tight fit of this joint and the strong connective tissue bands across the articulation immovably join the dentary and angulo-articular into a single functional unit. Thus in *Xenocharax* all motion of the dentary relative to the suspensorium is a consequence of the mobility between the angulo-articular and quadrate. This form of articulation is generalized for characoids and most teleosts (see Nelson, 1973*c*), and undoubtedly represents the plesiomorphous condition for the Citharinidae and Distichodontidae. Such an immobile articulation is common to citharinids and the distichodontid genera *Xenocharax*, *Neolebias*, *Nannaethiops* and *Paradistichodus*. All other distichodontid genera, in contrast, have a mobile joint between the angulo-articular and dentary. The least restructured form of the articulation is found in *Hemistichodus* which retains the plesiomorphous insertion of the triangular anterior process of the angulo-articular into a notch formed by posterodorsal and posteroventral dentary processes. However, in contrast to the primitive condition, the dentary in *Hemistichodus* is not in tight contact with the anterior process of the angulo-articular and the connective tissue bands joining these bones are flexible. These modifications result in a limited mobility between the dentary and angulo-articular. Such motion approximates the hypothesized first stage in the phylogenetic development of the more mobile *Distichodus*, *Ichthyborus* and *Mesoborus* types of articulations between these bones.

The second form of mobile joint between the dentary and the angulo-articular, the *Distichodus* type (Fig. 3b) is synapomorphous for *Distichodus*, *Nannocharax* and *Hemigrammocharax* among characoids. In these genera the primitively elongate dentary is horizontally foreshortened and its posteroventral process greatly reduced. Furthermore, the axis of the body of the dentary is reorientated distinctly anteroventrally from the horizontal or anterodorsal orientation common to most characoids. This reorientation, which shifts the plesiomorphously anterior face of the dentary posteroventrally, is particularly pronounced in bottom-dwelling *Nannocharax* species which have a nearly vertical axis through the body of the dentary. An additional consequence of this dentary foreshortening and reorientation is the reduction of the dentary portion of the mandibular sensory canal in *Distichodus* and its loss in *Nannocharax* and *Hemigrammocharax*.

Congruent with these dentary alterations are a series of modifications of the angulo-articular and of its relationship to the dentary. In the *Distichodus* type lower jaw, the angulo-articular is expanded dorsally or anterodorsally into a large flat plate which lies along and is ligamentously movably attached to the medial face of the dentary. These alterations in angular-articular form and position together with the previously described dentary modifications result in a highly mobile joint between the dentary and angulo-articular, in addition to the usual mobility of the latter on the quadrate. This mode of articulation of these elements, the 'chevauchement lateral' of Monod (1950), along with the previously described reorientation of the dentary permits a marked degree of horizontal motion of the dentary.

The two final forms of mobile articulation between the dentary and angulo-articular, the *Ichthyborus* and *Mesoborus* types, share several derived characters. In both of these lower jaw forms the posteroventral ramus of the dentary is lacking as a distinct process contrary to its plesiomorphous elongate form. Congruent with this change in dentary structure is an anterior expansion of the angulo-articular and its shift onto the medial surface of the dentary. Such an expansion, which compensates for the loss of support primitively provided by the posteroventral dentary ramus, differs from that of the *Distichodus* type jaw in two ways. Firstly, the anterior process of the angulo-articular in the *Ichthyborus* and *Mesoborus* jaw forms is directed horizontally forward rather than having the dorsal or anterodorsal orientation that characterizes the *Distichodus* type jaw. Furthermore, rather than simply abutting the medial surface of the dentary the angulo-articular in these taxa inserts into a depression (*Ichthyborus*) or fossa (*Mesoborus* type) on the posteromedial surface of the dentary. These modifications and other adaptations permit an apomorphic greatly increased mobility between the dentary and angulo-articular.

The *Ichthyborus* type articulation (Fig. 3c) is specific to that genus and characterized by an elongate angulo-articular considerably thickened posterior to the rear margin of the dentary. This expanded posterior portion of the angulo-articular is undercut anteriorly to form a deep notch into which the posteroventral corner of the dentary fits. Both the thickening of the posterior portion of the angulo-articular and its relationship to the dentary are apomorphic characters seemingly unique to this genus among characoids. The *Mesoborus* form of articulation between the angulo-articular and dentary is common, with some variation, to *Mesoborus*, *Microstomatichthyoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. In these genera the anterior portion of the angulo-articular inserts into a definite socket on the medial surface of the dentary. Along with the pronounced overlap of the dentary and angulo-articular, this adaptation shifts the pivot point of the dentary anteromedially. Within the assemblage characterized by the *Mesoborus* type articulation several subunits are distinguished by further modifications of the angulo-articular. In contrast to its plesiomorphously elongate state, the angulo-articular in *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* is a thickened element that is both shortened horizontally and shifted practically entirely onto the medial surface of the dentary (Fig. 3d). As a consequence the rear of the dentary extends nearly to the vertical through the joint of the angulo-articular with the quadrate. This apomorphic shortening of the angulo-articular is especially notable in *Eugnatichthys* in which the greatly thickened bone is barely visible laterally.

Keeping in mind the difficulties in determining the mode of action of a complex system on the basis of preserved material, it nonetheless appears that the two lower jaw pivot points (dentary-angulo-articular and angulo-articular-quadrate) in the *Ichthyborus* and *Mesoborus* jaw forms result in systems that are functionally unique among characoids. In *Ichthyborus* the ventral border of the dentary makes an oblique angle with that of the angulo-articular when the mouth is closed. As the mouth opens, the pivoting of the premaxilla on the supraethmoid causes the rear of the premaxilla to move ventrally. This motion is imparted *via* the reduced maxilla to the rear of the dentary. The entire lower jaw in turn shifts ventrally, with the dentary pivoting on the angulo-articular simultaneous with the pivoting of the entire dentary-angulo-articular complex on the quadrate. Both motions continue until the ventral borders of the angulo-articular and dentary achieve their plesiomorphous straight line orientation. During the second phase of jaw motion the mobility of the dentary relative to the angulo-articular ceases and these elements act as a rigid unit pivoting on the quadrate. Thus during the opening of the mouth, two functional phases are discernible; an apomorphic first phase characterized by mobility at both pivot points, and a second phase demonstrating only the plesiomorphous motion of the angulo-articular on the quadrate. Such a two-phase system is common to *Ichthyborus*, *Mesoborus* and *Microstomatichthyoborus*, and is the basis for the more derived jaw motion of *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* which have continual mobility between the angulo-articular and dentary throughout the entire cycle of jaw action. In these latter genera the ventral borders of the angulo-articular and dentary pass from the oblique concave angle of the closed jaw, to a straight-line orientation and then to a distinct convex relationship in the fully open mouth (see Gregory & Conrad, 1938, Fig. 35). This last apomorphic phase of the motion is, as far as can be determined, unique to these four genera among characoids.

Upper jaw

The plesiomorphous condition of the upper jaw in characoids appears to have the premaxilla immovably attached by tight syndesmotic articulations to the supraethmoid and lateral supraethmoid wings. Such attachment occurs either along the medial surface of the premaxilla (e.g. *Hepsetus*, *Acestrorhynchus*) or more usually to a posteriorly-directed ascending process of the premaxilla (e.g. *Brycon*, *Alestes*). Medially the premaxillae are completely or nearly completely separated symphyseally by an elongate supraethmoid spine. Plesiomorphously the maxilla is a moderately to markedly elongate element movably articulated with the posterodorsal edge of the premaxilla, and bearing anterodorsally a medially-directed process which attaches ligamentously to the palatine and *ligamentum primordiale*. Citharinids and distichodontids differ from this plesiomorphous upper jaw plan both in the relationships of the premaxilla with its partner and the supraethmoid, and in the form of the maxilla and its relationship to the premaxilla and dentary.

All citharinids and distichodontids lack the prominent premaxillary ascending process and tight connective tissue bands which plesiomorphously attach the premaxilla immovably to the supraethmoid. Instead a series of modifications of the premaxilla and supraethmoid result in a mobile articulation of the upper jaw with the supraethmoid. The various adaptations of the supraethmoid will be discussed in detail later in the paper. For the purposes of the discussion at this point, it suffices to note that among citharinids and distichodontids the plesiomorphous state of the forward edge of the supraethmoid is hypothesized to be an anteriorly trifurcate complex. In this condition a median plate extends anteriorly over the premaxillary symphysis, and ventrolateral articular processes insert into articular fossae on the rear of the premaxillae. In *Xenocharax* the articular fossa of the premaxilla has the form of a deep horizontal depression open to its partner across the symphysis and extending from the symphysis midway across the transverse width of the premaxilla. Such a horizontal fossa is hypothesized to be plesiomorphous for citharinids and distichodontids in so far as the corresponding horizontal supraethmoid process represents the least pronounced alteration of the primitively horizontal edge of the supraethmoid. Within citharinids and distichodontids, several derived modifications of this form of premaxillary fossa are found.

Among citharinids there occurs a progressive ontogenetic reduction of the roof of the basically *Xenocharax* form of articular fossa that characterizes juveniles of *Citharinus* and *Citharidium*. As a consequence in adult citharinids the fossa roof is reduced to a small shelf at the lateral margin of the depression. Thus the primitively ventral surface of the fossa is now exposed dorsally and is ligamentously attached to the median process of the supraethmoid. Such an attachment contrast with the latter's plesiomorphous attachment to the dorsal surface of the roof of the fossa.

Within the complex formed by *Distichodus*, *Hemigrammocharax* and *Nannocharax* there occurs a phylogenetic transition in the form, position and extent of development of the premaxillary fossa. *Distichodus notospilus* and *D. brevipinnis* have a basically *Xenocharax* form of wide horizontal fossa on the posterior surface of the premaxilla. In comparison in *Distichodus lusosso*, *D. niloticus* and *D. fasciolatus* the fossa is a conical pit located on the posterodorsal surface of the premaxilla. These adaptations are correlated with the posteroventral shift of the premaxillae in these species, a repositioning carried further in *Nannocharax* and *Hemigrammocharax*. In these latter genera the premaxillae are located distinctly ventral to the supraethmoid and the articular fossae are reduced either to small conical depressions on the dorsal surface of the premaxillae or are entirely lacking. An evidently independent shift of the fossa to the dorsal surface of the premaxilla occurs in *Hemistichodus* in which the articular fossa is a rounded groove on the posterodorsal surface of the premaxilla. Finally, in *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* the articular fossa is a transversely directed pit on the medial surface of the longitudinally-oriented posterior portion of the premaxilla. This adaptation is especially pronounced in the last two genera.

The above modifications, those of the supraethmoid and a series of other alterations permit varying degrees of mobility of the premaxilla on the supraethmoid. Such motion is limited in citharinids but more pronounced in distichodontids, especially in *Distichodus*, *Nannocharax*, *Hemigrammocharax*, *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. The upper jaw motion of these genera takes two forms. In *Distichodus*, *Nannocharax* and *Hemigrammocharax* the posteroventrally shifted premaxillae are notably mobile in the horizontal plane. In contrast, in the other distichodontids listed, the jaw modifications permit a pronounced pivoting of the premaxillae on the supraethmoid with a consequent increase in the vertical extent of the gape.

Among characoids other than citharinids and distichodontids, mobile premaxillary–supraethmoid articulations occur in the African characid genus *Hydrocynus*, and the Neotropical characoid families Anostomidae, Chilodontidae, Prochilodontidae, Parodontidae and Hemiodontidae (Roberts, 1974). *Argonectes* and *Bivibranchia*, in turn, have radically altered protrusible upper jaws in which the premaxilla separates from the supraethmoid during opening of the mouth. Comparison of the mobile upper jaw in *Hydrocynus* with that of citharinids and distichodontids reveals pronounced anatomical and functional differences between these systems. The consequent likelihood that these complexes represent independent acquisitions of upper jaw mobility is supported by the series of derived characters uniting *Hydrocynus* to African characids having immovable premaxillary–supraethmoid articulations (see Comments on the African Characidae). *Argonectes*, *Bivibranchia* and the family Hemiodontidae differ from citharinids and distichodontids both in their mode of premaxillary mobility and in their possession of a rhinosphenoid. The rhinosphenoid is a median orbital ossification unique to various South American characoid groups, most of which are characterized by a plesiomorphous immobile upper jaw. On the basis of the common possession of a rhinosphenoid and other characters, it is most parsimonious to assume that hemiodontids, *Bivibranchia* and *Argonectes* are closely related to Neotropical rhinosphenoid-bearing characoids with immovable upper jaws. In light of this, and the differences in the type of supraethmoid–premaxillary articulation, it appears that upper jaw mobility in these groups has been achieved independent of that in citharinids and distichodontids. Finally, prochilodontids, anostomids and the closely related chilodontids achieve upper jaw mobility by motion of the ascending arm (Anostomidae, Chilodontidae) or body (Prochilodontidae) of the premaxilla along the edge of the supraethmoid spine rather than *via* the citharinid and distichodontid type of hinging of the premaxilla on anterior processes of the supraethmoid. As such, the premaxillary mobility of these South American families appears to be non-homologous with that of citharinids and distichodontids. The closest approximation among charcoids to the citharinid and distichodontid type of premaxillary–supraethmoid articulation is found in the Neotropical family Parodontidae. The members of this family have a distinct dorsomedial premaxillary fossa articulating with anterolateral processes of the supraethmoid. However, as discussed in the Conclusions section, the parodontid fossa appears to be convergent with that of citharinids and distichodontids rather than an indicator of close relationship between the groups.

As was the case with the dentary symphysis, the interpremaxillary articulation among citharinids and distichodontids demonstrates several apomorphous modifications of varying levels of universality. Contrary to the plesiomorphous, limited syndesmotic contact of the premaxillae anterior to the supraethmoid spine citharinids and distichodontids have the medial surfaces of the premaxillae broadly in contact. Within these families, however, the exact form and extent of the contact varies significantly. In *Xenocharax*, *Nannaethiops* and *Neolebias* the combination of a syndesmotic joint and a somewhat narrow premaxillary symphysis permits a limited mobility between the premaxillae. Although retaining the plesiomorphous syndesmotic joint, *Paradistichodus*, *Distichodus*, *Nannocharax*, *Hemigrammocharax* and *Hemistichodus* are immovably joined symphyseally. This immobility is a consequence of the expanded cross-sectional extent of the jaws around the widened replacement tooth trenches. Finally, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* have a series of interdigitating convolutions at the rear of the premaxillary symphysis. This synarthritic joint eliminates all motion between the premaxillae, a trend that is carried further in *Ichthyborus monodi* in which the premaxillae are fused symphyseally. This fusion is, as far as can be determined, unique to this species among characoids and perhaps a function of its markedly elongate jaws.

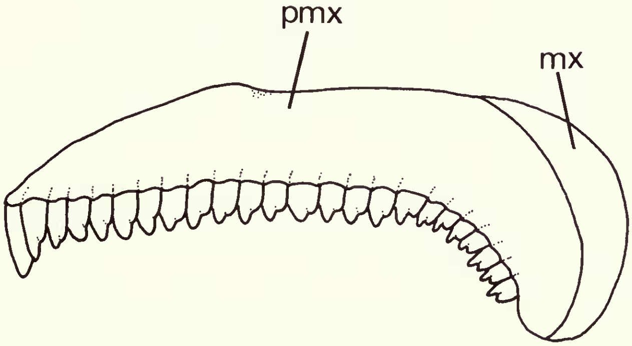

Fig. 4 *Ichthyborus quadrilineatus*, upper jaw, left lateral view.

A second form of synarthritic interpremaxillary joint characterizes the family Citharinidae. In *Citharinus* and *Citharidium* the longitudinal extent of the premaxillary symphysis is increased by the expansion of the median portions of the premaxillae posteriorly to form a prominent symphyseal bulge. This posterior expansion of the premaxillae along with a series of highly developed symphyseal interdigitations tightly join the premaxillae synarthrically. These premaxillary sutures differ, however, from those of some distichodontids both in the form and extent of the interdigitations, and in their association with the posteriorly expanded portion of the premaxilla. The consequent likelihood that the premaxillary sutures in the two groups are non-homologous is supported by the overall distribution of derived characters in these families.

Although the possession of interpremaxillary sutures is considered an apomorphous character on the basis of outgroup comparisons, such adaptations are not unique to citharinids and distichodontids within the Characoidea. Such sutures have been previously reported for the Neotropical genus *Brycon* (Weitzman, 1962) and the old world characid *Hydrocynus* (Eastman, 1917). Interpremaxillary sutures have also been found during this study in the South American characid genera *Triportheus* and *Serrasalmus*, and the African characids *Bryconaethiops* and *Alestes*. However, on the basis of a series of derived characters (the possession of a rhinosphenoid, tooth form and distribution, etc.) the South American genera appear to be most closely related to Neotropical characoids lacking interdigitating premaxillary sutures. Similarly, the old world groups form a monophyletic unit with African genera lacking the synarthritic joint (see p. 341). Consequently, the interpremaxillary suturing in these South American and African characoids appears to have been acquired independently of that in citharinids and distichodontids.

The final jaw character of interest is the form of the maxilla and its relationship to the premaxilla and dentary. The hypothetical plesiomorphous state of the maxilla among characoids is a relatively large, tooth-bearing element movably attached to the premaxilla, and with a dorsomedially directed process for the attachment of the palatine and *ligamentum primordiale*. In *Citharinus* and *Citharidium*, in contrast, the maxilla is relatively reduced but retains its mobility, flattened plate-like form and dorsomedially directed process. The maxilla in the distichodontid genera *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* is also reduced. However, in these genera the relative reduction of the bone is much more pronounced than in citharinids. Furthermore, the maxilla in these genera is unique among characoids examined in its lack of a dorsomedial process and in being immovably joined, but not fused, to the rear of the enlarged premaxilla (Fig. 4). These maxillary alterations are most pronounced in *Hemistichodus* in which the bone is greatly reduced both relative to the generalized characoid condition and also with respect to that in the other genera listed. Furthermore, the maxilla in *Hemistichodus* is autapomorphically shifted onto the dorsal surface of the premaxilla (see Daget, 1968, Fig. 2) and is consequently totally removed from the ventral border of the upper jaw. Finally, the assemblage consisting of *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* is characterized by a recontouring and expansion of the posteroventral portion of the reduced maxillary into a rounded somewhat bulbous process. During movements of the jaws this portion of the maxilla closely articulates with and slides along the previously described groove on the lateral surface of the posterodorsal dentary ramus.

In summary, the diverse apomorphic jaw modifications described above are:

1 the outward rotation of the replacement tooth trench in citharinids, and the great expansion of the trenches in distichodontids other than *Xenocharax*, *Nannaethiops* and *Neolebias*.
2 the lack of an interdigitating symphyseal hinge joint in citharinids and distichodontids.
3 the fused dentaries of *Ichthyborus*.
4 the bony interdigitations along the posterior portion of the dentary symphysis in *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.
5 the posteriorly directed process lateral to the dentary symphysis in *Nannocharax* and *Hemigrammocharax*.
6 the pronounced posterodorsal dentary ramus in *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. This process is laterally modified to form a groove articulating with the maxilla in the last four genera and is greatly developed autapomorphically in *Hemistichodus*.
7 the mobile joint between the dentary and angulo-articular in all distichodontids other than *Xenocharax*, *Neolebias*, *Nannaethiops* and *Paradistichodus*. The four forms of this mobile articulation are:
  (A) the *Hemistichodus* type limited to that genus and plesiomorphous with respect to the *Ichthyborus*, *Mesoborus* and *Distichodus* forms of the joint.
  (B) the *Distichodus* type occurring in *Distichodus*, *Nannocharax* and *Hemigrammocharax*.
  (C) the *Ichthyborus* type limited to that genus.
  (D) the *Mesoborus* type common to *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. The last four genera share an apomorphic further reduction of the horizontal extent of the angulo-articular.
8 the premaxillary articular fossa in citharinids and distichodontids.
9 the ontogenetic reduction of the premaxillary fossa roof in citharinids.
10 the reduction in the extent, and the shift of the articular fossa to the dorsal surface of the premaxilla in *Nannocharax*, *Hemigrammocharax* and some *Distichodus* species.
11 the rounded articular fossa on the dorsal surface of the premaxilla in *Hemistichodus*.
12 the laterally-directed articular fossa in *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.
13 the reduced maxilla of citharinids.
14 the greatly reduced, immobile maxilla in *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.
15 the bulbous, posteroventrally expanded maxilla in *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

16 the position of the maxilla on the dorsal surface of the premaxilla in *Hemistichodus*.

17 the interdigitating premaxillary symphyseal processes in citharinids and some distichodontids.

Dentition

Characoids are notable for, and largely classified on, the basis of their broad range in tooth form and arrangement. Such variation is evident in the morphology, distribution and mode of implantation of the dentition in the Citharinidae and Distichodontidae. Roberts (1967, p. 231) hypothesized that 'the most primitive dentition in characoids consists of conical teeth on the premaxillary, a single row of conical teeth extending beyond the gap of the maxillary, and two rows of conical teeth in the lower jaw separated by a shallow replacement trench'. Such a dental plan is consistent with our present knowledge of characoid ontogeny and phylogeny and would, with the exception of the tooth form, appear to have been the condition in the common ancestor of citharinids and distichodontids.

A bicuspidate equally-cusped tooth (Fig. 2) is common to all citharinids and distichodontids at some point in ontogeny. Multicuspidate dentition, either in the form of linearly arranged cusps (e.g. cheirodontines) or an arched cusp series along the edge of a wide tooth (e.g. *Brycon*, *Alestes*), is widespread among characoids. However, the bicuspidate tooth form of citharinids and distichodontids appears to be unique to, and apomorphic for, these families among characoids.

Within the Distichodontidae two assemblages have sequential ontogenetic replacement of the equally-cusped dentition by teeth demonstrating a relative enlargement of one cusp. In *Ichthyborus* this takes the form of a markedly developed anterior cusp, while *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* have the posterior cusp enlarged. The shift from the equally-cusped tooth form, plesiomorphous for distichodontids, to the unequally-cusped condition can be followed ontogenetically in representative species demonstrating each form of enlarged cusp.

Among species with an enlarged anterior cusp, an ontogenetic series of *Ichthyborus besse* reveals a progressive shift to teeth with a relatively larger anterior cusp (Fig. 5a). In 30 mm SL specimens, the anterior cusp of the teeth at the front of each jaw is somewhat enlarged relative to the posterior cusp. This relative difference in cusp size decreases posteriorly so that the teeth at the rear of each jaw have equally-sized cusps. By 70 mm SL the anterior cusps of all teeth are larger than the posterior, with this difference again most pronounced anteriorly. Appreciably enlarged anterior cusps occur on all teeth in 100 mm SL specimens with the posterior cusp of the anterior teeth very small. *Ichthyborus besse* specimens of 150 mm SL have the posterior cusp on most teeth so reduced relative to the anterior cusp as to give the teeth a unicuspidate appearance. A similar, though not as pronounced, ontogenetic transition in tooth-cusp size occurs in *Ichthyborus ornatus* and *I. quadrilineatus* over the limited size range of specimens examined. It was not possible, however, to confirm the predicted ontogenetic transition in tooth form for *I. monodi* which is only known from adult specimens.

A size range of *Mesoborus crocodilus*, a species with an enlarged posterior tooth cusp, shows a progressive ontogenetic increase in the size of the posterior cusp (Fig. 5b). In 45 mm SL specimens the anterior teeth, particularly of the upper jaw, show a distinct enlargement of the posterior tooth cusp, with the remaining teeth retaining the plesiomorphous equally-cusped condition. By 55 mm SL nearly all the teeth in the upper jaw and those in the anterior half of the lower jaw exhibit an enlarged posterior cusp to varying degrees. At 70 mm SL the anterior cusp is totally lacking on the anterior teeth and greatly reduced on the remaining teeth of both jaws. The dentition of *Mesoborus* specimens of greater than 120 mm SL is nearly unicuspidate with a rudimentary anterior cusp remaining only on the posterior teeth of each jaw. It should be emphasized, however, that the relative difference in tooth cusp size found in *Mesoborus* is not universal among genera having an enlarged posterior tooth cusp. In *Microstomatichthyoborus* the posterior tooth cusp is only slightly enlarged. A slightly greater relative development of the cusp occurs in *Belonophago* (see Poll, 1957, Fig. 141), while *Eugnatichthys*, *Paraphago* and *Phago* show a marked enlargement of the posterior cusp, although the difference is not as appreciable as that of *Mesoborus*.

The mode of implantation of the outer tooth row also varies within the complex formed by citharinids and distichodontids. In all citharinids and the distichodontid genera *Xenocharax*, *Nannaethiops* and *Neolebias* the teeth attach by flattened or slightly oblique bases to a series of sockets along the distal edge of the replacement tooth trench ridges (Fig. 1a). Such an acrodont type of tooth attachment is generalized, though not universal, for characoids and tooth-bearing ostariophysans and is thus hypothesized to be plesiomorphous for citharinids and distichodontids.

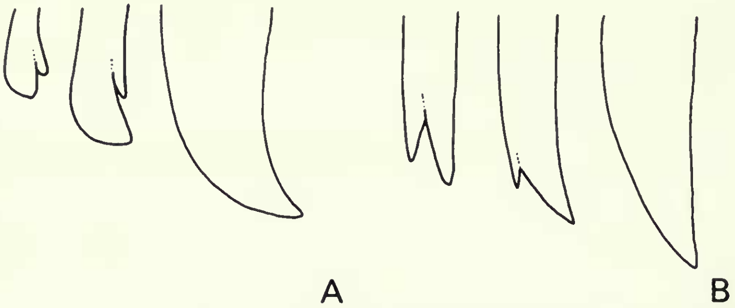

Fig. 5 Ontogenetic variation in dentition of A. *Ichthyborus besse* (fifth premaxillary tooth at 32, 50 and 115 mm SL), B. *Mesoborus crocodilus* (fourth premaxillary tooth at 55, 85 and 130 mm SL), left lateral view.

The outer row of dentition in all remaining distichodontid genera, in comparison, has the tooth form and mode of attachment illustrated in Figs 1b and c. In this condition, the teeth of the outer tooth row taper gradually to fit the anterior contours of the replacement tooth trench to which they have a ligamentous (pleurodont) attachment. As a consequence, the total relative length of the teeth is increased, with this elongation most pronounced in *Distichodus*, *Nannocharax* and *Hemigrammocharax*. The genera *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*, in turn, are characterized by relatively stronger teeth than those of citharinids and other distichodontids. Although the forward extension of the posterior wall of the replacement tooth trench results in what appear to be a series of interconnected sockets for the enlarged outer tooth row, in actuality these teeth retain their pleurodont attachment to the anterior wall of the trench (Fig. 1c).

The distribution pattern of the dentition within citharinids and distichodontids shows both reductions and increases relative to the previously described hypothetical plesiomorphous condition for characoids (see p. 275). The plesiomorphously present inner dentary tooth row is lacking in citharinids, *Nannocharax*, *Hemigrammocharax*, *Hemistichodus* and all *Ichthyborus* species other than *I. besse*. On the basis of the hypothesized phylogeny (see p. 338) this absence of the inner row of dentary teeth appears, however, to have arisen *via* multiple independent losses. The opposite trend of an increase in the number of inner tooth rows on the dentary occurs in *Xenocharax* and some *Neolebias trilineatus* specimens (Daget, 1965, p. 7) which have two inner tooth rows, and in *Ichthyborus besse* where the inner row of dentary dentition is expanded into a broad band.

In the upper jaw, the dentition of both the premaxilla and maxilla varies within the assemblage formed by the Citharinidae and Distichodontidae. Contrary to the hypothesized plesiomorphous state of a tooth-bearing maxilla, citharinids and all distichodontids with the exception of *Xenocharax*, *Nannaethiops* and *Neolebias* have edentulous maxillae (the reported absence of maxillary teeth in some *Neolebias* species is erroneous, see p. 330). An inner premaxillary tooth row occurs in all distichodontids other than *Nannocharax*, *Hemigrammocharax*, *Hemistichodus*, *Ichthyborus ornatus* and *I. monodi*, all of which also lack the inner dentary tooth row. The lack of the inner row of premaxillary dentition in these taxa and in citharinids would appear to be apomorphous though considered to represent several independent losses on the basis of the hypothesized phylogeny. *Ichthyborus besse*, in contrast, has the inner row of premaxillary dentition expanded into a broad tooth patch. Finally, *Hemistichodus* is distinguished by the autapomorphous lack of the medial premaxillary teeth (see Poll, 1957, Fig. 134).

The final tooth character of phylogenetic interest among citharinids and distichodontids involves the canine dentition in *Ichthyborus* and *Mesoborus*. *Ichthyborus* has an enlarged unpaired tooth in the midline of the fused dentaries, an adaptation unique to this genus among characoids examined. The median dentary tooth and that flanking it on each side interdigitate with a pair of enlarged teeth at the anterior of the premaxillae (see Poll, 1957, Figs 132 & 136). In *Ichthyborus quadrilineatus* these dentary and premaxillary teeth are only slightly enlarged, with a limited overlap between the anterior teeth of the upper and lower jaws. However, in *I. ornatus*, *I. besse* and *I. monodi* these teeth are produced into prominent, significantly overlapping canines.

A different form of caniniform dentition characterizes *Mesoborus*. Although sharing with *Ichthyborus* an enlargement of the anterior premaxillary teeth, the dentary dentition in this genus is markedly different. *Mesoborus* lacks the unpaired median dentary tooth and the enlarged teeth flanking it that occur in *Ichthyborus*. Instead, the anteriormost dentary teeth of *Mesoborus* are quite small and the second to fourth teeth are strongly developed. These enlarged teeth arise from a distinct convex portion of the dorsal edge of the dentary and fit lateral to a series of relatively small teeth on a corresponding concave region of the premaxilla (see Gregory & Conrad, 1938, Fig. 34). Such a pattern of dentary and premaxillary dentition is not encountered elsewhere in the families under study, and is hypothesized to be derived relative to the graded dentition of most characoids.

In summary, the derived states of the dentition among citharinids and distichodontids are hypothesized to be:

1. the common possession in these families of a bicuspidate tooth. This tooth form is secondarily apomorphically modified by an enlargement of the anterior cusp in *Ichthyborus*, and of the posterior cusp in *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.
2. the pleurodont tooth attachment in all distichodontids other than *Xenocharax*, *Nannaethiops* and *Neolebias*.
3. the loss of maxillary teeth in citharinids and all distichodontids other than *Xenocharax*, *Nannaethiops* and *Neolebias*.
4. the loss of the inner dentary tooth row in *Nannocharax*, *Hemigrammocharax*, *Hemistichodus* and all *Ichthyborus* species other than *I. besse*.
5. the loss of the inner dentary tooth row in citharinids, *Nannocharax*, *Hemigrammocharax*, *Hemistichodus*, *Ichthyborus ornatus* and *I. monodi*.
6. the lack of the medial premaxillary teeth in *Hemistichodus*.
7. the enlarged median dentary tooth of *Ichthyborus*.
8. the form of caniniform dentition in *Mesoborus*.

Supraethmoid

The supraethmoid form hypothesized plesiomorphous for characoids is an anteriorly triangular bone extending between, and completely or nearly completely separating, the premaxillae. The supraethmoid usually bears along its lateral margin a somewhat triangular process, the lateral supraethmoid wing, which is, however, lacking in many characoids with an elongate skull. As discussed previously, the supraethmoid of citharinids and distichodontids is greatly modified anteriorly as part of a system permitting upper jaw mobility. The least derived condition of the supraethmoid in these families occurs in *Xenocharax* in which the bone is relatively short longitudinally and lacks the plesiomorphously present lateral supraethmoid wings. More significant from a functional viewpoint are the marked modifications of its anterior edge. In contrast to the simple supraethmoid spine of the hypothesized plesiomorphous characoid state, in *Xenocharax* the supraethmoid is elaborated anteriorly into a wide trifurcate complex (Fig. 6a). Medially a short horizontal shelf extends forward from the anterodorsal edge of the supraethmoid to overlie and attach ligamentously to the dorsomedial portion of the premaxillae. On either side of, and slightly ventral to, this median process there is an anteriorly directed horizontal articular process which partially inserts into, and ligamentously attaches to, the previously described premaxillary fossa. As discussed earlier, the *Xenocharax* condition of a wide horizontal articular process is considered plesiomorphous for citharinids and distichodontids in that it represents the least derived modification of the primitively horizontal edge of the supraethmoid. Although the exact homology, if any, of the three supraethmoid processes with the primitively present supraethmoidal spine and lateral wings is unknown, these modifications of the anterior region of the supraethmoid appear to be apomorphous within characoids and as such are indicative of the monophyletic nature of the unit formed by the Citharinidae and Distichodontidae. The somewhat similar articular processes present in the South American characoid family Parodontidae differ in overall form and are considered to be independently acquired (see p. 340).

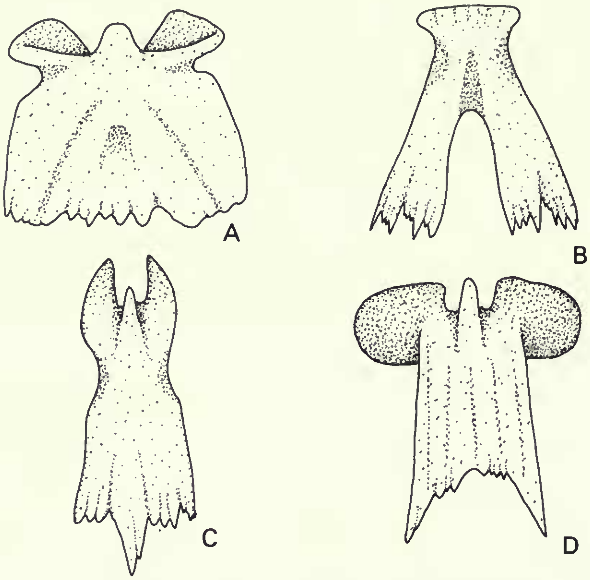

Fig. 6 Supraethmoid of A. *Xenocharax spilurus*, B. adult *Citharinus citharus*, C. *Distichodus niloticus*, D. *Phago loricatus*, dorsal view.

Various modifications of the *Xenocharax* form of supraethmoid distinguish the Citharinidae and subunits of the Distichodontidae. Juvenile citharinids have a basically *Xenocharax* type of supraethmoid with the anteromedial supraethmoid process overlying the premaxillae and prominent articular processes inserting into the premaxillary fossae. Congruent with the previously described ontogenetic alterations of the premaxillary fossae, citharinids demonstrate an ontogenetic increase in the extent of median supraethmoid process and a reduction of the lateral articular processes. The broad articular processes that are present in juvenile citharinids are progressively reduced along their lateral margins until the remaining medial portions coalesce with the enlarged median process. These alterations result in a single enlarged median supraethmoid process (Fig. 6b), in contradistinction to the juvenile anteriorly trifurcate supraethmoid. As a consequence of this restructuring of the supraethmoid and the correlated changes of the premaxillary articular fossa, in adult citharinids the enlarged median process of the supraethmoid overhangs and directly contacts the ventral surface of the articular fossa. Such an association contrasts with the plesiomorphous, and ontogenetically earlier, attachment of the median supraethmoid process to the dorsal surface of the fossa roof. In addition to the above adaptations of the anterior edge of the supraethmoid, *Citharinus* and *Citharidium* have the cranial fontanelle extending midway along the longitudinal extent of the bone. Such a forward extension of the fontanelle is lacking among distichodontids and rare among characoids in general. As such it is considered apomorphous for citharinids among characoids.

Several subunits of the Distichodontidae demonstrate distinctive modifications to the articular processes of the supraethmoid, and of overall supraethmoid form. In *Distichodus*, *Nannocharax* and *Hemigrammocharax* the median supraethmoid process is greatly reduced relative to the lateral articular processes. The latter, in turn, show a transition in form and orientation within these genera. The articular processes of *Distichodus notospilus* and *D. brevipinnis* retain the plesiomorphous flattened, horizontal form, although being somewhat more medially directed than in *Xenocharax*. The other *Distichodus* species examined, along with the genera *Hemigrammocharax* and *Nannocharax*, have the lateral articular processes modified into pointed, anteroventrally-directed prongs (Fig. 6c). In these taxa the articular processes either insert into a conical fossa on the posterodorsal face of the premaxilla (*Distichodus*) or attach ligamentously to the dorsal surface of that element (*Hemigrammocharax* and *Nannocharax*). Congruent with these alterations of the articular processes are changes in the overall form of the supraethmoid. Whereas the supraethmoid in *D. notospilus* and *D. brevipinnis* is relatively square, as it is in *Xenocharax*, those *Distichodus* species with prong-like articular processes have narrow elongate supraethmoids (Fig. 6c). This supraethmoid elongation and that of the articular processes appear to be correlated with the posteroventral shift of the premaxilla relative to the supraethmoid in these taxa. The distichodontid genus *Paradistichodus* also has a long, slender supraethmoid which in overall proportions resembles that of *Hemigrammocharax* and *Nannocharax*. However, contrary to the state of the supraethmoid in those genera. *Paradistichodus* retains the plesiomorphous condition of wide horizontal articular processes and a relatively large median process.

Two other supraethmoid modifications of note occur among distichodontids. In *Hemistichodus* the supraethmoid is greatly reduced to a small element totally lacking the median supraethmoid process, and with the articular processes rounded and laterally directed (see Daget, 1968, Fig. 3). Similarly, but evidently independently, the median supraethmoid process is reduced to approximately one-half of its plesiomorphous size in *Microstomatichthyoborus* and *Mesoborus*, and further diminished to a small pointed element in *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. Congruent with this reduction of the median supraethmoid process is an enlargement and reorientation of the articular processes in these genera. In *Microstomatichthyoborus* and *Mesoborus* these processes retain the plesiomorphous form of anteriorly-directed, horizontal plates. *Eugnatichthys* and *Paraphago*, in contrast, have less flattened articular processes that are both relatively larger and more distinctly orientated. Finally, in *Phago* and *Belonophago* the articular processes are markedly enlarged, bulbous, laterally-oriented structures (Fig. 6d).

The apomorphous modifications of the supraethmoid among citharinids and distichodontids are summarized as follows:

1 the anteriorly trifurcate form of the supraethmoid or a further derived state of the structure that is common to citharinids and distichodontids.
2 the reduction of the articular processes of the supraethmoid and their fusion with the enlarged median supraethmoid process in citharinids.
3 the reduction of the median supraethmoid process and restructuring of the lateral articular processes into pointed, anteroventrally-directed prongs in *Hemigrammocharax*, *Nannocharax* and some *Distichodus* species. Congruent with these changes, these taxa demonstrate a pronounced elongation of the supraethmoid.
4 the elongation of the supraethmoid in *Paradistichodus*.
5 the greatly reduced supraethmoid in *Hemistichodus*.
6 the progressive reduction of the median supraethmoid process, and the enlargement and lateral reorientation of the articular processes in *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

Anterior orbital region

The plesiomorphous condition of the anterior orbital region for characoids is hypothesized to have the orbitosphenoid separated from the lateral ethmoid. In this condition the olfactory nerve exits either from the anteromedian opening of the orbitosphenoid or through a foramen along its anterior face. The nerve then extends obliquely across the anteromedial region of the orbital cavity to the olfactory foramen of the lateral ethmoid. In contrast, citharinids and distichodontids, together with various South American and African characoid groups, have a direct contact of the lateral ethmoid and orbitosphenoid, with the olfactory bulb and tract covered laterally. In the following discussion the forms of this contact in the Citharinidae and Distichodontidae are first described and then contrasted to those in characoid outgroups.

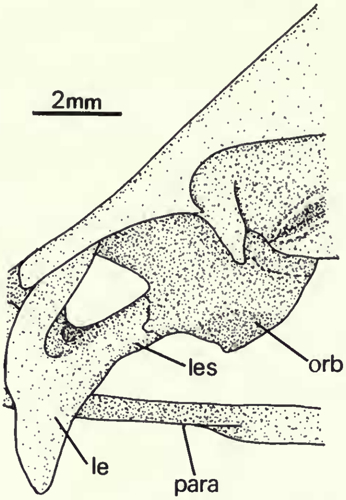

Fig. 7 *Xenocharax spilurus*, anterior orbital region, left lateral view.

Distichodontids other than *Nannaethiops* and *Neolebias* are characterized by the type of lateral ethmoid–orbitosphenoid contact illustrated in Fig. 7 or a further derived state of such an articulation. In the simplest condition, such as that of *Xenocharax*, the lateral ethmoid bears a prominent horizontal or posterodorsally sloping process which extends posteriorly from the postermedial portion of the lateral ethmoid to contact the anterolateral edge of the orbitosphenoid. This lateral ethmoid process forms a strut that laterally overlaps the olfactory bulb and tract and extends between the superior and inferior oblique muscles. As a consequence the entrance into the anterior myodome is horizontally divided posteriorly.

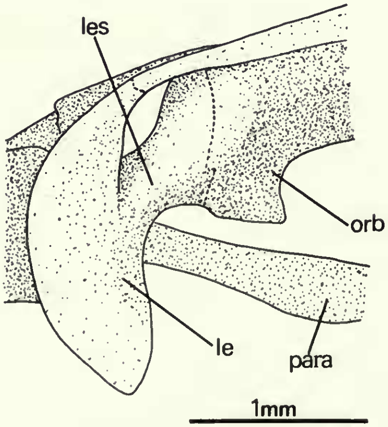

Fig. 8 *Nannocharax elongatus*, anterior orbital region, left lateral view.

The distichodontid genera *Hemigrammocharax* and *Nannocharax* share a further derived form of this type of contact between the lateral ethmoid and orbitosphenoid (Fig. 8). In these genera the posterior process of the lateral ethmoid undergoes a progressive vertical expansion phylogenetically, with a consequent increase in the vertical extent of the articulation between the lateral ethmoid and orbitosphenoid. Although the posterior process of the lateral ethmoid in *Hemigrammocharax monodi* and *Nannocharax multifasciatus* is vertically deeper than that occurring in *Xenocharax*, it is nonetheless distinctly separated dorsally from the ventral surface of the frontal. Thus these species retain a large opening dorsally for the passage of the superior oblique muscle into the anterior myodome. In *Nannocharax gobioides*, *N. fasciatus* and *N. intermedius*, however, the posterior process of the lateral ethmoid is greatly expanded vertically. This expansion both increases the vertical contact between the posterior process of the lateral ethmoid and the orbitosphenoid and further reduces the dorsal aperture into the anterior myodome.

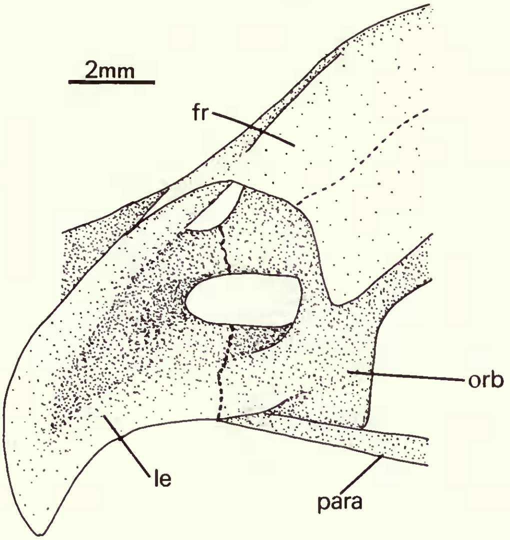

Fig. 9 *Citharinus citharus*, adult, anterior orbital region, left posterolateral view.

In contradistinction to the condition in all other distichodontids, the genera *Nannaethiops* and *Neolebias* lack any direct contact between the lateral ethmoid and orbitosphenoid. This absence of the lateral ethmoid strut is, however, hypothesized to be a secondary loss rather than a primary lack of such a structure. Such an hypothesis is congruent with the most parsimonious reconstruction of relationships among distichodontids, and with the myriad reductional trends demonstrated by the monophyletic unit formed by *Nannaethiops* and *Neolebias*. Furthermore, in *Nannaethiops unitaeniatus*, in which the reductional trends characteristic of these genera are least pronounced, there occurs a short posteriorly-directed lateral ethmoid process lateral to the olfactory foramen. This process may very well represent a reduced form of the *Xenocharax* strut.

The form of lateral ethmoid–orbitosphenoid contact common to all citharinids differs entirely from that in distichodontids. In *Citharinus* and *Citharidium* the orbitosphenoid is shifted to the anteroventral edge of the pterosphenoid as a consequence of the deep orbital lamella of the frontal characteristic of citharinids. The orbitosphenoid of citharinids extends ventrally, as a nearly vertical pillar, to contact the parasphenoid dorsally, and then continues forward as a large, anteriorly-directed, anterolaterally diverging process which articulates with a posterolateral process of the lateral ethmoid (Fig. 9). Juveniles of *Citharinus* and *Citharidium* possess solely this ventral bony contact of the lateral ethmoid and orbitosphenoid. In the anterodorsal region of the orbit, juvenile citharinids have a large cartilage block in the area between the anterior edge of the orbital lamella of the frontal and the posteromedial portion of the lateral ethmoid. This cartilage mass undergoes a progressive ontogenetic ossification from the anterodorsal portion of the orbitosphenoid. As a consequence in all larger citharinid specimens examined (*Citharinus latus*, *C. citharus*, *C. congicus*, *C. distichoides* and *C. gibbosus*) the area occupied earlier in ontogeny by the cartilagenous block is filled by a prominent process of the orbitosphenoid. This ossification extends anterior of the orbital lamella of the frontal along the ventral surface of that bone to either coalesce or synchondrally join with a smaller posterodorsal process of the lateral ethmoid. Although large specimens of all citharinid species were not available for examination, it appears that such an anterodorsal orbitosphenoid process probably occurs in the adults of *Citharidium* and other *Citharinus* species. These dorsal processes of the lateral ethmoid and orbitosphenoid, along with the aforementioned ventral articulation of these bones, restrict the entrance to the anterior myodome in citharinids to a single horizontally elongate fenestra.

Neither the dorsal nor the ventral articulation between the orbitosphenoid and lateral ethmoid among citharinids can be homologized with the bony lateral ethmoid strut joining these elements in most distichodontids. The distichodontid strut passes between the superior and inferior oblique muscles and arises directly lateral to the olfactory foramen through the lateral ethmoid. In citharinids, in contrast, the superior and inferior oblique muscles pass between the processes joining the orbitosphenoid and lateral ethmoid rather than around either or both of them. Furthermore, the lateral ethmoid olfactory foramen is located directly anterior to the central elongate fenestra between these processes, rather than medial to either of them. Consequently, other than by hypothesizing a highly complex series of alterations of the above bones, muscles and nerves, it is not possible to homologize either of the lateral ethmoid–orbitosphenoid contacts in citharinids with the bony lateral ethmoid strut of distichodontids. Thus it is most parsimonious to assume that the citharinid and distichodontid types of lateral ethmoid–orbitosphenoid articulation are distinct, independently acquired, apomorphous systems.

Outgroup comparisons have revealed various ostariophysan groups with articulations of the lateral ethmoid and orbitosphenoid somewhat similar to those of citharinids and distichodontids. Some of these in non-characoid ostariophysans (e.g. the bony tube between the orbitosphenoid and lateral ethmoid in the catfish *Diplomystes*) are undoubtedly convergent with those in the groups under discussion. Within characoids, however, a direct contact of the lateral ethmoid and orbitosphenoid occurs within African characids in *Hydrocynus*, *Bryconaethiops* and various *Alestes* species and in the Neotropical families Anostomidae, Curimatidae, Prochilodontidae, Paradontidae and Lebiasinidae. Consequently, the mere fact of a direct articulation between these bones is not a distinguishing character among characoids for either the citharinid or distichodontid type of contact. Nonetheless, in each case the particular form of lateral ethmoid–orbitosphenoid contact appears to be unique to citharinids and distichodontids among characoids.

The presence in distichodontids of a strut-like process between the orbitosphenoid and lateral ethmoid was noted by Starks (1926, p. 167) in *Distichodus fasciolatus*, *D. lusosso* and *Mesoborus crocodilus*. The same author also described a somewhat similar tubular process in the African characids *Alestes grandisquamis* and *A. liebrechstii*. This process of these characids was later noted for *Hydrocynus*, *Bryconaethiops*, *Alestes baremose*, *A. imberi* and *A. macrolepidotus* by Roberts (1969, p. 441), and has been found in *A. dentex* and *A. macrophthalmus* during these studies. Although the tubular process in African characids seems homologous with the distichodontid strut on a purely topographical basis, closer observation reveals several major differences between these structures. As previously noted, the distichodontid strut is formed primarily by the lateral ethmoid and covers only the lateral face of the olfactory bulb and tract. The process in the above characids, in contrast, is a bony tube formed primarily or entirely by the orbitosphenoid and completely surrounding the olfactory bulb and tract to varying degrees. Differences between these structures are also apparent in the phylogenetic and ontogenetic development of the orbitosphenoid tube of characids. Commencing in some *Alestes* species as a short anteriorly-directed lip around the orbitosphenoid olfactory foramen, the characid orbitosphenoid process becomes increasingly elongate anteriorly through the phylogenetic series until in *Hydrocynus* it is a thick tube extending to the rear of the lateral ethmoid. At no point during this phylogenetic sequence, or the similar ontogenetic transition of *Hydrocynus*, is there found a distichodontid type strut. Thus the characid tube and the distichodontid strut would appear to be analogous but non-homologous structures.

A closer approximation to distichodontid form of contact between the lateral ethmoid and orbitosphenoid occurs in the South American characoid family Parodontidae. Among parodontids, the genus *Saccodon* has a posterior lateral ethmoid process contacting the orbitosphenoid (see Roberts, 1974, Fig. 57). This lateral ethmoid process is rather similar to the *Xenocharax* strut between these elements. In *Parodon*, in contrast, the expanded contact between these bones is comparable to that of *Nannocharax*. These similarities are, however, considered to be convergent with those of distichodontids rather than an indicator of close relationship between the Parodontidae and Distichodontidae (see p. 340).

It is interesting to note that distichodontids and parodontids, together with the African characids having a bony tube between the orbitosphenoid and lateral ethmoid all have a forward shift of the olfactory bulb (see p. 341). It seems likely that the various adaptations of the anterior orbital region in these groups are correlated with this anterior position of the bulb and the consequent necessity to protect it from compression by the superior and inferior oblique muscles. Similarly, the dorsal and ventral articulations of the lateral ethmoid and orbitosphenoid in citharinids separate the olfactory bulb, nerve and tract from the orbital cavity and the inferior and superior oblique muscles. The only characoid found during this study to have a forward position of the bulb, but lacking some form of bony protection for it, was the Neotropical genus *Salminus*. However, in that genus the bulb is, nonetheless, surrounded laterally by a very heavy, inflexible connective tissue capsule.

An approximation to the citharinid form of contact between the orbitosphenoid and lateral ethmoid is found among the Neotropical families Anostomidae, Curimatidae, Prochilodontidae and Lebiasinidae. A variety of differences discriminate the form of contact in these families from that in citharinids. However, rather than dealing with these in detail, for the purposes of this study, it suffices to note that in none of them is the ventral articulation between the orbitosphenoid and lateral ethmoid as massive as in citharinids. Neither has there been found among these families any form of dorsal contact between the lateral ethmoid and orbitosphenoid comparable to that in citharinids.

Citharinids also demonstrate yet another modification of this region of the neurocranium. These genera have a prominent horizontal shelf extending along the rear portion of the orbitosphenoid and onto the anterior part of the pterosphenoid. The functional significance of this process, which is unique to *Citharinus* and *Citharidium* among the families under study, is presently unknown.

Derived states of the anterior orbital region among citharinids and distichodontids include:

1 the dorsal and ventral lateral ethmoid–orbitosphenoid contacts in citharinids.
2 the bony strut between the orbitosphenoid and lateral ethmoid in distichodontids. This strut is vertically expanded in *Nannocharax* and *Hemigrammocharax*, but is hypothesized to be secondarily reduced in *Nannaethiops* and *Neolebias*.
3 the shelf-like process on the lateral surface of the orbitosphenoid and pterosphenoid in citharinids.

Posterior orbital and anterior otic regions

Among citharinids and distichodontids the posterior orbital and anterior otic regions undergo a series of interrelated modifications and thus are most easily discussed as a unit. The plesiomorphous state of this portion of the neurocranium, within the complex formed by the Citharinidae and Distichodontidae, is hypothesized to be similar to that of *Xenocharax* (Fig. 10). This genus has the dorsal margin of the orbit formed by a distinct lateral process of the frontal. The posterodorsal wall of the orbital cavity is formed by the prominent sphenotic spine. This process extends distinctly lateral to the frontal and is orientated along the vertical through the trigemino-facialis foramen. Ventrolaterally the sphenotic bears a short vertical process which is continuous dorsally with the sphenotic spine, and ventrally with the prominent sharp-edged ridge of the lateral commissure of the prootic. This lateral commissural ridge, in turn, contacts the lateral flange present on the anterior edge of the ascending process of the parasphenoid. Together these lateral processes of the sphenotic, prootic and parasphenoid form a nearly continuous, laterally-directed flange at the rear of the orbital cavity. Along its ventral border the sphenotic forms the anterodorsal portion of the hyomandibular fossa which extends anteriorly to below the sphenotic spine and contacts the posterior edge of the orbital cavity. The prootic in *Xenocharax* is an angular element whose lateral surface nearly forms a right angle horizontally at the ridge of the lateral commissure. As a consequence the anterior portion of the prootic faces onto the orbital cavity while the posterior section contributes to the lateral surface of the neurocranium. In *Xenocharax* the prootic forms the dorsal and dorsolateral borders of the entrance into the posterior myodome, and the ventrolateral and ventral borders of the median opening into the braincase. Thus this bone broadly separates the posteroventral border of the pterosphenoid from the dorsal edge of the ascending process of the parasphenoid. Finally, the pterosphenoid and orbitosphenoid of *Xenocharax* are rather flat, square bones.

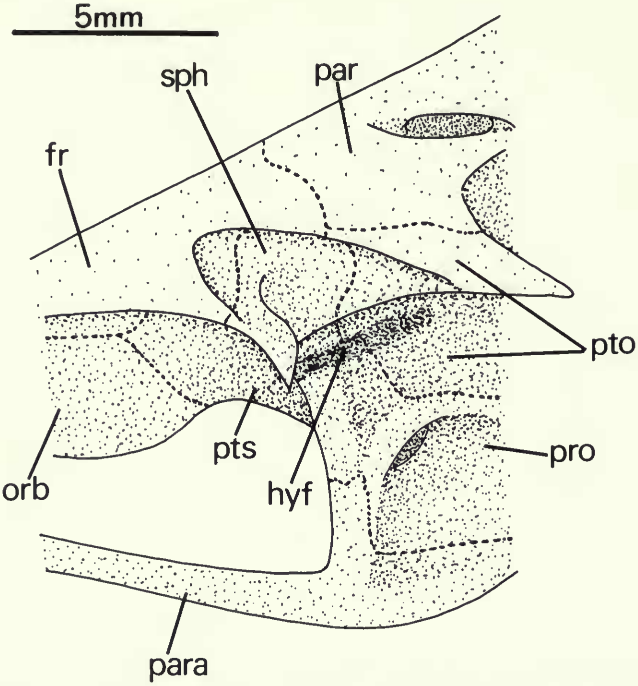

Fig. 10 *Xenocharax spilurus*, posterior orbital and anterior otic regions, left lateral view.

The *Xenocharax* plan of the posterior orbital and anterior otic regions agrees in general morphology, although not necessarily specific detail, with that in non-specialized members of most groups of characoids. Thus this plan is hypothesized to represent the plesiomorphous condition of this region for citharinids and distichodontids. Apart from a difference in the extent of the contribution of the supraorbital to the orbital rim (see p. 301), this arrangement of the posterior orbital and anterior otic regions is shared with minor variations by citharinids and the distichodontid genera *Xenocharax*, *Nannaethiops*, *Neolebias*, *Paradistichodus* and *Hemistichodus*. The remaining distichodontid genera can be divided into two assemblages on the basis of their distinct adaptations of this neurocranial region.

Within the subunit of distichodontids formed by *Distichodus*, *Nannocharax* and *Hemigrammocharax* there occurs a progressive transition from the plesiomorphous ventrally sharp-edged sphenotic spine to a reduced, ventrally concave sphenotic process. *Distichodus* species such as *D. notospilus* retain the plesiomorphous condition of a large, nearly vertical sphenotic spine tapering ventrally to a thin edge. In *D. niloticus* and *D. fasciolatus* the central portion of the ventral edge of the spine is rotated slightly anteriorly, resulting in an oblique anteroventrally sloping central portion of the ventral margin of the spine. This alteration is further pronounced in species such as *D. lusosso* where this section of the sphenotic spine is expanded ventrally into a broad concave surface. Such a restructuring of the sphenotic spine is carried further in *Nannocharax* and *Hemigrammocharax* where the ventrally reduced spine has the form of a short, ventrally concave, posteroventrally sloping shelf.

The genera *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*, in turn, exhibit a different series of alterations and reductions of the bones of the posterior orbital and anterior otic regions (note: the osteology of *Paraphago*, known only from the type series of *P. rostratus*, was examined primarily by radiographs). Progressive modifications of several levels of universality characterize this region of the neurocranium among these distichodontids. In the following discussion these adaptations will be dealt with sequentially. First, those apomorphic alterations found in *Ichthyborus* and common to, or further modified in, the other genera listed above will be described. The further derived characters that characterize less universal groups within this unit will be discussed in light of the modifications in *Ichthyborus*.

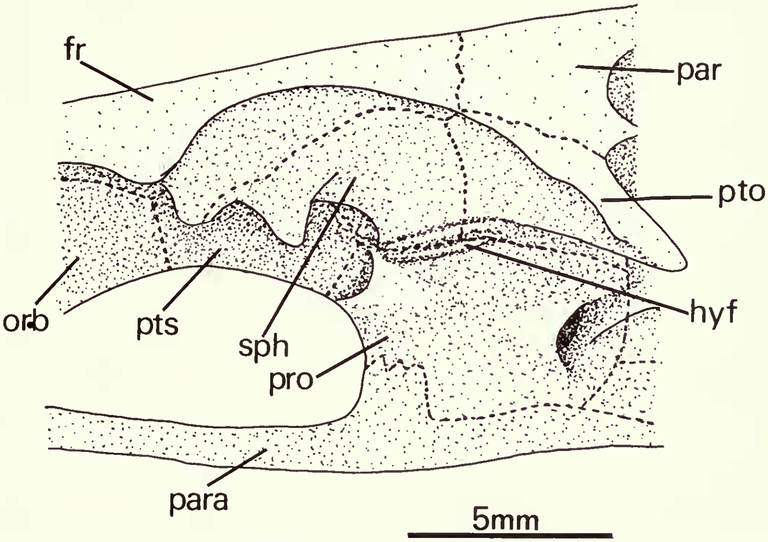

Fig. 11 *Ichthyborus besse*, posterior orbital and anterior otic regions, left lateral view.

The most pronounced alterations of this neurocranial region are those of the sphenotic, in particular the reduction and reorientation of the sphenotic spine. In *Ichthyborus* (Fig. 11), the entire sphenotic spine is rotated so that its primitively ventral edge is shifted posterodorsally. This reorientation results in the spine forming a posteroventrally sloping shelf in contrast to its plesiomorphous state of a nearly vertical wall. In addition, the lateral extent of the spine is reduced, resulting in a truncate process that barely extends beyond the lateral margin of the frontal. The overall form of the sphenotic in *Ichthyborus* is horizontally elongate relative to the hypothesized plesiomorphous state. Along with a posterior shift of the prootic, this elongation has resulted in a horizontal separation of the anterior margin of the hyomandibular fossa from the posterior edge of the sphenotic spine and the vertical through the trigemino-facialis foramen. Such a separation is considered derived relative to the close approximation of these structures in the plesiomorphous condition. The prootic of *Ichthyborus* is also markedly restructured from the plesiomorphous condition in which the lateral commissure bears a sharp-edged lateral ridge. In this genus the prootic is a gently curved, flattened element unelaborated laterally apart from the slightly raised lips around the facialis and trigemino-facialis foramina. The prootic of *Ichthyborus* is also shifted posteriorly, resulting both in the aforementioned repositioning of the hyomandibular fossa and in the reduction of the contribution of the prootic to the edge of the opening into the posterior myodome. As a consequence of the latter change, there is a significant reduction in the plesiomorphously wide separation between the posterior border of the pterosphenoid and the ascending arm of the parasphenoid.

The final noteworthy adaptation of this neurocranial region in *Ichthyborus* involves the ventral surface of the orbital process of the frontal. In citharinids and most distichodontids that portion of the frontal forming the roof of the orbital cavity is a ventrally smooth, slightly concave surface; a condition probably plesiomorphous for characoids. The ventral surface of the frontal in *Ichthyborus*, in contrast, bears a strong transverse ridge capped laterally by an anterodorsal extension of the sphenotic spine. This ridge is continuous with the orbital lamella of the frontal and extends transversely along the ventral surface of the bone just anterior to the suture of the frontal with the anterodorsal edge of the sphenotic spine.

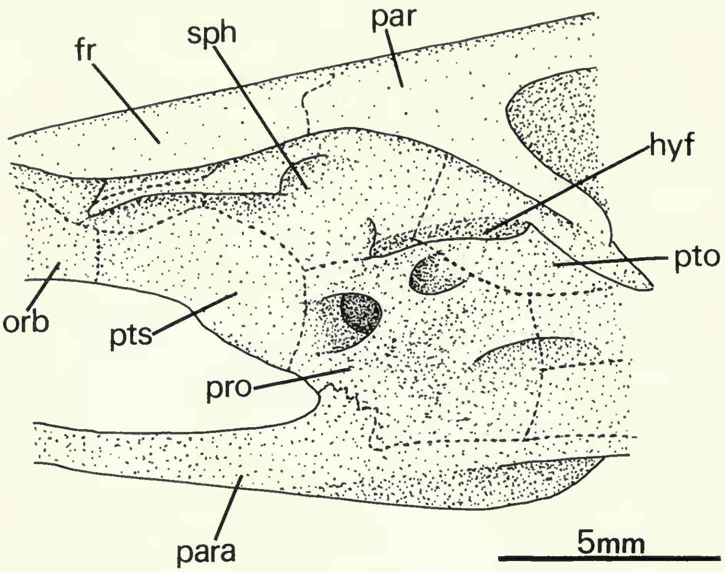

Fig. 12 *Mesoborus crocodilus*, posterior orbital and anterior otic regions, left lateral view.

These apomorphous modifications of the posterior orbital and anterior otic regions are common to *Ichthyborus* and *Microstomatichthyoborus*, and are the basis for a series of further derived adaptations in *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. Congruent with the overall elongation of the neurocranium, the orbitosphenoid and pterosphenoid of these latter genera are notably elongate both relative to the *Ichthyborus* condition, and more notably with respect to the hypothesized plesiomorphous characoid state. These taxa also have in common a further restructuring of the sphenotic spine. The primitively ventral edge of the sphenotic has rotated posterodorsally nearly to the level of the horizontal through the anterodorsal margin of the spine. Thus in these genera the spine has the form of a nearly horizontal shelf (Figs 12, 13, 14) rather than the near vertical wall at the rear of the orbital cavity of *Xenocharax*, or the posteroventrally slanting process of *Ichthyborus*. As described earlier, the plesiomorphous sphenotic spine extends distinctly lateral to the edge of the frontal, with *Ichthyborus* having the lateral extent of the spine significantly reduced. *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* show a further reduction of the *Ichthyborus* form of the sphenotic. In *Mesoborus* the sphenotic spine barely extends lateral of the edge of the frontal, and it falls distinctly short of the margin in *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. Within the latter assemblage, the anterior sphenotic process which caps the transverse ridge of the frontal is significantly reduced in *Eugnatichthys* and completely lost in *Phago* and *Belonophago* (the condition of the process is unknown in *Paraphago*). In addition, *Belonophago* lacks, evidently secondarily, the transverse strut along the ventral edge of the frontal that characterizes other members of its monophyletic unit.

Phago and *Belonophago* can be further distinguished within distichodontids by the broad contact between the posteroventral portion of the pterosphenoid and the dorsal margin of the ascending arm of the parasphenoid (Fig. 14). The extensive articulation between these bones totally separates the prootic from its plesiomorphous location along the anterior margin of the entrance into the posterior myodome. Furthermore, radiographs of *Paraphago rostratus* reveal what appears to be a less extensive suture between these bones. Therefore *Phago*, *Belonophago* and perhaps *Paraphago* share a synapomorphous contact of the pterosphenoid and parasphenoid.

Belonophago is a highly specialized genus characterized by long jaws and an extreme elongation of the skull, particularly in the posterior orbital region (Fig. 14). In this genus the pterosphenoid is expanded posteriorly and ventrally to form the entire anterior surface of the braincase. As a consequence of this elongation, the lateral commissure and hyomandibular fossa are markedly shifted posteriorly and are removed from the rear of the orbit by a distance equal to the orbital diameter. Such an extensive separation is derived relative to the *Ichthyborus* condition of a slight distance between these structures, and is a pronounced apomorphous change relative to the plesiomorphous close proximity of the anterior portions of the lateral commissure and hyomandibular fossa to the rear of the orbital cavity. As noted previously, the pterosphenoid in *Belonophago* is broadly in contact posteroventrally with the ascending process of the parasphenoid. In addition, *Belonophago* has a median articulation between these elements. Arising from the anterior face of the pterosphenoid is a ventrally-directed medial process which contacts a corresponding dorsally-orientated medial parasphenoid strut. Together these processes form a pedicle between the pterosphenoid and the parasphenoid (Fig. 14), an adaptation that is evidently unique to this genus among characoids.

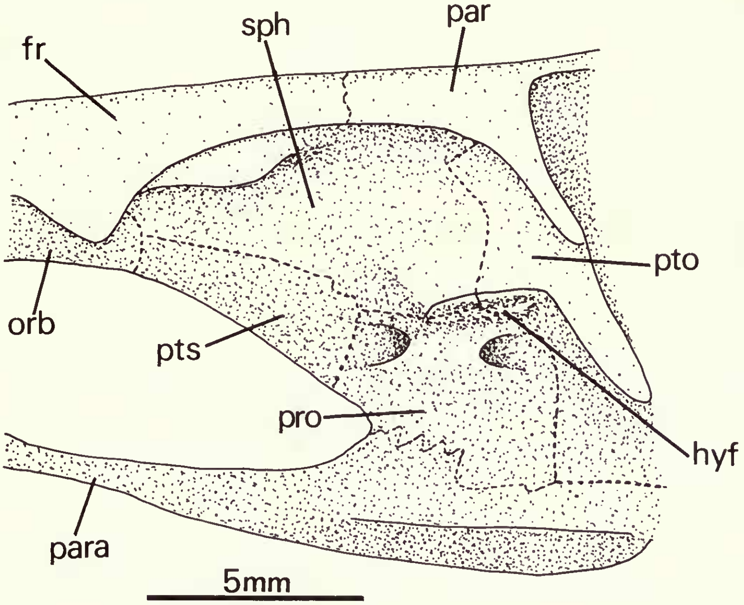

Fig. 13 *Eugnatichthys eetveldii*, posterior orbital and anterior otic regions, left lateral view.

A series of autapomorphous adaptations of the posterior orbital and anterior otic regions distinguish *Eugnatichthys* among distichodontids. The pterosphenoid in this genus is shifted posteroventrally by the ventral expansion of the orbital lamella of the frontal. This shift, along with the horizontal elongation of the sphenotic, results in a marked separation, both vertically and horizontally, between the rear of the sphenotic spine and anterior margin of the hyomandibular fossa. Together with a horizontal expansion of the pterosphenoid, this sphenotic elongation has shifted the prootic and associated lateral commissure posteriorly relative to the *Ichthyborus* condition. Although *Eugnatichthys* and *Belonophago* both possess a pronounced posterior shift of the hyomandibular fossa and lateral commissure, the method by which this realignment is achieved differs greatly in the two genera. In *Eugnatichthys* this restructuring is primarily a consequence of the elongation of the sphenotic and the ventral expansion of the orbital lamella of the frontal. In *Belonophago*, in contrast, the realignment is largely the result of the horizontal extension of the pterosphenoid.

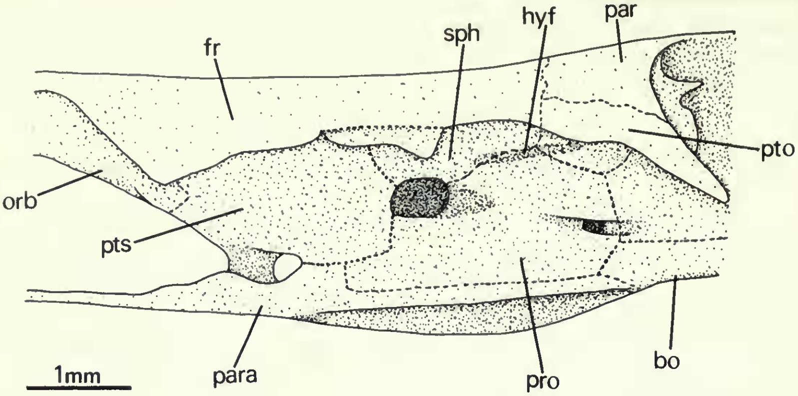

Fig. 14 *Belonophago tinanti*, posterior orbital and anterior otic regions, left lateral view.

Several modifications of the parasphenoid are of interest for an understanding of relationships within the Citharinidae and Distichodontidae. The plesiomorphous characoid parasphenoid form appears to be a flat, straight or ventrally convex element, extending posteriorly to below the basioccipital. In *Citharinus* and *Citharidium*, in contrast, the parasphenoid is markedly flexed ventral to its ascending processes and ontogenetically develops a bulbous process ventral to this point of flexure. This process serves as the area of attachment for the anteriorly shifted suspensory pharyngeals characteristic of this family. Posteriorly the citharinid parasphenoid has two slightly divergent lateral wings separated by a deep groove. Although such a condition occurs in many characoids in which the posterior myodome is posteroventrally open, in citharinids the myodome is closed at the rear, and the posterolateral wings of the parasphenoid surround the anterior portion of the dorsal aorta. In juveniles of *Citharinus* and *Citharidium* these parasphenoid processes are separate both from the basioccipital and the highly modified pars sustentaculum of the Weberian apparatus. In adults, however, the posterior parasphenoid processes fuse dorsally with the basioccipital and posteriorly with the ventral projections of the pars sustentaculum (see discussion on the Weberian apparatus). The overall modifications in pharasphenoid form, and the changes in its relationships to the basioccipital and pars sustentaculum are hypothesized to be apomorphous.

The distichodontid genera *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* have the parasphenoid expanded ventrally into a flattened median ridge. This process serves as a point of attachment for the posteroventrally shifted suspensory pharyngeals occurring in these genera and is most developed in *Eugnatichthys* in which the shift is most pronounced (Fig. 13).

In summary, the hypothesized apomorphous states of the posterior orbital and anterior otic regions in citharinids and distichodontids include:

1. the vertical reduction and horizontal expansion of the sphenotic spine in *Hemigrammocharax*, *Nannocharax* and some *Distichodus* species. The restructuring of the spine is particularly pronounced in the first two genera.
2. the lack of lateral flanges on the prootic and ascending arm of the parasphenoid in *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. These genera also share a laterally reduced sphenotic spine whose plesiomorphously ventral edge is shifted posterodorsally; the development of a transverse process on the ventral surface of the frontal; a posterior shift of the hyomandibular fossa; and a reduction in the gap between the parasphenoid and pterosphenoid.

3 the restructuring of the sphenotic spine to form a horizontal shelf in *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. The lateral extent of the spine is slightly further reduced relative to the *Ichthyborus* condition in *Mesoborus*, and greatly so in the other genera listed.

4 the reduction of the sphenotic process capping the transverse process of the frontal in *Eugnatichthys*, and its loss in *Phago*, *Belonophago* and perhaps *Paraphago*.

5 the broad articulation between the pterosphenoid and parasphenoid in *Phago*, *Belonophago* and perhaps *Paraphago*, with *Belonophago* having an autapomorphous median contact between these elements.

6 the pronounced posterior expansion of the pterosphenoid in *Belonophago*.

7 the ventral expansion of the orbital lamella of the frontal and a horizontal lengthening of the sphenotic in *Eugnatichthys*.

8 the distinctive flexure in the parasphenoid and the development of a ventral bulbous parasphenoid process in citharinids. In these genera the posterior processes of the parasphenoid straddle the dorsal aorta and fuse with the pars sustentaculum and basioccipital.

9 the median ventral parasphenoid ridge in *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

Occipital region

The character of phylogenetic interest in the occipital region of citharinids and distichodontids is the number, form and extent of development of the posttemporal fossae. The most widespread, and the hypothesized plesiomorphous, state of these openings among characoids consists of a dorsal and posterolateral pair of fossae on either side of the neurocranium. The horizontal or slightly oblique dorsal fossa is bordered by the supraoccipital medially, the parietal anteriorly and the epioccipital posteriorly. The remaining fossa is located at the posterolateral corner of the neurocranium and is bordered anteriorly and ventrally by the pterotic, and posteriorly and dorsally by the epioccipital.

Citharinids and distichodontids, in contrast, also possess an additional vertically ovate fossa bordered by the epioccipital and exoccipital (Fig. 15) (citharinids although possessing this 'third' fossa have, however, lost the dorsal fossa and thus retain only two sets of openings, see below). On the basis of outgroup comparisons the possession of a third fossa appears to be derived among ostariophysans in general and characoids in particular. However, although not widespread, a third posttemporal fossa *per se* is not unique to citharinids and distichodontids among charcoids. Such a feature has been found in most African characids and among South American characoids in the families Curimatidae, Hemiodontidae (Roberts, 1974), Parodontidae (Roberts, 1974) and the characid tribe Cynodontini (*sensu* Howes, 1976). However, the third posttemporal fossa in these taxa, with the exception of the Cynodontini, is a small round opening entirely within the epioccipital. This condition contrasts with the large ovoid fossa bordered by the deeply incut exoccipital and epioccipital in citharinids, distichodontids and cynodontines.

Although the Cynodontini possess a form of third posttemporal fossa very similar to that of citharinids and distichodontids, they do not, however, appear to be the sister group to the latter families. As discussed by Howes (1976), cynodontines possess a series of derived characters uniting them to the neotropical characid tribe Characini which lacks a third posttemporal fossa. Furthermore, the members of both the Cynodontini and Characini have a rhinosphenoid, an element unique to various South American characoids, most of which lack any form of third posttemporal fossa. In light of the lack of the third fossa both in the sister group to cynodontines and in the more inclusive unit of Neotropical characoids defined by the presence of a rhinosphenoid, it is most parsimonious to assume that the cynodontines arose from an ancestor possessing a rhinosphenoid but lacking a third posttemporal fossa. It thus appears that although convergently derived in cynodontines, the possession of a vertically ovate third posttemporal fossa bordered by the epioccipital and exoccipital is apomorphous for, and indicative of the monophyly of the unit formed by citharinids and distichodontids within characoids.

The genera *Citharinus* and *Citharidium* lack the plesiomorphously present posttemporal fossa on the posterodorsal surface of the neurocranium. In *Eugnatichthys*, in turn, there occurs a greatly reduced fossa in the same area. Both the reduction of the fossa in *Eugnatichthys* and its loss in citharinids are considered derived in so far as the possession of a large dorsal posttemporal fossa is generalized among characoids.

Cranial fontanelle

The extent of the dorsomedian fontanelle varies considerably within the unit formed by citharinids and distichodontids. Although the plesiomorphous condition of the fontanelle for these families or indeed any otophysans is difficult to ascertain, this variation does permit certain assumptions to be made. Of particular note is the extension of the fontanelle into the posterior half of the supraethmoid in *Citharinus* and *Citharidium* (Fig. 6c). Such an elongate fontanelle is rarely encountered among characoids and appears apomorphous for the superfamily. Among distichodontids, *Xenocharax* possesses an elongate fontanelle that separates the frontals, which are only in contact at the epiphyseal bar, and the parietals. The remaining distichodontids demonstrate a progressive phylogenetic reduction of this extensive fontanelle. All distichodontids apart from *Xenocharax* have a shorter opening which at the maximum extends slightly anterior to the epiphyseal bar. *Ichthyborus*, *Microstomatichthyoborus*, *Belonophago*, *Mesoborus*, *Eugnatichthys*, *Paraphago* and *Phago* have a further reduced fontanelle limited to the interparietal region, with this reduction particularly pronounced in the last four genera. The hypothesis that a progressive reduction of the fontanelle is apomorphic among distichodontids is congruent with the large fontanelle that characterizes the Citharinidae, the family which is hypothesized as the sister group to distichodontids. Such a hypothesis also agrees with the distribution of a large suite of derived characters within distichodontids. This reductional trend appears, however, to have been slightly reversed in *Belonophago* where the fontanelle is enlarged relative to the condition in other members of its monophyletic group.

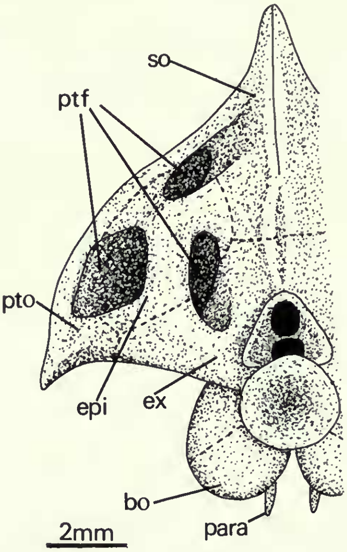

Fig. 15 *Xenocharax spilurus*, neurocranium, posterior view.

Suspensorium

The diverse modifications of the dentition, jaws and neurocranium that characterize the Citharinidae and subunits of the Distichodontidae are reflected in a series of alterations to the suspensorium. Two different types of suspensorium can be discriminated among citharinids and distichodontids on the basis of the relative position of the articulation of the angulo-articular with the quadrate. In *Citharinus*, *Citharidium*, *Xenocharax*, *Neolebias* and *Nannaethiops* the horizontal distance between the ventral portion of the hyomandibula and the articular condyle of the quadrate is relatively short. As a consequence, the articulation of the angulo-articular with the quadrate occurs below the centre of the orbit and distinctly posterior to the vertical through the body of the lateral ethmoid. In the remaining distichodontid genera, in contrast, the symplectic, metapterygoid and quadrate are relatively elongate resulting in a forward shift of the articular condyle of the quadrate to below or anterior to the vertical through the lateral ethmoid.

The polarity of such changes in the position of the articulation of the angulo-articular with the quadrate is somewhat problematical in that both anterior and posterior positions of this joint occur within a variety of seemingly monophyletic characoid groups. Consequently, a shift in the position of the articulation has evidently occurred independently within the Characoidea on several occasions. It is nonetheless interesting to note that those characoid groups which have been considered to be 'primitive' (Hepsetidae and Erythrinidae) have the posterior position of this joint; a location also common to generalized members of most characoid groups. If these families do indeed possess the plesiomorphous jaw form, then the primitive joint position and type of suspensorium among citharinids and distichodontids would be the posterior articulation common to *Citharinus*, *Citharidium*, *Xenocharax*, *Neolebias* and *Nannaethiops*. It is furthermore noteworthy that distichodontids with an anterior articulation of the quadrate and angulo-articular have derived forms of jaws and dentition. This congruence of the forward position of the angulo-articular-quadrate joint with a series of apomorphous jaw characters, contrasted with the posterior articulation among 'primitive' and generalized characoids, supports the hypothesis that an anterior articulation of these elements is the derived condition.

These adaptations in the suspensorium are reflective of the relative mouth sizes of the two groups of genera. In characoids with a non-protrusible mouth, the length of the jaws and consequently the extent of the gape is primarily a function of the position of the articulation of the quadrate with the angulo-articular. Thus in small-mouthed characoids the joint occurs under or forward of the ventral process of the lateral ethmoid. In large-mouthed, often predacious forms, in contrast, the articulation is distinctly posterior to the lateral ethmoid, and is sometimes also shifted ventrally. The distichodontid genera *Hemistichodus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Ichthyborus*, *Paraphago*, *Phago* and *Belonophago*, particularly the latter four genera, would appear to invalidate this distinction in being large-gaped fish with a forward angulo-articular-quadrate articulation. However, this seeming incongruity is a function of the autapomorphous manner in which the elongation of the jaws is achieved in these genera. Among other characoids the premaxilla extends little, if at all, anterior to the tip of the supraethmoid. Thus the effective gape is a function of the distance between the anterior margin of the supraethmoid and the articular condyle of the quadrate. In the distichodontid genera noted above, however, the elongation of the gape is a function of the lengthening of the premaxillae anterior to the supraethmoid. This adaptation together with the congruent changes in the supraethmoid, lower jaw and suspensorium permits an elongation of the gape despite the retention of an anterior position of the articulation between the angulo-articular and quadrate.

In addition to the above broad differences in overall suspensorium form, modifications of portions of this system characterize groups of varying levels of universality with the Distichodontidae. Two multigeneric assemblages within this family demonstrate a restructuring of the generalized characoid condition of a somewhat rectangular hyomandibula having a slightly concave anterior face. In *Nannocharax* and *Hemigrammocharax* the hyomandibula is markedly widened anteroposteriorly and has a relatively elongate articulation with the hyomandibular fossa (see Daget, 1961, Fig. 10). *Ichthyborus*, *Mesoborus*, *Microstomatichthyoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*, in contrast, have an elongate hyomandibula with a deeply concave anterior margin (see Daget, 1967, Fig. 9). Both this form of hyomandibula and that occurring in the unit formed by *Hemigrammocharax* and *Nannocharax* appear to be derived characters serving to define these multigeneric units.

The hyomandibula exhibits several other modifications of note among distichodontids. In *Eugnatichthys* this bone has a dorsally-directed process arising from its dorsolateral border

(Fig. 16). A similar, although not as well-developed, process occurs in *Phago* and appears to be present in *Paraphago*. *Eugnatichthys* also possesses a medially-directed process on the medial surface of the hyomandibula. This structure both braces the bone against the ventral surface of the neurocranium and serves as a point of origin for portions of the *adductor mandibulae* muscles.

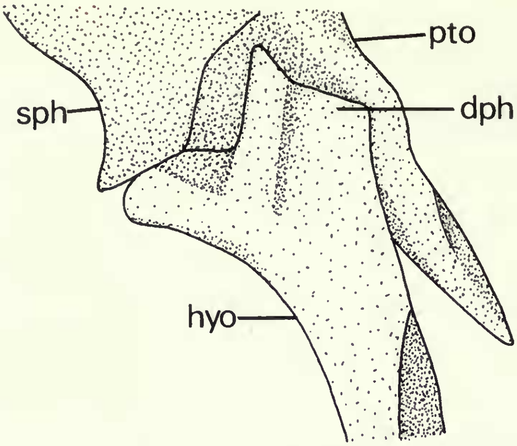

Fig. 16 *Eugnatichthys eetveldii*, posteroventral otic region and dorsal portion of the hyomandibula, left lateral view.

The final hyomandibular modifications of note among distichodontids involve the relationships of this element to the dorsal portion of the preopercle. Citharinids and distichodontids other than *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* retain the plesiomorphous characoid condition of a slight overlap of the lateral face of the vertical arm of the preopercle by the posterior border of the hyomandibula. In the listed genera, however, the posterior surface of the hyomandibula bears a vertically elongate depression just ventral to the articular condyle. This groove, which appears to be unique to these genera among characoids, tightly surrounds the dorsal tip of the preopercle (Fig. 17) and further reduces the possibility of motion between these elements.

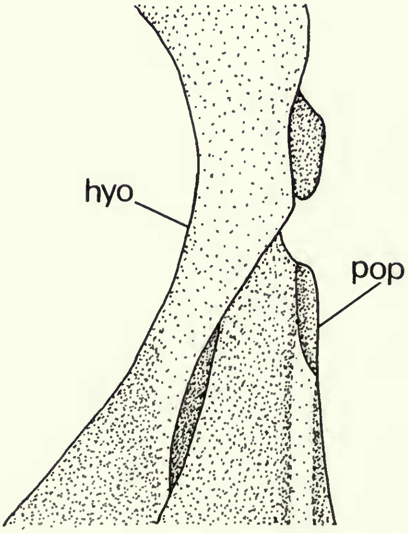

Fig. 17 *Phago loricatus*, central portion of the hyomandibula and posterodorsal section of the preopercle, left lateral view.

The preopercle, in turn, has undergone several modifications that distinguish groups of varying levels of universality within distichodontids. In *Hemistichodus*, *Ichthyborus*, *Microstomatichthyborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* the laterosensory canal segment in the vertical arm of the preopercle is shifted medially relative to the condition in citharinids and other distichodontids. This shift, which is especially pronounced in *Ichthyborus*, results in a broad separation of the laterosensory canal segment from the posterolateral edge of the bone. These genera, with the exception of *Ichthyborus* and *Hemistichodus*, are also characterized by the separation of the posterolateral portion of the preopercle as a distinct dorsally-directed process (Fig. 18). Both this lateral preopercular flange and the medial shift of the posterior portion of the preopercular laterosensory canal are hypothesized to be apomorphous characters.

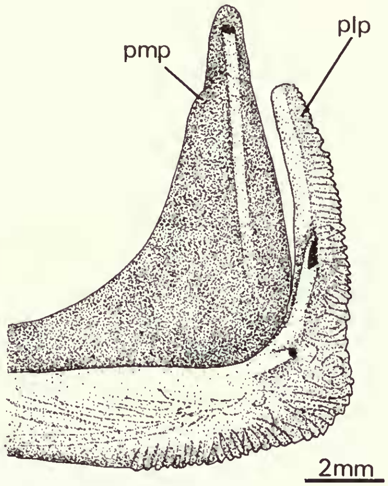

Fig. 18 *Phago loricatus*, posterior portion of the preopercle, left lateral view.

The final preopercular modification of note involves the development of a lateral preopercular shelf in some distichodontids. The lateral surface of the preopercle in citharinids and the distichodontid genera *Xenocharax*, *Nannaethiops* and *Neolebias* is nearly flat except for the slightly raised laterosensory canal. *Paradistichodus*, *Distichodus*, *Nannocharax*, *Hemigrammocharax* and *Hemistichodus*, in contrast, have a horizontal, laterally-directed ridge along the anterior portion of the preopercle. This lateral preopercular ridge is further elaborated, both posteriorly and laterally, in *Ichthyborus*, *Microstomatichthyborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* where it extends posteriorly to the vertical arm of the preopercle. In these genera these processes of the quadrate and preopercle form a distinct trough from which the expanded origin of the large A_1 and A_2 portions of the *adductor mandibulae* muscles partially arise. Such an elaboration of the preopercle and quadrate is hypothesized apomorphous for these genera, although occurring evidently independently in the South American characoid family Anostomidae.

The metapterygoid–quadrate fenestra undergoes a series of apomorphic alterations in various generic and multigeneric units among distichodontids. The plesiomorphous condition of the fenestra among characoids appears to be an horizontally ovoid opening bordered primarily by the metapterygoid dorsally and the quadrate ventrally, and with the symplectic forming a limited portion of its posteroventral border. A complete eradication of the fenestra occurs in *Neolebias spilotaenia* in which the enlarged symplectic fills the space primitively occupied by the fenestra. Correlated with the decreased vertical extent of the suspensorium in *Nannocharax* and *Hemigrammocharax* is a reduction or elimination of the fenestra as a consequence of the approximation of the quadrate and metapterygoid (see Daget, 1961, Fig. 10).

Hemistichodus, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*, in contrast, have a horizontally elongate metapterygoid–quadrate fenestra (see Daget, 1967, Fig. 9). In these genera the contribution of the symplectic to the border of the fenestra is greatly increased, with a congruent reduction of the portion of the border formed by the quadrate. Such seemingly apomorphous modifications are correlated with the lengthening of the metapterygoid and symplectic necessitated by the posterior shift of the hyomandibular fossa in these genera. This elongation of the fenestra is particularly pronounced in *Phago* and *Belonophago* in which the bones are exceptionally long and slender.

The final modifications of the suspensorium to be discussed involve the relationship of the anterior portion of the suspensorium to the upper jaw. The generalized characoid condition has a ligamentous or cartilaginous attachment of the palatine to the anteromedial maxillary process, and a loose ligamentous connection of the palatine to the vomerine region. In *Citharinus* and *Citharidium*, however, a large cartilage pad joins the palatine to the anteromedial process of the maxilla. Furthermore, citharinids have a second cartilaginous mass joining the palatine to the posterior surface of the premaxilla. Although a cartilaginous connection between the maxilla and palatine occurs in other characoid groups, both the size of the cartilage in citharinids, and the presence of a cartilaginous body between the palatine and premaxilla is unique to, and thus considered apomorphous for, these genera among the families under study.

Some species of *Nannocharax*, in contradistinction, have a partially ossified cartilaginous rod joining the palatine to the maxilla. Further study is necessary to determine whether this ontogenetically variable ossification, termed the submaxilla by Daget (1961), is a defining character for the genus or some subunit of it.

In distichodontids, other than *Xenocharax*, *Nannaethiops*, *Neolebias* and *Paradistichodus*, the mesopterygoid is more tightly joined to the lateral ethmoid than in the hypothesized plesiomorphous condition. Furthermore, the palatine in these genera is distinctly more enveloped by the ectopterygoid and mesopterygoid than in the generalized state. This trend is most pronounced in *Ichthyborus* and the unit formed by *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* which have a reduced palatine fitting into a depression along the dorsal surface of the ectopterygoid and lacking the plesiomorphous ligamentous attachment to the maxilla.

Finally, it should be noted that the quadrate and palatine have been found to be separate in all *Paradistichodus* specimens examined, contrary to Daget (1968, Fig. 10) who illustrated these elements are fused.

In summary, derived characters in the suspensorium of the citharinids and distichodontids are:

1. the anterior position of the articulation of the angulo-articular and quadrate in all distichodontids other than *Xenocharax*, *Neolebias* and *Nannaethiops*.
2. the broadened hyomandibula in *Hemigrammocharax* and *Nannocharax*.
3. the slender, anteriorly concave hyomandibula in *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.
4. the dorsolateral and dorsomedial hyomandibular processes present in various distichodontids.
5. the groove on the posterior surface of the hyomandibula in *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.
6. the lateral horizontal preopercular shelf in all distichodontids other than *Xenocharax*, *Nannaethiops* and *Neolebias*. This shelf is most distinctly developed, both posteriorly and laterally, in *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.
7. the medial shift of the laterosensory canal segment in the vertical arm of the preopercle in *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. This assemblage, with the exception of *Ichthyborus*, is also characterized by the development laterally of a distinct posterodorsal preopercular flange.
8. the reduction or loss of the metapterygoid–quadrate fenestra in *Neolebias spilotaenia* and the unit formed by *Nannocharax* and *Hemigrammocharax*.
9. the elongate metapterygoid–quadrate fenestra of *Ichthyborus*, *Mesoborus*, *Microstomatichthyoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

10 the two large cartilage pads between the palatine and upper jaw of citharinids.
11 the increased attachment of the palatine and mesopterygoid to the neurocranium in distichodontids other than *Xenocharax*, *Neolebias*, *Nannaethiops* and *Paradistichodus*.
12 the loss of the ligamentous connection between the palatine and the maxilla in *Ichthyborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

Opercle

On the basis of outgroup comparisons, the plesiomorphous form of the opercle among characoids is hypothesized to be a flat and unfenestrated bone. Such an opercular form occurs in the distichodontid genus *Xenocharax*, but is variously modified in citharinids and all other distichodontids.

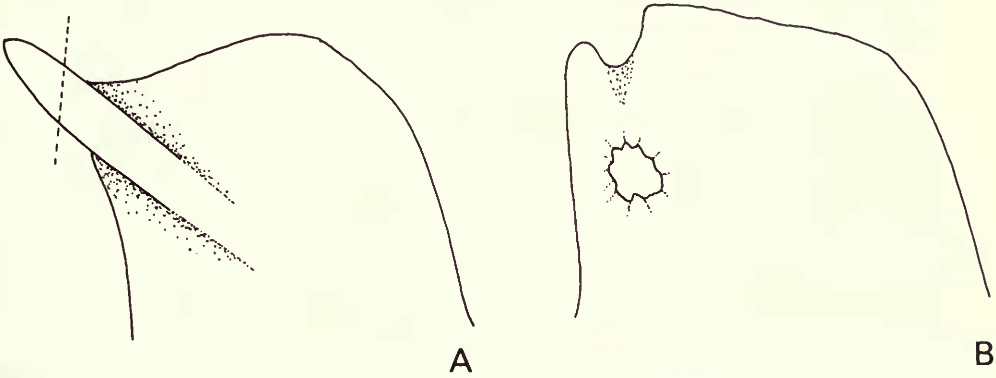

Fig. 19 Dorsal portion of the opercle of A. *Citharinus citharus* (dotted line denotes position of the suprapreopercle), B. *Distichodus notospilus*, left lateral view.

Laterally the opercle of *Citharinus* and *Citharidium* bears a prominent, anterodorsally oriented ridge aligned at an acute angle relative to the anterior border of the opercle (Fig. 19a). This ridge extends dorsally from the body of the opercle to the tip of the elongate anterodorsal corner of the bone. Such a lateral opercular ridge has not been encountered elsewhere among charcoids except in the Neotropical characoid family Curimatidae (Roberts, 1974). The opercular flange of curimatids differs, however, from that of citharinids in its less extensive vertical development, and in not extending to the anterodorsal edge of the bone.

Among distichodontids other than *Xenocharax*, the opercle undergoes a progressive fenestration. The simplest condition of this opening occurs in *Nannaethiops* and *Neolebias* which have a series of small, closely apposed holes extending through the opercle. These foramina, which are located slightly posterior to the facet for articulation with the hyomandibula, appear to be the precursors of the distinct opercular fenestra occupying this region in the remaining distichodontids with the exception of *Xenocharax* (Fig. 19b). As far as can be determined, neither this distinct fenestra nor the series of small openings in *Nannaethiops* and *Neolebias* serve for the passage of any nerves, blood vessels or muscle fibres. In *Hemigrammocharax* and *Nannocharax* the opercle is reduced dorsally with a consequent opening of the opercular fenestra to the dorsal margin of the bone. The resultant vertical slit separates the anterodorsal portion of the opercle, to which the *dilator operculi* muscles attach, from the posterodorsal plate-like portion of the bone. None of these forms of fenestrated opercle have been encountered elsewhere in characoids, or among the non-characoid ostariophysans examined. Consequently, these modifications are considered to represent apomorphous characters of varying levels of universality.

In summary, the hypothesized derived opercular characters among citharinids and distichodontids are:

1 the prominent lateral opercular ridge in citharinids.

2 the fenestrated opercle in all distichodontids other than *Xenocharax*. Three increasingly apomorphous forms of the opening occur in these genera:

(A) the series of small holes in *Nannaethiops* and *Neolebias*.

(B) the distinct fenestra of all distichodontids other than *Nannaethiops*, *Neolebias* and *Xenocharax*.

(C) the vertical slit along the dorsal margin of the opercle in *Nannocharax* and *Hemigrammocharax*.

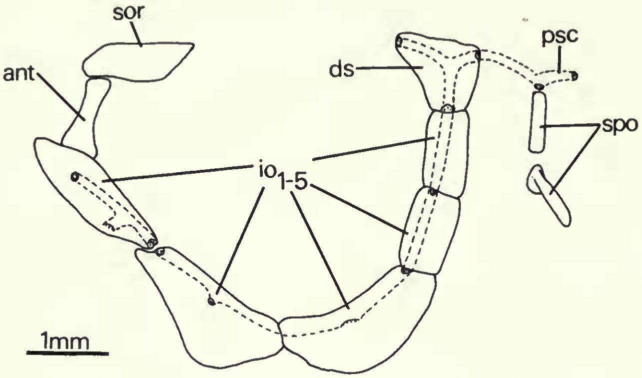

Fig. 20 *Xenocharax spilurus*, supraorbital, antorbital, infraorbitals, dermosphenotic, pterotic sensory canal and suprapreopercle, lateral view.

Dermosphenotic, pterotic and suprapreopercle

The general morphological diversity of the family Citharinidae and Distichodontidae is reflected in the overall structure and in the patterns of the sensory canals of the dermosphenotic, pterotic and suprapreopercle. Prior to a discussion of these characters, however, it is necessary to comment on the nomenclature of some of the sensory canal-bearing bones of the lateral edge of the skull. Daget, in a series of publications (1958–1968), distinguished the canal-bearing dermosphenotics and dermopterotics from the underlying sphenotics and pterotics. Similarly, Gregory (1933) and Gregory & Conrad (1938) illustrate a separate dermosphenotic in *Distichodus langi*, *Mesoborus* and *Phago*, and distinguish the scale bone (the dermopterotic of Daget) from the underlying pterotic.

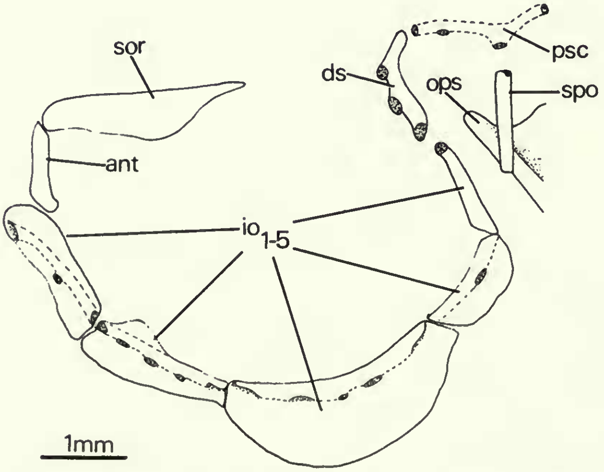

Fig. 21 *Citharidium ansorgei*, supraorbital, antorbital, infraorbitals, dermosphenotic, pterotic sensory canal and suprapreopercle, lateral view.

When present the dermosphenotic (or infraorbital 6) of characoids is independent throughout ontogeny from the underlying sphenotic. In light of such a separation, this element should obviously be recognized as a distinct bone, the dermosphenotic. However, in none of the characoids examined are the pterotic (*sensu stricto*) and the lateral canal-bearing element (Daget's dermopterotic and Gregory & Conrad's scale bone) separate elements. Neither has such a separation been reported in the literature for any adult characoid. Indeed, a separate dermopterotic is rare among teleosts (Patterson, 1977, p. 97). Although these elements arise independently from cartilaginous and intramembranous elements (Weitzman, 1962, p. 25) they fuse early in ontogeny and I will follow Weitzman in considering the resultant bone as a single unit, the pterotic. The pterotic in this sense is equivalent to the pterotic plus scale bone of Gregory & Conrad, and the pterotic plus dermopterotic of Daget.

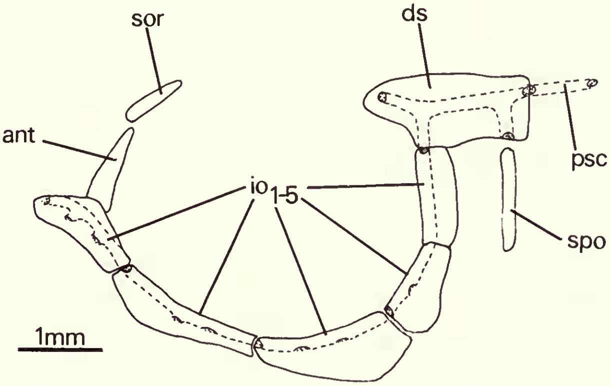

Fig. 22 *Paradistichodus dimidiatus*, supraorbital, antorbital, infraorbitals, dermosphenotic, pterotic sensory canal and suprapreopercle, lateral view.

Within the families Citharinidae and Distichodontidae four main patterns of the dermosphenotic and pterotic and of their relationships to the infraorbitals and supraperopercle can be discerned. On the basis of outgroup comparisons, the plesiomorphous form of these bones and the associated canals among characoids appears to be similar to that of *Xenocharax* (Fig. 20). The moderately sized dermosphenotic completely roofs over the dilatator fossa and carries a Y-shaped segment of the laterosensory canal system. The ventral segment of the dermosphenotic sensory canal communicates with that of the fifth infraorbital, the anterior branch with the supraorbital sensory canal of the frontal and the posterodorsal section with the pterotic sensory canal. The pterotic, in turn, is broadly exposed laterally and bears a trifurcate sensory canal system. The anterior branch of the pterotic sensory canal contacts the posterior portion of the dermosphenotic sensory canal, the posterior segment communicates with the extrascapular sensory canal, and the ventral branch receives the preopercular sensory canal by way of the suprapreopercle.

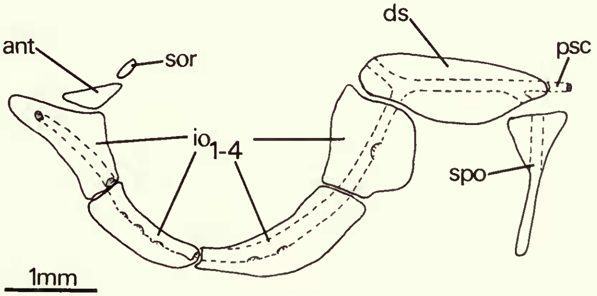

Fig. 23 *Ichthyborus besse*, supraorbital, antorbital, infraorbitals, dermosphenotic, pterotic sensory canal and suprapreopercle, lateral view.

The remaining genera in the families Citharinidae and Distichodontidae exhibit a series of apomorphous modifications of the above plan of these bones and sensory canals. *Citharinus* and *Citharidium*, although retaining the plesiomorphous sensory canal pattern, have greatly reduced the dermosphenotic into a tube-like element which no longer contacts the edges of the dilatator fossa and only partially covers the lateral surface of the *dilatator operculi* muscle (Fig. 21). In contradistinction, in all distichodontids other than *Xenocharax*, the dermosphenotic, when present, is posteriorly expanded relative to the hypothesized plesiomorphous condition. As a consequence of this expansion, the dermosphenotic overlaps much of the primitively exposed lateral surface of the pterotic and separates the suprapreopercle from its direct contact with the pterotic laterosensory canal system (see below with respect to *Nannaethiops* and *Neolebias*).

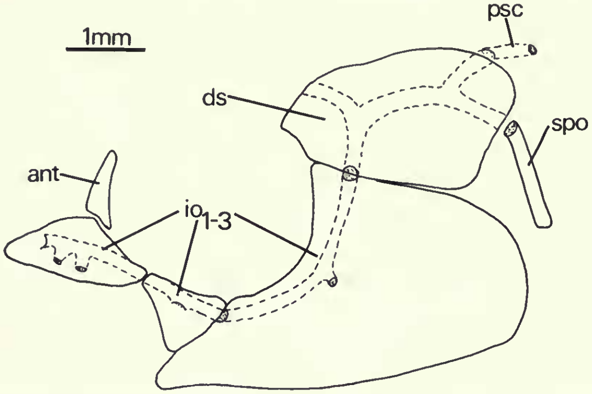

Fig. 24 *Phago intermedius*, antorbital, infraorbitals, dermosphenotic, pterotic sensory canal and suprapreopercle, lateral view.

This shift of the contact of the suprapreopercle and the expansion of the dermosphenotic results in a marked change in the sensory canal system in these bones. Whereas the dermosphenotic sensory canal is bifurcate anteriorly as in *Xenocharax*, the posterior branch of the canal is drawn out along the horizontally elongate dermosphenotic and bifurcates posteriorly (Figs 22, 23, 24). As a consequence the posteroventral branch of the canal contacts the dorsal tip of the suprapreopercle while the posterodorsal segment communicates with the pterotic sensory canal. This expansion of the dermosphenotic sensory canal results in a horizontally elongate, somewhat H-shaped system. Outgroup comparisons among characoids have failed to reveal a comparable posterior expansion of the dermosphenotic. Neither have there been discovered any other characoids in which the dermosphenotic directly communicates both with the infraorbital and preopercular sensory canal systems. Furthermore, the reduced lateral exposure of the pterotic and the shift in the contact of the suprapreopercle has resulted in a pronounced reduction of the pterotic sensory canal segment. Rather than the plesiomorphous Y-shaped system of most characoids, in these genera the pterotic laterosensory canal is a simple, short tube joining the dermosphenotic and the extrascapular sensory canals. Such a reduction is particularly pronounced in *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* in which the laterally exposed portion of the pterotic is a small wedge of bone between the rear of the dermosphenotic and the margin of the extrascapular.

Autapomorphous modifications of the above form of dermosphenotic and of the associated laterosensory canals characterize several subunits of the assemblage having this pattern of these bones. In *Ichthyborus* the dermosphenotic is shifted posterodorsally and thus is totally removed from the orbital rim. This shift, along with the dorsal elongation of the suprapreopercle in this genus, is reflected in the posteroventral reduction of the dermosphenotic and in the shortening of the posterodorsal and posteroventral portions of the dermosphenotic sensory canal system (Fig. 23). In *Paraphago*, in contrast, the dermosphenotic is somewhat expanded ventrally. This expansion is a precursor of the markedly expanded dermosphenotic in *Phago* and *Belonophago* where the large plate-like bone extends ventrally midway along the posterior rim of the orbit (Fig. 24). The enlarged dermosphenotic of *Belonophago* is autapomorphously further modified by the total loss of its sensory canal system.

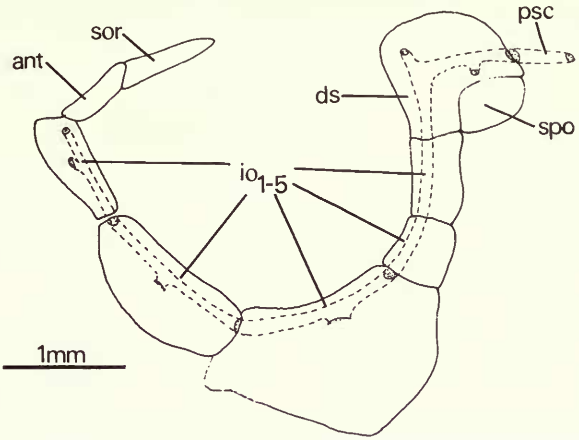

Fig. 25 *Nannaethiops unitaeniatus*, supraorbital, antorbital, infraorbitals, dermosphenotic, pterotic sensory canal and suprapreopercle, lateral view.

The monophyletic unit formed by *Nannaethiops* and *Neolebias* is characterized by a progressive apomorphic reduction of the dermosphenotic and pterotic sensory canals common to distichodontids other than *Xenocharax*. The least pronounced reduction is found in *Nannaethiops unitaeniatus* (Fig. 25) which has a slight shortening of the posteroventral branch of the dermosphenotic sensory canal. The reduction of this canal segment, which primitively communicates with the suprapreopercle, is congruent with the loss of the suprapreopercular sensory canal in *Nannaethiops* and *Neolebias* (see discussion on the suprapreopercle). The dermosphenotic, pterotic and their sensory canals in *Neolebias unifasciatus* (see Daget, 1965, Fig. 7) and *N. trewavasae* are similar to that of *Nannaethiops* other than for the pronounced reduction or loss of the anterodorsal and posterodorsal branches of the dermosphenotic sensory canal system. Apomorphic reduction of the dermosphenotic laterosensory canals is further advanced in *N. trilineatus*, *N. bidentatus* and *N. axelrodi* where the sensory canals of the dermosphenotic and pterotic are totally lacking. This reductional trend reaches its terminal stage in *N. spilotaenia* in which the dermosphenotic is lost, together with that portion of the pterotic which plesiomorphously carries the pterotic sensory canal segment. These progressive reductions of the dermosphenotic sensory canals and the eventual loss of the bone itself are considered to be a series of derived characters of decreasing levels of universality (see the Phylogenetic analysis).

The marked modifications of the dermosphenotic and pterotic described above appear to have resulted in several misinterpretations of distichodontid skull osteology by Gregory & Conrad. In their figure of the skull of *Phago* (1938, Fig. 35) those authors illustrate the dermosphenotic and pterotic as part of a single ossification. The bone indicated is, however, the dermosphenotic which almost totally overlaps the pterotic in this genus. The exposed portion of the pterotic is actually the small scale bone of those workers. The same authors in their drawing of the skull of *Mesoborus* (1938, Fig. 34), show an unlabelled dermosphenotic which incorporates the sensory canals of the pterotic and extrascapular along its posterodorsal margin. Examination of this species, however, shows that these sensory canals are actually separate tubes in their respective bones.

In the course of the above discussion, it was noted that the preopercular sensory canal of citharinids and distichodontids communicates with the sensory canal system of the pterotic or expanded dermosphenotic by way of an ossified suprapreopercle. Such a canal-bearing suprapreopercle or a derived form of the bone is common to all citharinids and distichodontids other than some *Neolebias* species in which it is hypothesized to be secondarily lost (see below). The possession of a suprapreopercle would appear apomorphous in characoids although occurring in a variety of ostariophysan groups. Despite the uncertainty on the exact distribution of this element and on the interrelationships of the groups possessing it, at the least, the common possession of this element is congruent with the hypothesized monophyletic nature of the unit formed by the families Citharinidae and Distichodontidae. In its simplest form the suprapreopercle is a bony tube extending from the dorsal opening of the preopercular sensory canal to the sensory canal system of the pterotic or dermosphenotic. Such a suprapreopercular form, which represents an ossification of the primitively unossified tube joining these systems, is modified in the Citharinidae and subunits of the Distichodontidae.

In *Citharinus* and *Citharidium* the elongate tube-like suprapreopercle extends over the lateral surface of the anterodorsal corner of the opercle (Fig. 21). Such a transversing of the opercle by the suprapreopercle has not been encountered elsewhere among characoids examined and thus appears autapomorphous for these genera. Among distichodontids the plesiomorphous tubular suprapreopercle is modified in several distinctive apomorphous modes. The simplest of these adaptations occurs in *Ichthyborus besse* where the suprapreopercle bears anterodorsal and posterodorsal flanges that give it a somewhat triangular form (Fig. 23). In *Xenocharax*, in contrast, the suprapreopercle retains its basically tubular shape, but is subdivided horizontally into two short tubes (Fig. 20). The remaining and most radical restructuring of the suprapreopercle occurs in *Nannaethiops* and *Neolebias*. As illustrated in Fig. 25 for *Nannaethiops unitaeniatus* these genera have an independent ossification fitting the posteroventrally concave border of the dermosphenotic (see also Daget, 1965, Fig. 7). Although it carries no sensory canal segment, this independent ossification is hypothesized to represent a highly modified suprapreopercle. Such an hypothesis is congruent with its location in the region primitively occupied by the plesiomorphous tubular suprapreopercle. Furthermore, this element contacts the posteroventral dermosphenotic sensory canal segment which plesiomorphously communicates with the suprapreopercle. In light of this association and the relative position of the element, it is most parsimonious to assume that this plate-like, non-canal-bearing element is homologous with the tubular suprapreopercle of citharinids and other distichodontids. This flattened suprapreopercle is lost, evidently secondarily, in *Neolebias spilotaenia* which is characterized by an extreme reduction of various dermal elements of the skull.

Daget, in his illustration of *Neolebias unifasciatus* (1965, Fig. 7), identified the element herein considered the suprapreopercle as an infraorbital (the postorbital of Daget). It would appear that Daget believed this bone to be a posteriorly shifted fourth or fifth infraorbital. Such an homology would give a full series of five infraorbitals plus the dermosphenotic for the species. However, the identification of this independent ossification as an infraorbital appears erroneous if we examine the infraorbital series of *Neolebias trewavasae* and *Nannaethiops unitaeniatus* (Fig. 25). These species, which have the infraorbital reductional trends characteristic of these genera least pronounced, retain a full series of infraorbitals in addition to the independent ossification termed an infraorbital by Daget. In light of this condition and the previously discussed information indicating that the independent ossification is a modified suprapreopercle, the identification of the element as an infraorbital is herein considered incorrect.

Hypothesized apomorphic states of the dermosphenotic, pterotic, suprapreopercle and their associated sensory canals among citharinids and distichodintids are:

1 the reduced tubular dermosphenotic of citharinids.
2 the posterior expansion of the dermosphenotic in all distichodontids other than *Xenocharax*. These genera have a congruent reduction of the laterally exposed portion of the pterotic and a shift of the contact of the suprapreopercular sensory canal to the dermosphenotic.
3 the posterodorsal shift of the dermosphenotic in *Ichthyborus*.
4 the ventral expansion of the dermosphenotic in *Paraphago*, *Phago* and *Belonophago*. This expansion is particularly pronounced in the last two genera.
5 the loss of the dermosphenotic sensory canal system in *Belonophago*.

6 the progressive reduction of the dermosphenotic and pterotic sensory canal systems in *Nannaethiops* and *Neolebias*.
7 the suprapreopercle common to citharinids and distichodontids.
8 the subdivision of the suprapreopercle in *Xenocharax*.
9 the extension of the suprapreopercle across the opercle in citharinids.
10 the modification of the dermosphenotic into a flat, non-canal-bearing plate in *Neolebias* and *Nannaethiops*.

Supraorbital and infraorbitals

The hypothetical plesiomorphous infraorbital series for characoids consists of a chain of six canal-bearing bones (a dermosphenotic and five infraorbitals) which, together with the supraorbital, form a bony rim to the orbit. The modifications of the dermosphenotic (infraorbital 6) and its associated sensory canals were discussed in the previous section. Reductions, expansions and losses of the supraorbital, infraorbitals 1 to 5 and the infraorbital sensory canal system characterize subunits of varying levels of universality among distichodontids.

A large supraorbital forming the anterodorsal portion of the orbital rim is common to *Citharinus* and *Citharidium* (Fig. 21). Although somewhat enlarged relative to that of many characoids, the citharinid form of supraorbital nonetheless appears to be plesiomorphous among citharinids and distichodontids in forming a large portion of the anterodorsal rim of the orbit and in extending beyond the posterior margin of the lateral ethmoid. The distichodontid genera *Xenocharax* (Fig. 20), *Nannaethiops*, *Neolebias*, *Paradistichodus* (Fig. 22), *Distichodus*, *Nannocharax*, *Hemigrammocharax*, *Hemistichodus* and *Ichthyborus* (Fig. 23) differ from citharinids and the generalized characoid condition in having an anteriorly shifted supraorbital which is variously reduced. The remaining distichodontid genera, in turn, have the supraorbital totally lacking, a loss that is considered apomorphous within distichodontids (in *Neolebias spilotaenia*, a supraorbital ossification was found only in the largest specimens examined). Although David & Poll's illustration (1937, Fig. 9) of the jaws and dermal bones of the anterior portion of the head of *Microstomatichthyoborus bashforddeani* and *M. katangae* includes a prominent 'supraorbital', examination of these species has shown that those 'supraorbitals' are actually the antorbitals.

Subunits of the Distichodontidae also differ in the total number of infraorbitals, their relative sizes and the extent of the infraorbital sensory canal system. Three different types of reduction from a full series of five canal-bearing infraorbitals are discernable in different subunits of the family (see the previous section for a discussion of the variation in the dermosphenotic, infraorbital 6). Two of these reductions result in a partially unossified orbital rim, while the third retains a continuous infraorbital series.

The first of these modifications to be discussed is the progressive reduction of the infraorbital series within the genus *Neolebias*. *Neolebias trewavasae* has a full series of five infraorbitals, with two elements (infraorbitals 4 and 5) forming the posterior rim of the orbit. In *N. unifasciatus* and *N. bidentatus*, in contrast, there is only a single infraorbital at the rear of the orbit, with the remaining elements shifted so as to retain a fully ossified orbital rim (see Daget, 1965, Fig. 7). The remaining infraorbital at the posterior margin of the orbit is lost in *N. trilineatus*, *N. ansorgei*, *N. axelrodi* and *N. spilotaenia* in which the posterior orbital border is unossified. This reductional trend reaches its terminal stage in *N. spilotaenia* which additionally lacks infraorbitals 2 and 3 and the sensory canal segment in infraorbital 1. The progressive reduction of the infraorbital series from a chain of five canal-bearing elements to a single non-canal-bearing bone is considered to represent a series of derived reductional characters of varying levels of universality, and is congruent with the overall reduction of the dermal skull elements in these genera.

The second reduction of the infraorbital series among distichodontids occurs in *Nannocharax* and *Hemigrammocharax*. In *Nannocharax multifasciatus*, *N. fasciatus* (Daget, 1961, Fig. 7) and *Hemigrammocharax wittei* the fourth and fifth infraorbitals are reduced to two bony tubes dorsal to an expanded third infraorbital. In contrast, the specimens of *Nannocharax niloticus*, *N. ansorgei*, *N. gobioides*, *N. intermedius*, *Hemigrammocharax machadoi* and *H. polli* examined have infraorbitals 4 and 5 totally lacking. Although this reduction results in an unossified posterior orbital border similar to that in some *Neolebias* species, the phylogenetic sequence of the reductions and losses leading up to this condition differ significantly from that in *Neolebias*. Consequently, the unossified posterior orbital rim in the listed *Nannocharax* and *Hemigrammocharax* species and that of the previously noted *Neolebias* species are considered to be non-homologous.

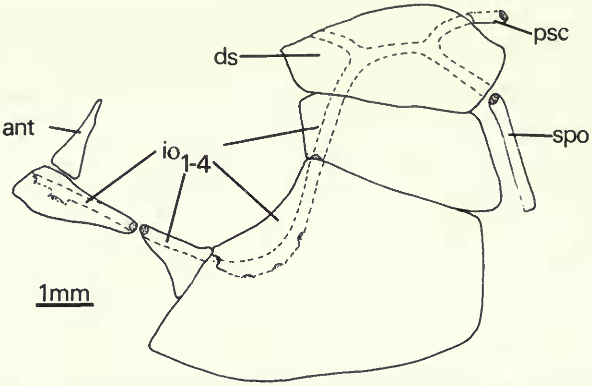

Fig. 26 *Eugnatichthys eetveldii*, antorbital, infraorbitals, dermosphenotic, pterotic sensory canal and suprapreopercle, lateral view.

The final reductional transition series of the infraorbitals among distichodontids occurs within the assemblage consisting of *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. Contrary to the hypothesized plesiomorphous condition of an infraorbital series with five elements, these genera are characterized by a maximum of four infraorbitals. This reduced infraorbital count appears to be a consequence of the loss of an infraorbital at the posterior margin of the orbit. The exact homology of the remaining element, that is whether it represents the plesiomorphous infraorbital 4, infraorbital 5 or a fusion of these bones, is uncertain. However, for simplicity in the following discussion the bone is arbitrarily termed infraorbital 4. Within this assemblage, *Ichthyborus* (Fig. 23) has a relatively narrow infraorbital series, but with infraorbital 4 expanded posterodorsally so as to separate distinctly the dermosphenotic from the orbital rim. In contrast, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys* (Fig. 26), *Paraphago*, *Phago* (Fig. 24) and *Belonophago* have the posterior infraorbital elements widened, with infraorbital 3 expanded posteriorly so as to cover a major portion of the cheek. Anteroventrally infraorbital 3 is produced into a distinct process extending ventral to infraorbital 2 and almost to the vertical through the articular condyle of the quadrate. Within this assemblage *Paraphago* has the fourth infraorbital reduced to a narrow, horizontally elongate element and it is completely lacking in *Phago* (Fig. 24) and *Belonophago*. As a consequence of these changes the enlarged third infraorbital of *Phago* and *Belonophago* completely covers the cheek and is in direct contact dorsally with the expanded dermosphenotic. Among members of these families, the enlarged third infraorbital in *Belonophago* is also unique in its total lack of a sensory canal segment. The loss of infraorbitals 4 and 5 in these genera differs from that among the previously described *Neolebias*, *Nannocharax* and *Hemigrammocharax* species in that the expansion of the remaining infraorbitals fills the space primitively occupied by the missing elements, and a fully ossified orbital rim is thus retained.

Two differences between the observations of this study and those of Gregory & Conrad (1938) and Daget (1968) should be noted. In their illustration of the skull of *Mesoborus*, Gregory & Conrad (1938, Fig. 34) show a single infraorbital (the suborbital of those authors) in the region plesiomorphously occupied by infraorbitals 1 and 2. However, examination of the specimen probably illustrated by those workers, along with other *Mesoborus* material, shows there to be two distinct infraorbitals preceding the expanded infraorbital 3. Similarly, Daget (1968, Fig. 4) in his illustration of the skull of *Hemistichodus vaillanti* shows a single large infraorbital in the region normally occupied by infraorbitals 2 and 3. However, all specimens of the three nominal *Hemistichodus* species examined have the second and third infraorbitals as separate elements.

In summary, hypothesized apomorphous supraorbital and infraorbital characters among distichodontids are:

1 the reduction and anterior shift of the supraorbital in *Xenocharax*, *Nannaethiops*, *Neolebias*, *Paradistichodus*, *Distichodus*, *Nannocharax*, *Hemigrammocharax* and *Ichthyborus*. This reduction is a precursor of the further apomorphous loss of the element in *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

2 the reduction to a single infraorbital at the rear of the orbit in *Neolebias unifasciatus* and *N. bidentatus*, with the remaining element lost in *N. trilineatus*, *N. ansorgei*, *N. axelrodi* and *N. spilotaenia*.

3 the loss of infraorbitals 2 and 3 and the sensory canal of infraorbital 1 in *N. spilotaenia*.

4 the reduction of infraorbitals 4 and 5 to bony tubes or a loss of these elements in *Nannocharax* and *Hemigrammocharax*.

5 the loss of infraorbital 5 in *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

6 the expansion of infraorbital 4 to exclude the dermosphenotic from the orbital rim in *Ichthyborus*.

7 the reduction of infraorbital 4 in *Paraphago* and its loss in *Phago* and *Belonophago*.

8 the loss of the sensory canal segment of infraorbital 3 in *Belonophago*.

9 the anterior and posterior expansion of infraorbital 3 in *Microstomatichthyoborus*, *Eugnatichthys*, *Mesoborus*, *Paraphago*, *Phago* and *Belonophago*.

Branchial apparatus

The morphology of the branchial apparatus among members of the families Citharinidae and Distichodontidae demonstrates a significant degree of variation for a system that is otherwise rather stable among characoids. Major branchial apparatus modifications occur in *Citharinus* and *Citharidium*, whereas less pronounced adaptations distinguish various distichodontid subunits.

The fifth ceratobranchial (lower pharyngeal) of citharinids is highly modified with respect to the relatively flat, anteromedially tooth-bearing elements common to most characoids. In *Citharinus* and *Citharidium* the medial portion of the fifth ceratobranchial is a dorsally bulbous, highly fenestrated structure bearing only a few greatly reduced, loosely attached teeth (Fig. 27). These genera also demonstrate a comparable reduction and modification of the upper pharyngeal tooth plates and their associated dentition. Among most characoids, the fourth epibranchial and cartilaginous fourth pharyngobranchial articulate with the tooth-bearing fourth and fifth upper pharyngeal tooth plates respectively (see Rosen, 1973, Fig. 3). In contradistinction, citharinids either have the upper pharyngeal dentition totally lacking or reduced to a few loosely-attached minute spicules. More significantly, the fourth and fifth upper pharyngeal tooth plates of citharinids are fused to form an elongate bony plate (Fig. 28). Such a distinctive upper pharyngeal ossification has not been encountered elsewhere among characoids and would appear to be apomorphous, as is its edentulous nature. Similarly, the highly modified lower pharyngeals of *Citharinus* and *Citharidium* are, as best as can be determined, autapomorphous for these genera among characoids. Further apomorphic characters in the branchial apparatus of citharinids include their loss of the first pharyngobranchial and the elongation and reorientation of the second and third pharyngobranchials. These alterations result in a close approximation of the tips of the first epibranchial and the second and third pharyngobranchials.

The marked restructuring of the branchial apparatus among citharinids would seem to be an adaptation to their filter-feeding mode of life. An additional gill arch character congruent with this feeding method is the presence of micro-gillrakers in all citharinids. Micro-gillrakers are a series of parallel bands of small, bony spicules located along both faces of the gill arch between the gillrakers and gill filaments (Gosse, 1956; Daget, 1962). On the basis of our present knowledge on micro-gillraker distribution, it appears that these structures are unique to citharinids among characoids.

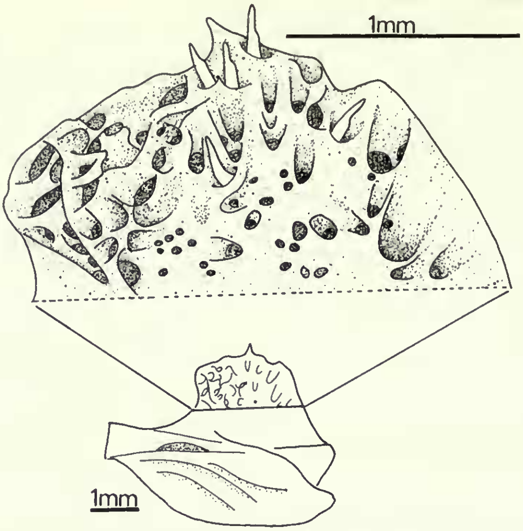

Fig. 27 *Citharidium ansorgei*, fifth ceratobranchial, right side, medial portion enlarged, dorsal view.

Alterations of the branchial apparatus among distichodontids are not as radical as those in citharinids and are primarily reductional. In most *Neolebias* species the fourth upper pharyngeal tooth plate is slightly ossified, with this element and its associated dentition totally lacking in *N.* spilotaenia (Fig. 29). Furthermore, in *N. spilotaenia* the fifth upper pharyngeal tooth plate is a reduced rounded ossification bearing approximately only six teeth. Similarly, the tooth-bearing portion of the lower pharyngeals is reduced to a small ovoid patch with a correlated reduction in the number of teeth.

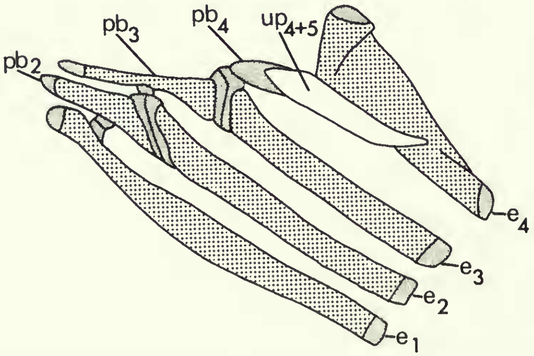

Fig. 28 *Citharidium ansorgei*, gill arches, dorsal parts of right side, ventral view.

An ossified fourth upper pharyngeal tooth plate and its associated dentition is also lacking in *Hemigrammocharax machadoi*, *Nannocharax fasciatus* and *N. niloticus*. However, based on the most parsimonious reconstruction of the phylogeny of citharinids and distichodontids, this loss is considered to have occurred independently of that in *Neolebias*. Furthermore, it is noteworthy that the lack of a fourth upper pharyngeal tooth plate is not universal within *Nannocharax*. *Nannocharax intermedius* has a small, slightly ossified fourth upper pharyngeal tooth plate, whereas *N. gobioides* and *N. ansorgei* have a larger but still reduced form of the bone. The resolution of the question of whether this variation in the extent of the ossification of this element represents a phylogenetic reductional trend within the genus or whether it is a function of ontogenetic variation awaits further study.

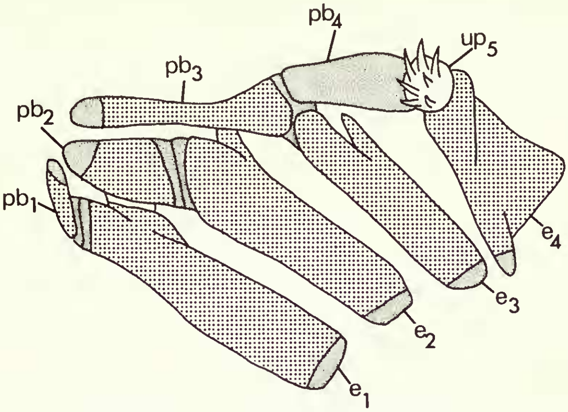

Fig. 29 *Neolebias spilotaenia*, gill arches, dorsal parts of right side, ventral view.

Among the remaining distichodontid genera no alterations of branchial apparatus structure have been found. However, congruent with their restructured neurocranial form, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* have a posterior shift in the attachment of the suspensory pharyngeals to the neurocranium. Within this assemblage *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* have an additional shift of this attachment ventrally, a trend that is most pronounced in the latter four genera where the pharyngeal attachment is to the previously described median parasphenoid ridge. It would appear that these shifts of gill arch attachment in these genera are a function of the extension of the *adductor mandibulae* muscle onto the medial surface of the hyomandibula and its expansion into regions plesiomorphously occupied by the branchial apparatus.

In summary, hypothesized derived states of the branchial apparatus among citharinids and distichodontids are:

1. the highly fenestrated, dorsally bulbous, nearly edentulous lower pharyngeal in citharinids.
2. the fusion of the fourth and fifth upper pharyngeal tooth plates in citharinids.
3. the loss of the first pharyngobranchial and the anterior elongation of the second and third pharyngobranchials in citharinids.
4. the loss of the fourth upper pharyngeal tooth plate and its associated dentition in *Neolebias spilotaenia*. This species also demonstrates a reduction of the fifth upper pharyngeal tooth plate and of the dentition associated with that element and the fifth ceratobranchial.
5. the micro-gillrakers in citharinids.
6. the reduction or loss of the fourth upper pharyngeal tooth plate in various *Nannocharax* and *Hemigrammocharax* species.
7. the posterior shift of the attachment of the suspensory pharyngeals in *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.
8. the ventral shift of the suspensory pharyngeals onto the median parasphenoid ridge in *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

Weberian apparatus

The common possession of the Weberian apparatus, an otophysic connection between the anterior chamber of the swimbladder and the middle ear, characterizes the series Otophysi of the superorder Ostariophysi (Rosen & Greenwood, 1970). The Weberian apparatus is composed of the Weberian ossicles (the pars auditum) and their supporting vertebrae (the pars sustentaculum). The Weberian ossicles are four small bones, the tripus, intercalarium, scaphium and claustram (the intercalarium and claustrum are lacking in some groups), that are joined by ligamentous bands and pivot on the anterior vertebrae. It is believed that vibrations induced in the anterior chamber of the swimbladder by soundwaves in the surrounding medium are transmitted by these ossicles to the middle ear, thereby aiding in sound reception (see Alexander, 1966, for a discussion of the mechanism). The pars sustentaculum is derived from the four or more anterior vertebrae and serves as a base for the Weberian ossicles and the shortened first pleural rib. In the generalized characoid condition the vertebrae of the pars sustentaculum are ventrally unfused and unmodified, with the fourth vertebrae bearing a pair of shortened, modified pleural ribs. Arising from the medial surface of each of these ribs is a distinct process, the os suspensorium, which serves for the support and attachment of the peritoneal layer of the anterior swimbladder chamber. The dorsal aorta, which is in contact with the ventral surface of these vertebrae, is surrounded laterally and to varying degrees ventrally by the shortened first pleural rib and os suspensorium.

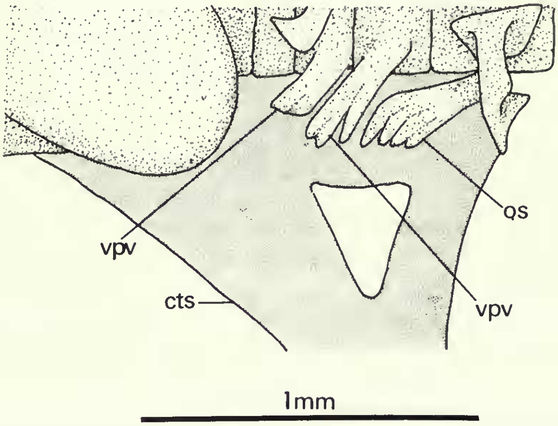

Fig. 30 *Nannaethiops unitaeniatus*, posteroventral section of neurocranium, ventral portion of pars sustentaculum and connective tissue sheath, left lateral view, Weberian ossicles removed.

All characoids examined have a triangular connective tissue system associated with the pars sustentaculum, the anterior section of the coeliac artery and the peritoneal covering of the anterior chamber of the swimbladder. This complex (Fig. 30) arises anterodorsally from the parasphenoid and basioccipital and posterodorsally from the os suspensorium. Dorsally it encompasses the dorsal aorta and anteriorly surrounds the anterior portion of the coeliac artery. The posterior section of this complex is formed by a medial thickening in the peritoneal covering over the anterior swimbladder chamber. This connective tissue band extends from the os suspensorium to the point of contact of the coeliac artery with the anterodorsal surface of the swimbladder chamber. Alexander (1962) applied the term 'coeliac sheath' to that portion of the system encompassing the coeliac artery in the Neotropical characoid genus *Leporinus*. In the following discussion, however, the term sheath is applied to the entire complex, unless a specific section (e.g. coeliac sheath) is cited.

Although the Weberian apparatus, particularly portions of the pars sustentaculum, undergoes pronounced restructuring in various ostariophysan groups (see Alexander, 1962, 1964*a*, 1964*b*) it has been traditionally considered morphologically conservative among characoids. However, an examination of the Weberian apparatus in the families Citharinidae and Distichodontidae has revealed a series of modifications of the pars sustentaculum, os suspensorium and of their relationships to the connective tissue sheath. Four major types of modifications to this complex are distinguishable in these families. These are hereafter termed the *Nannaethiops*, *Citharinus*, *Xenocharax* and *Nannocharax* types of pars sustentaculum.

Nannaethiops possesses the simplest form of modification to the pars sustentaculum and os suspensorium in the families Citharinidae and Distichodontidae. In the *Nannaethiops* type pars sustentaculum (Fig. 30) the second and third vertebrae bear paired, ventrally-directed projections arising from their ventrolateral borders, contrary to the plesiomorphous, ventrally unelaborated state of these bones. Furthermore, the os suspensorium in *Nannaethiops* is enlarged and extends anteriorly to contact the posterior margin of the ventral process of the third vertebra. The ventral projections of the second and third vertebrae, together with this anterior process of the os suspensorium, form a longitudinally orientated vertical wall lateral to the dorsal aorta. This structure also serves as a broad area of attachment for the connective tissue sheath associated with the dorsal aorta and coeliac artery. Such adaptations, either in the *Nannaethiops* form or further derived states, are common to all species of the families Citharinidae and Distichodontidae. On the basis of their unique nature within characoids these modifications are hypothesized as being synapomorphous for these families.

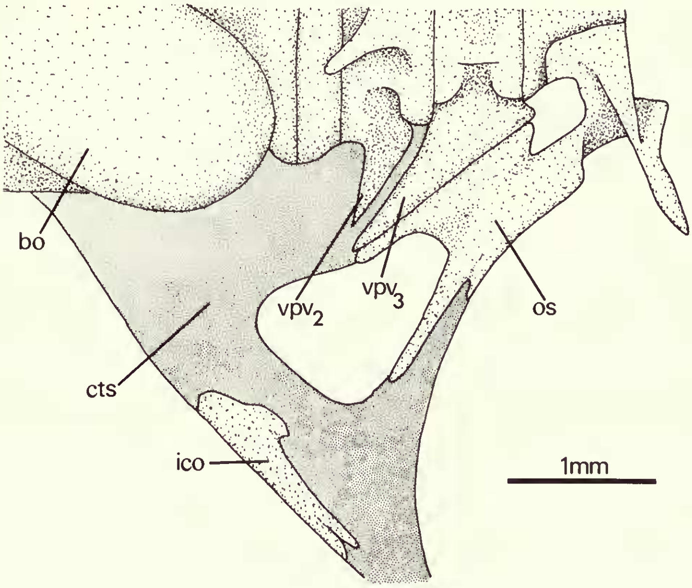

Fig. 31 *Citharinus citharus*, juvenile, posteroventral section of neurocranium, ventral portion of pars sustentaculum, connective tissue sheath and independent coeliac ossifications, left lateral view, Weberian ossicles removed.

As noted previously, the *Nannaethiops* type of pars sustentaculum and os suspensorium is the ontogenetic precursor of more complex structures in citharinids and some other distichodontids. One of the more elaborate alterations of this system is common to *Citharinus* and *Citharidium*. In the smallest individuals of *Citharinus* examined, the pars sustentaculum is similar to the *Nannaethiops* type other than for the slightly more anteroventrally expanded os suspensorium and a pair of slight ossifications along the anterior surface of the coeliac sheath. Later in ontogeny, juveniles of *Citharinus* and *Citharidium* possess the pars sustentaculum and os suspensorium form illustrated in Fig. 31. The ventral processes of the second and third vertebrae are more anteroventrally produced than in the *Nannaethiops* pattern or earlier in ontogeny. Similarly, the os suspensorium is anteroventrally expanded into a prominent, ventrally-directed process that partially encompasses the connective tissue band on the anteromedial surface of the swimbladder. The os suspensorium is also expanded anterodorsally to surround the lateral surface of the dorsal aorta and tightly contact the rear of the expanded ventral process of the third vertebrae

Finally, the coeliac sheath is encompassed anteroventrally by a prominent ossification derived from the independent ossifications present earlier in ontogeny.

With increasing age the os suspensorium, the ventral process of the second and third vertebrae and the independent ossifications of the coeliac sheath coalesce with each other and with the posterior projections of the parasphenoid and ventral projections of the basioccipital. In large individuals of *Citharinus* and *Citharidium* this results in a triangular, highly ossified structure which corresponds in shape to, and largely replaces, the connective tissue sheath present earlier in ontogeny (Fig. 32). This complex is anteriorly continuous with the elongate posterior ramus of the parasphenoid and encompasses the dorsal aorta laterally, ventral to the first three vertebrae.

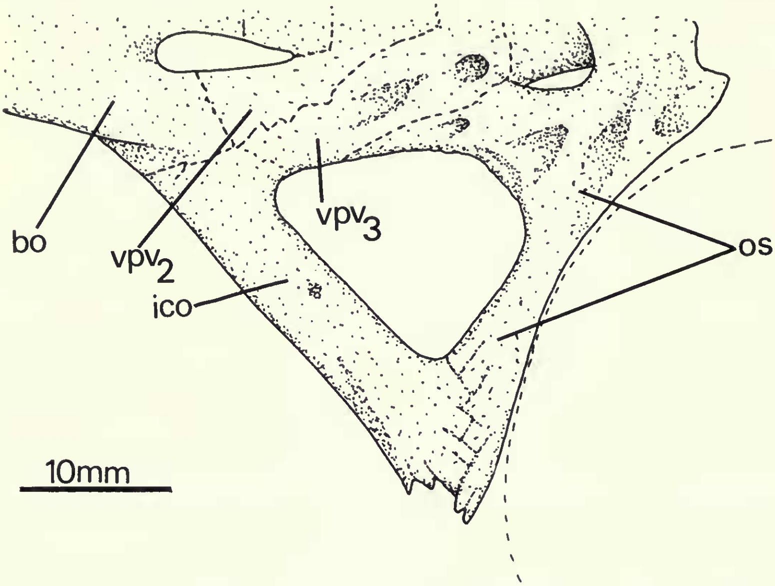

Fig. 32 *Citharinus citharus*, adult, posteroventral section of neurocranium and ventral portion of pars sustentaculum complex, left lateral view, Weberian ossicles removed. The dotted line indicates the position of the anterior chamber of the swimbladder.

Similarly, the coeliac artery is surrounded laterally and ventrally from its divergence from the dorsal aorta to its point of contact with the peritoneal covering of the anterior chamber of the swimbladder. Posteriorly the third portion of this structure consists of a thick bony strut formed by a ventral projection of the os suspensorium. This portion of the complex serves as an expanded area of attachment for the peritoneal layer covering the anterior swimbladder chamber. These modifications of the pars sustentaculum and os suspensorium, together with the strong attachment of the neural process of the Weberian apparatus to the supraoccipital, eliminate any possibility of motion, either between the vertebrae forming the pars sustentaculum or between the pars sustentaculum and the skull. With increasing age, these ossifications expand further so that in the largest citharinid examined (a skull of *Citharinus citharus*, 170 mm from snout to rear of the fourth vertebrae) the processes surrounding the dorsal aorta and coeliac arterly are nearly in contact with their fellows along the internal midline of the complex.

Examination of the Weberian apparatus in characoid outgroups has failed to reveal modifications homologous to those of citharinids, nor have such adaptations been encountered among other ostariophysans. An analogous envelopment of the dorsal aorta and coeliac sheath has been found in the Neotropical characoid genera *Anostomus*, *Leporinus*, *Schizodon* and *Laemolyta*. In these genera the parasphenoid bears posteriorly-directed processes which laterally encompass the dorsal aorta ventral to the basioccipital and first vertebra. In large individuals of these genera, these parasphenoid processes extend posteroventrally along the lateral surface of the strongly developed coeliac sheath, and an independent ossification overlies the dorsal aorta laterally under the first three vertebrae. Although similar in superficial form to those of citharinids, these ossifications in anostomids differ in their ontogenetic origins and are thus considered non-homologous with those of citharinids although synapomorphous for some or all anostomids.

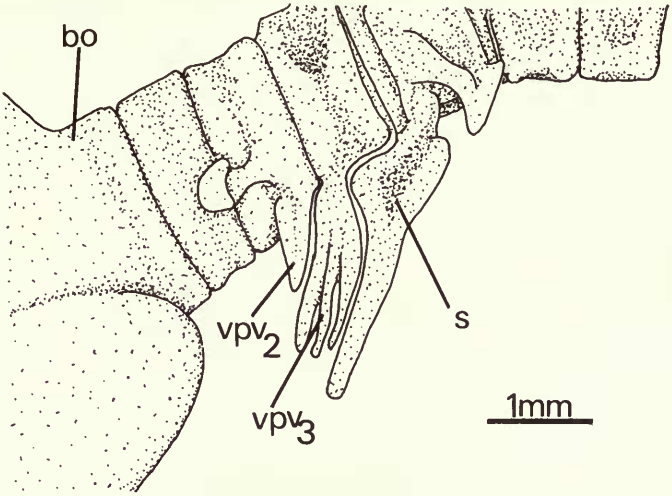

Fig. 33 *Xenocharax spilurus*, posteroventral section of neurocranium and ventral portion of pars sustentaculum, left lateral view, Weberian ossicles removed.

The second apomorphous modification of the *Nannaethiops* type of pars sustentaculum and os suspensorium occurs in the monotypic distichodontid genus *Xenocharax*. In this species the longitudinal axis of the first four vertebrae is strongly angled posterodorsally with respect to the skull and anteroventrally relative to the longitudinal axis through the remaining abdominal vertebrae (Fig. 33). The shift in the axis of these vertebrae is reflected in two adaptations. Firstly, the axis through the chain of the Weberian ossicles is nearly horizontal in *Xenocharax*, rather than demonstrating the posteroventral slope generalized for characoids. This shift is, however, a consequence of the reorientation of the anterior vertebrae with respect to the skull, rather than a repositioning of the ossicles relative to the pars sustentaculum. The second adaptation of the *Xenocharax* os suspensorium is consequent upon the retention by this genus of the primitive relationship of the os suspensorium and the anterior chamber of the swimbladder. Due to the reorientation of the pars sustentaculum with respect to the vertebral column, this alignment represents a marked decrease in the angle between the axis of the os suspensorium and that of the longitudinal axis of the vertebrae of the pars sustentaculum. This alteration is of sufficient magnitude so that the ventral tip of the os suspensorium extends to below the first or second vertebrae. This contrasts to the generalized characoid condition where it reaches only to below the third vertebra.

The fourth and final form of pars sustentaculum among citharinids and distichodontids occurs in some *Nannocharax* species. The species of this genus range from moderately deep-bodied, generalized forms such as *N. multifasciatus*, *N. ansorgei* and *N. minutus* to ventrally-flattened, bottom-dwelling species such as *N. brevis*, *N. gobioides*, *N. niloticus* and *N. intermedius*. One of the myriad adaptions to a bottom-dwelling habit demonstrated by the latter group of species is a restructuring of the pars sustentaculum and the first and second pleural ribs. Generalized *Nannocharax* species have the basically *Nannaethiops* type of pars sustentaculum. In the specialized forms, however, the proximal section of the first pleural rib is expanded anteriorly to form a prominent flange extending over the dorsal surface of the anterior swimbladder chamber. The second pleural rib has a similar, though posteriorly-directed and somewhat smaller, process proximally. Further distally this rib also bears an anteriorly directed flange extending along the lateral wall of the anterior chamber of the swimbladder. More notably, the ventral processes of the second vertebra are expanded into a common, transverse, plate-like structure covering the anterior and anteroventral surfaces of the anterior chamber of the swimbladder (Fig. 34). Associated with these expanded ventral processes of the second vertebra is the development of a bony tube along the anteromedial face of this plate. This canal surrounds the coeliac artery from its point of origin to the point where, plesiomorphously, it contacts the anterior chamber of the swimbladder. It should be emphasized that although superficially similar to the bony tube around the coeliac artery in citharinids, this channel in *Nannocharax* is formed by a process of the second vertebra rather than by the citharinid independent ossifications.

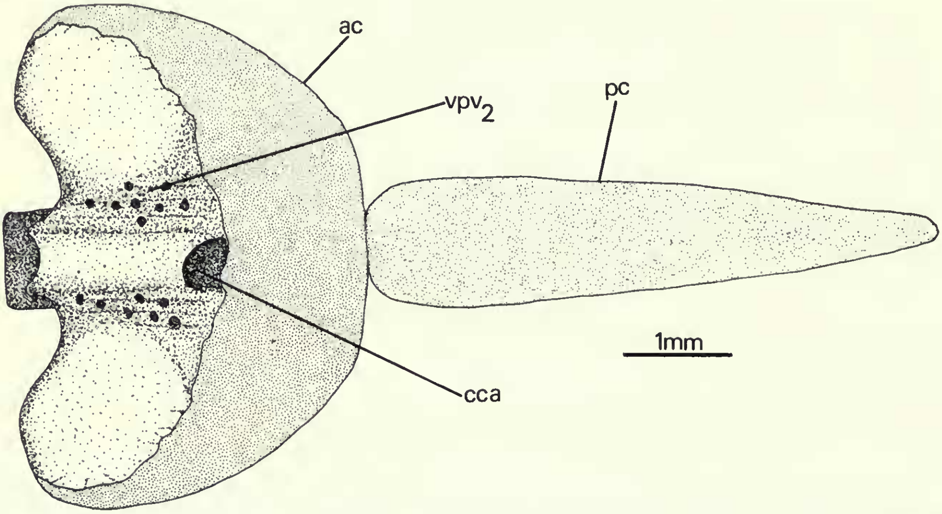

Fig. 34 *Nannocharax niloticus*, swimbladder and bony capsule of anterior swimbladder chamber, ventral view.

Such an encapsulation of the anterior swimbladder chamber has not been reported previously among characoids or encountered elsewhere in the superfamily during this study and undoubtedly represents a synapomorphy for some *Nannocharax* species. Functionally, this partial encapsulation of the swimbladder appears to be related to the bottom-dwelling habits of the species possessing it, as is the case in cobitids, various catfish groups and perhaps the small capsules around the anterior swimbladder chamber in some gymnotids (e.g. *Rhamphichthys rostratus*).

Derived states of the Weberian apparatus in the families Citharinidae and Distichodontidae are:

1 the expanded os suspensorium and the ventrolateral projections of the second and third vertebrae common to all citharinids and distichodontids at some point in ontogeny.
2 the highly ossified triangular pars sustentaculum complex of citharinids.
3 the marked reduction in the angle between the axis of the os suspensorium and that of the pars sustentaculum in *Xenocharax*.
4 the expansion of the ventral processes of the second vertebra and modifications of the first and second pleural rib to partially encapsulate the anterior chamber of the swimbladder in some *Nannocharax* species.

Postcleithra

The pectoral girdle of citharinids and distichodontids is distinctive in having a maximum of two postcleithra rather than the three postcleithral elements that characterize most characoids. The upper postcleithrum in these families overlaps the junction between the cleithrum and supracleithrum and is homologous with the element termed postcleithrum 1 in *Byrcon meeki* by

Weitzman (1962). The remaining postcleithrum in citharinids and distichodontids is located posteromedial to the cleithrum and has the form of an elongate plate with a pronounced anteroventral strut that is ventrally continuous with a rod-like process (Fig. 35a) (see also below with respect to *Phago* and *Belonophago*). In overall form this postcleithral element is very similar to the flat, ovoid postcleithrum 2 and the separate rod-like postcleithrum 3 overlapping and ventral to the former that occupy this region in most characoids. Because of this similarity in form, the ventral postcleithral element of citharinids and distichodontids is hypothesized to represent an apomorphous, fused postcleithrum 2 and 3. *Nannocharax* and *Hemigrammocharax*, in addition, lack the dorsal postcleithral element (postcleithrum 1) that plesiomorphously overlies the junction between the cleithrum and supracleithrum. A final postcleithral character of note in these families is the expansion of the ventral postcleithral element in *Phago* and *Belonophago* to form a rigid strut around the posterior border of the pectoral fin base (Fig. 35b).

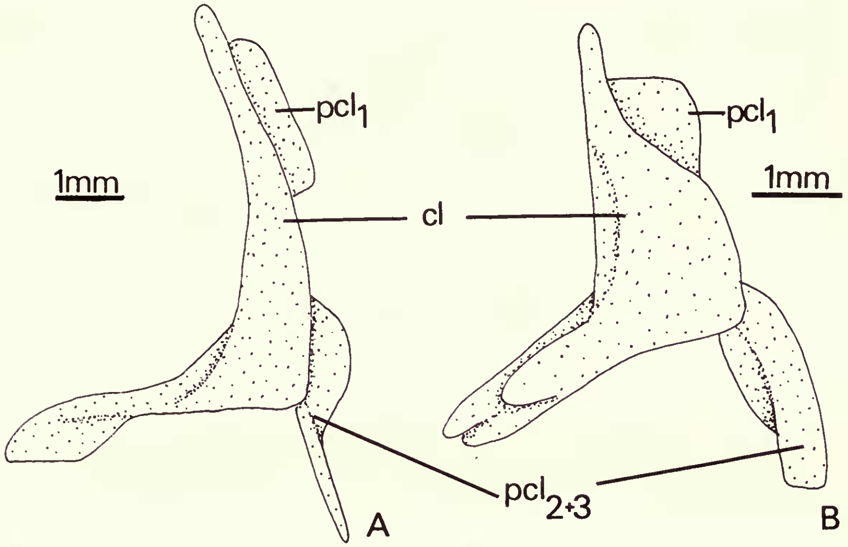

Fig. 35 Cleithrum and postcleithra of A. *Citharidium ansorgei*, B. *Phago intermedius*.

Pelvic bone

The form of the pelvic bone shows considerable variation from the generalized characoid condition both throughout and within the assemblage that constitutes the families Citharinidae and Distichodontidae. The pelvic bone of anotophysans and generalized characoids has anteriorly a single tapering process braced by a longitudinal ridge. However, among citharinids and particularly distichodontids, the pelvic bone has two anterior processes giving it an anteriorly bifurcate form (Fig. 36a). The longer lateral process extends almost directly anteriorly and bears a longitudinal ridge along its dorsal surface. The smaller medially slanting process, in turn, has a shorter ventral ridge. A somewhat bifurcate pelvic bone also occurs in various neotropical characoid groups, but in none of them is the bifurcation as pronounced as that in citharinids and distichodontids.

Further modifications to the pelvic bone occur in bottom-dwelling *Nannocharax* species (*N. niloticus*, *N. gobioides*, *N. intermedius* and *N. fasciatus*) in which the pelvic bone is distinctly widened anteriorly to form a broad plate-like structure (Fig. 36b). This modification, the congruent expansion of the ischiac process of the pelvic bone and the elongation of the pelvic fin rays is evidently an adaptation to the bottom-dwelling habits of these species.

Caudal skeleton

The caudal skeleton of citharinids and distichodontids exhibit several characters of interest both

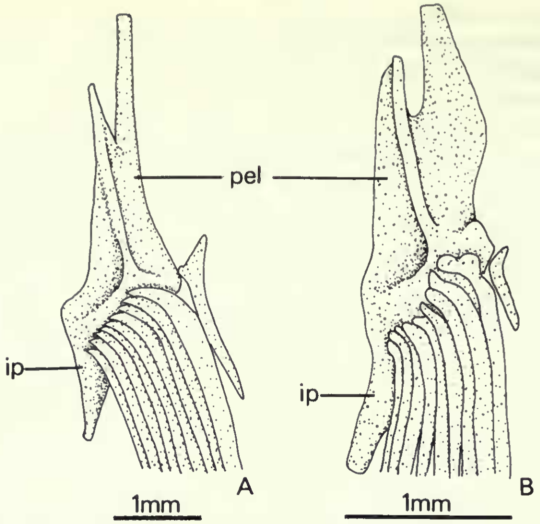

Fig. 36 Pelvic girdle of A. *Xenocharax spilurus*, B. *Nannocharax niloticus*.

relative to the question of the monophyletic nature of the complex formed by these families and to the hypothesis of relationships within the assemblage. The hypural fan form hypothesized plesiomorphous for characoids consists of six separate hypural elements. All citharinids and distichodontids differ from this condition in having hypurals 1 and 2 (the ventral elements) fused into a single unit not articulating with the fused PU_1 and U_1 (Fig. 37).

Such an apomorphic fusion of the two ventral hypurals also occurs within the Characoidea in the South American family Hemiodontidae (including *Anodus*), the characid subfamily Serrasalminae and the African characid *Lepidarchus adonis* (Roberts, 1966). As noted earlier the

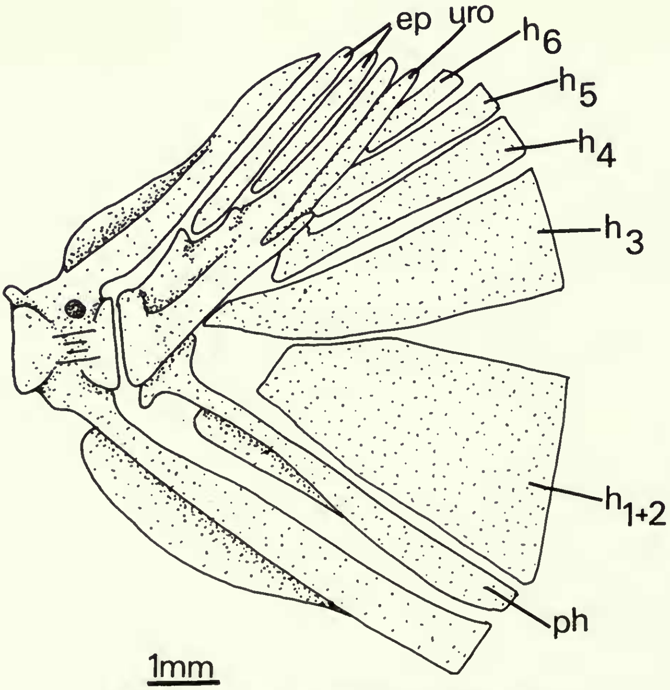

Fig. 37 *Xenocharax spilurus*, caudal skeleton.

members of the Hemiodontidae possess a rhinosphenoid; an apomorphous median ossification unique to various Neotropical characoids. With the exception of hemiodontids, all members of these rhinosphenoid-bearing groups examined during this study have separate hypurals. Similarly, although the exact relationships of the Serrasalminae are unknown, their multicuspidate dentition ties them to various Neotropical groups which lack any hypural fusions. Finally, *Lepidarchus* is a member of the African Characidae (Roberts, 1966) whose members are otherwise characterized by six separate hypurals.

Two other South American characoid groups have fused hypurals 1 and 2. However, in each of these cases the fused hypural plate differs from that of citharinids and distichodontids in such a way as to cast doubt on the homology of this fusion with that in the latter families. In the Cynodontini the genera *Hydrolycus* and *Cynodon* have hypurals 1, 2 and 3 joined into a large plate encompassing the ventral and part of the dorsal portions of the hypural fan. However, the cynodontine genus *Rhaphiodon*, has hypurals 2 and 3 fused, but separate from hypural 1. Finally, *Roestes*, the most plesiomorphous cynodontine (Howes, 1976), has a completely separate hypural fan. Thus it is most parsimonious to assume that the phylogenetic progression of hypural fusion of cynodontines is a joining of hypurals 2 and 3 followed by the fusion of the resultant plate with hypural 1. Such a sequence does not demonstrate a fusion homologous with the fused hypurals 1 and 2 that characterize citharinids and distichodontids. Finally, fused hypurals 1 and 2 have also been discovered in *Crenuchus* and *Poecilocharax*. The fused hypurals in these genera differ, however, from the pattern in citharinids and distichodontids in being joined to the fused PU_1 and U_1.

The number of separate hypural elements is further reduced in *Neolebias*, *Nannaethiops* and *Paradistichodus* in which only three upper hypurals exist. Although the question of whether this reduction is a consequence of the fusion of hypurals 5 and 6, or a loss of the latter, has not been resolved, such a reduction is nonetheless considered to be a derived feature. Finally, a reduction from the two epurals plesiomorphous for citharinids and distichodontids has occurred in *Paradistichodus*, *Phago* and *Belonophago* in which only one epural is present.

Scale form

Unlike most anatomical features, the scale form among members of the Characoidea exhibits little variation at the gross morphological level. The majority of characoids are characterized by the possession of a simple cycloid scale form. Within the families Citharinidae and Distichodontidae, however, this seemingly plesiomorphous scale form is limited to the genus *Citharinus*. *Citharidium* has ctenoid scales, while all distichodontids have a second, non-homologous form of serrate scales.

In *Citharidium* the prominent, distinctly pointed ctenii are continuous with the main body of the scale (Fig. 38a). In this scale form a strong ridge extends from the scale body radially along the centre of each cteni, with the distal circuli diverging outwards along the ridge. The members of the family Distichodontidae, in contrast, possess a very different type of ctenoid scale, the simplest form of which is illustrated in Fig. 38b. In the distichodontid ctenoid scale, the scale body is comparable to that of a typical characoid scale except for a shift of the scale focus towards the scale margin. Along the scale margin there occurs a line of irregular ctenii that vary in number between different taxa. These ctenii differ from those of *Citharidium* in being formed by a series of independent ossifications attached to the scale body and each other by unossified connective tissue.

Examination of the ctenoid scales reported in other characoid groups has shown the term to be applied to an assemblage of very different scale types characterized by various forms of serrate posterior margins. In *Cynopotamus* and other genera in the Neotropical tribe Characini the ctenoid nature of the scales is a consequence of a series of spicules along the posterior margin and exposed lateral surface of the scale. The ctenoid scales of the tetragonopterine *Ctenobrycon*, various curimatids and the prochilodontid genus *Prochilodus* are characterized by an irregularly notched posterior scale margin, whereas the curimatid genus *Psectrogaster* has definite although somewhat irregular ctenii. However, none of the above forms of ctenoid scales is comparable

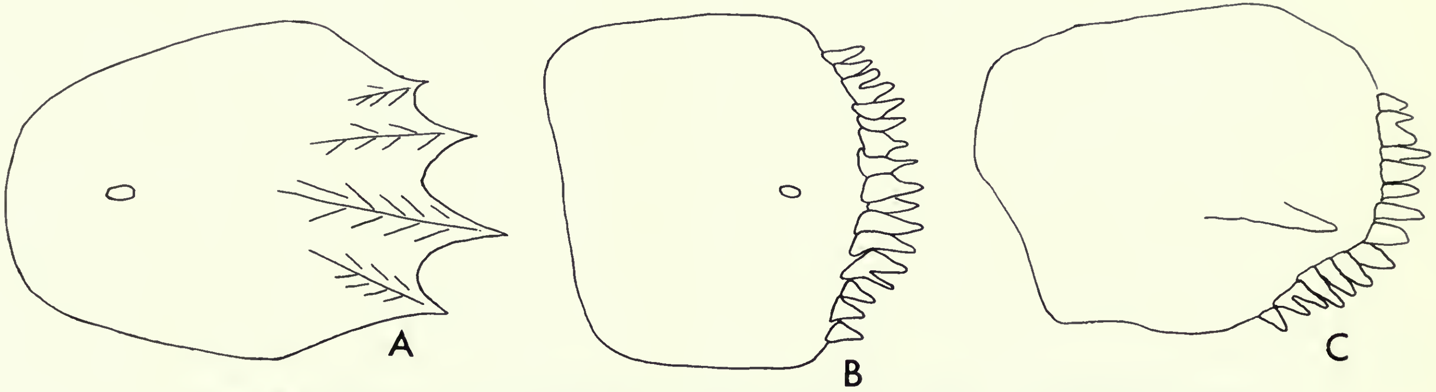

Fig. 38 Scale form of A. *Citharidium ansorgei*, B. *Xenocharax spilurus*, C. *Belonophago tinanti*.

to those in the African families under discussion. In the South American genus *Ctenolucius* the scales bear strong ctenii formed primarily by posterior continuations of the pronounced ridges that radiate outwards from the focus. In the closely related *Boulengerella* a less well-developed form of the same scale type occurs. Although these scale types approximate to that in *Citharidium*, they differ in the form of the ridges and in possessing strong radii which are totally lacking in that genus. These differences and the large number of derived characters uniting *Citharidium* into a monophyletic unit with *Citharinus* (which retains the plesiomorphous cycloid scale form) support the hypothesis that the *Ctenolucius* and citharinid forms of ctenoid scales were acquired independently.

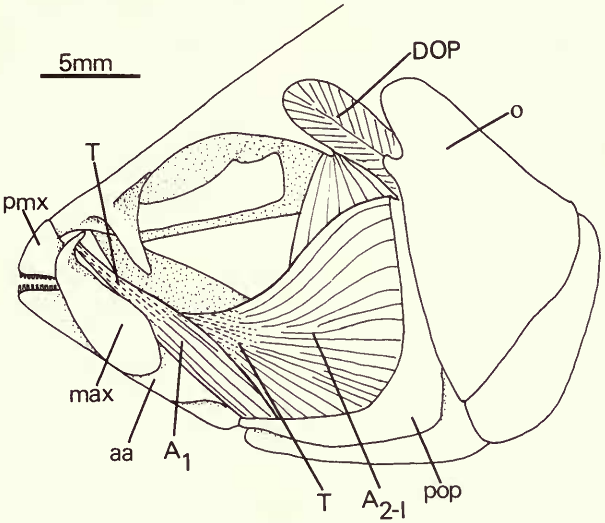

Fig. 39 *Xenocharax spilurus*, superficial cranial musculature, lateral view.

Although the distichodontid form of ctenoid scale does not appear to be approximated within characoids, a similar ctenoid scale with serrations formed by a series of independent ossifications occurs in the anatopysan ostariophysan *Gonorhynchus greyi*. However, the similarity in scale form between such phylogenetically separated members of the Ostariophysi undoubtedly represents independent acquisitions.

The distichodontid form of ctenoid scale undergoes further modifications in the genera *Phago* and *Belonophago*. In these taxa the greatly thickened scales and strong connective tissue bands joining them result in a bony but flexible body covering. Furthermore, as a consequence of their elongate cylindriform bodies, the relatively large scales in these genera are distinctly flexed horizontally. This flexure is especially pronounced in the vertically elongate scales of *Phago*. *Phago* and *Belonophago* have a distinct ossified bump overlying the scale focus, with this structure produced into a posteriorly directed spinous process in *Belonophago* (Fig. 38c).

The final character of note in the scalation of these families is the form and extent of development of the lateral line system. Although the plesiomorphous lateral line form among characoids is unknown, it is noteworthy that citharinids and distichodontids have a straight or nearly straight lateral line. This contrasts with the distinctly ventrally-curved lateral line in all other African and most Neotropical characoids. A reduction from a complete lateral line occurs in all *Neolebias* and *Hemigrammocharax* species. However, Roberts (1967) has questioned whether the reduced lateral line of *Hemigrammocharax* represents single or multiple reductions from the complete lateral line of *Nannocharax*. Two species of *Hemistichodus* (*lootensi* and *mesmaekersi*) have a distinctive medially interrupted lateral line.

Myology

The osteological characters described above have included a variety of alterations of the jaws, the jaw suspensorium, the operculum and the parts of the neurocranium associated with these systems. Congruent with these osteological changes are a series of adaptations in the cheek and opercular musculature of these genera.

In the following discussion the musculature of the distichodontid genus *Xenocharax* will first be described in detail. As far as can be determined from outgroup comparisons to generalized characoids, the myological plan of *Xenocharax* is the least derived overall among citharinids and distichodontids. Thus it serves as a useful basis of comparison for the myological variation that occurs in these families. In the case of *Paraphago*, which is known only from two syntypes and which was consequently not examined myologically, it is assumed that the myological characters of the genus are congruent with those of its monophyletic group. The muscles providing information relevant to a reconstruction of the hypothesized phylogeny of citharinids and distichodontids are the *adductor mandibulae*, the *levator arcus palatini* and the *dilatator operculi*.

The *adductor mandibulae* in *Xenocharax* (Fig. 39) is composed of sections A_1, A_2 (divisible into medial and lateral portions), A_3 and A_W. The A_1 portion of the *adductor mandibulae* is a somewhat tubular muscle extending anterodorsally from its origin on the lateral flange of the horizontal process of the quadrate. It is dorsally encompassed by a connective tissue sheath continuous with the strong tendon that runs along the anterior surface of the muscle. This tendon, in turn, inserts onto the maxilla at the point of merger between the anteromedial maxillary process and the broad lateral plate of the bone.

The remainder of the *adductor mandibulae* consists of the two sections of the A_2 portion of the muscle and medial to these an A_3. Posteriorly the two portions of the A_2 arise in common from the lateral face of the hyomandibula and vertical ramus of the preopercle. Along their posterodorsal borders these portions of the muscle contact the ventrolateral face of the dorsally widened *levator arcus palatini*. Ventrally A_2 has an origin from the lateral face of the horizontal portion of the preopercle and the posteroventral process of the quadrate (the medial portion of A_2 does not arise from the latter element). The A_2 divides into two sections parasagittally slightly anterior to the point where the *levator arcus palatini* passes between the A_2 and A_3 portions of the *adductor mandibulae*. The lateral section of A_2 extends forward over the posterodorsal surface of A_1 to insert onto the posterior edge of the dentary, just dorsal to the articulation of that element with the angulo-articular. The medial portion of A_2, in contrast, has its anterodorsal surface invested by a connective tissue band that is continuous with a prominent tendon extending anteriorly from the forward tip of the muscle and joining a comparable tendon from the A_3. This common tendon inserts onto the A_w and the coronomeckelian ossification (Fig. 40). The A_3 section of the *adductor mandibulae* is posteriorly separated from the medial section of A_2 by the ventral portion of the *levator arcus palatini*. The A_3 arises from the anteromedial surface of the hyomandibula and is surrounded anteriorly by a connective tissue sheath that is continuous with the tendon arising from the medial section of A_2. Finally, the A_w (intramandibular) section of the *adductor mandibulae* is a relatively flat muscle filling the meckelian fossa and attaching to the angulo-articular and dentary.

The *levator arcus palatini* of *Xenocharax* is a triangular muscle, laterally exposed along the posterodorsal region of the cheek. From its origin on the posteroventral portion of the sphenotic spine the *levator arcus palatini* extends ventrally between A_3 and the medial section of A_2 to insert on the anteroventral portion of the hyomandibula. The *dilatator operculi* is a pinnate muscle arising from the broad dilatator fossa of the sphenotic and pterotic and inserting onto a raised ridge along the anterodorsal corner of the opercle.

The above pattern of cheek and opercular musculature is common to *Xenocharax*, *Nannaethiops* and *Neolebias*. Citharinids and other distichodontids differ to varying degrees from the *Xenocharax* cheek musculature pattern. This variation in muscle origins, insertions, proportions and interconnections serves to define a series of multigeneric units within these families.

Citharinus and *Citharidium* have an elongate A_1 portion of the *adductor* mandibulae with a more extensive origin on the horizontal process of the quadrate and the ventral arm of the preopercle than in the *Xenocharax* condition (Fig. 41). More significantly, the citharinid A_1 differs from that of *Xenocharax* in attaching directly to the rear of the dentary rather than tendinously to the maxilla. Citharinids have, however, a ligament running from the point of contact of the A_1 with the dentary to the region of the maxilla where the tendon of A_1 inserts in *Xenocharax*. This ligament, the *ligamentum primordiale* of previous authors, may be homologous to the tendinous band along the anterior surface of the A_1 section of the *adductor mandibulae* in *Xenocharax*. On the basis of outgroup comparisons, the citharinid insertion of the A_1 to the dentary in conjunction with the retention of a distinct *ligamentum primordiale* is hypothesized to be the plesiomorphous characoid condition. The derived attachment of the A_1 to the maxilla in *Xenocharax* together with the seeming incorporation of the *ligamentum primordiale* into its tendon is evidently correlated with the increased upper jaw mobility of distichodontids.

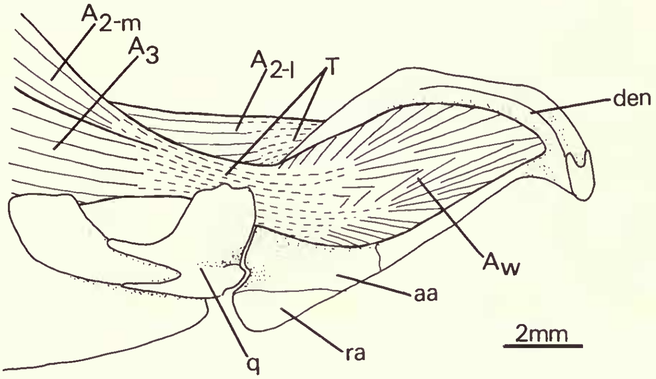

Fig. 40 *Xenocharax spilurus*, *adductor mandibulae*, anterior portions, medial view.

The A_2 portion of the *adductor mandibulae* in *Citharinus* and *Citharidium* arises posteriorly from the lateral surfaces of the hyomandibula and preopercle, but does not extend as dorsal on these elements as in *Xenocharax*. Anteriorly the lateral portion of the A_2 in citharinids inserts onto the rear of the A_w through a tendon that is anteriorly continuous with that of the medial section of A_2. This common insertion contrasts with the separate attachment of these muscles on the dentary and A_W respectively in *Xenocharax*. That portion of the *adductor mandibulae* of citharinids comparable to the A_3 of *Xenocharax* (that portion of the muscle medial to the *levator arcus palatini*) is greatly reduced and usually has the form of a series of muscle slips arising from the hyomandibula and metapterygoid. Furthermore, rather than having a distinct tendon, anteriorly continuous with the anterior tendon of A_2, the slips of muscles forming the A_3 of citharinids attach individually along the inner surface of the medial portion of A_2.

The A_w section of the *adductor mandibulae* in *Citharinus* and *Citharidium* is greatly expanded to fill entirely the large meckelian fossa and extends dorsally over the upper edge of the dentary. The *levator arcus palatini* of these genera, although relatively longer than in *Xenocharax*, has a similar origin and insertion apart from an expanded insertion posterodorsally on the preopercle. The *dilatator operculi* is significantly larger than that of *Xenocharax* and totally fills the large dilatator fossa on the sphenotic, pterotic and lateral edge of the frontal. This pinnate muscle inserts on the distinctive, elongate opercular spine that extends anterodorsally towards the middle of the fossa in citharinids.

Within distichodontids, several genera and generic assemblages show various modifications of the *Xenocharax* pattern of cheek musculature. In *Paradistichodus* the overall proportions of the muscles are changed, perhaps as a consequence of the elongate head that characterizes the genus. The A_1 portion of the *adductor mandibulae* is notably elongate and the muscle extends along the tendon anterodorsally, nearly to the maxilla. Overall, the A_2 is smaller than in *Xenocharax* and arises solely from the ventral half of the preopercle and hyomandibula. This reduction of the A_2 is especially notable in the longitudinal extent of the lateral section of the muscle which consequently attaches to the dentary through an elongate tendon.

Distichodus, *Nannocharax* and *Hemigrammocharax* have a series of modifications of the *adductor mandibulae* correlated with their unique jaw morphology (Fig. 42). The elongate A_1

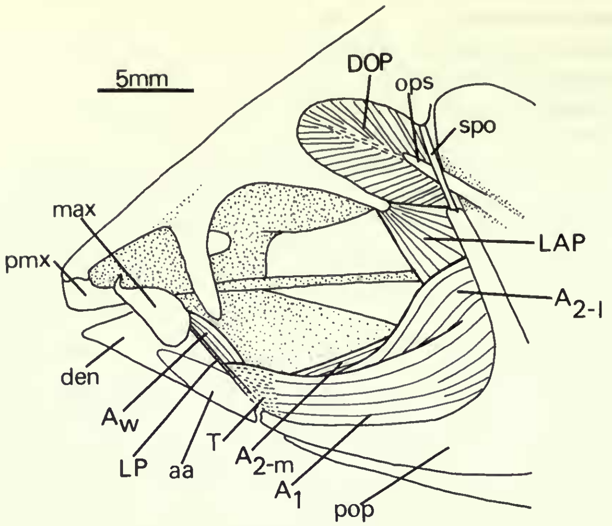

Fig. 41 *Citharinus citharus*, superficial cranial musculature, lateral view.

portion of this muscle arises from the quadrate and extends anteriorly to attach to the maxilla by way of a ligament running across the lateral face of the dorsally expanded dentary. As in *Xenocharax* the A_2 section of the *adductor mandibulae* is subdivided into medial and lateral segments with a prominent A_3 also present. However, as a consequence of the radically restructured jaw form of these genera, the relationships between the sections of the *adductor mandibulae* are somewhat altered. In other distichodontids the anterior sections of A_2 and A_3 run in parallel and the lateral portion of A_2 inserts lateral to, or only slightly dorsolateral to, the point where the joined tendon of A_3 and the medial portion of A_2 contacts the A_W. In *Distichodus*, *Nannocharax* and *Hemigrammocharax*, in contrast, the insertion of the lateral portion of A_2 is distinctly dorsal to the level where the combined tendon from A_3 and the medial section of A_2 attach onto the coronomeckelian ossification. The A_W of *Distichodus*, *Nannocharax* and *Hemigrammocharax* arises from the dorsal edge of the latter tendon and extends from distinctly posterior of the rear of the angulo-articular forward onto the bone. Both the origin of the A_W solely from the dorsal border of the ligament and its posterior position relative to the angulo-articular appear apomorphous relative to the generalized characoid condition. An additional

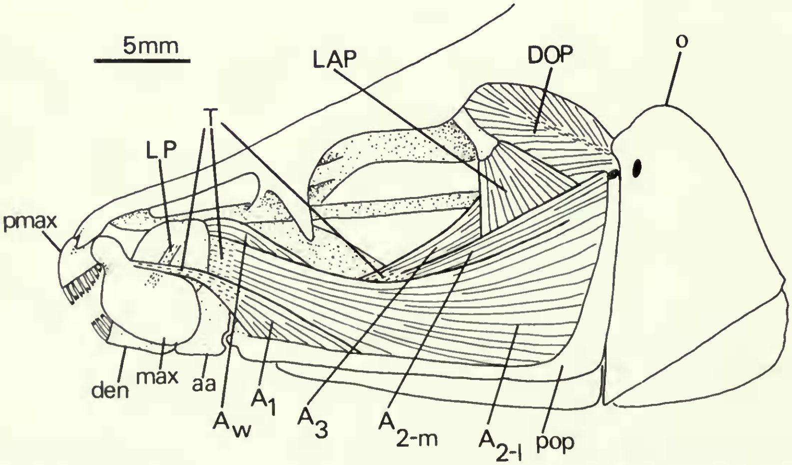

Fig. 42 *Distichodus lusosso*, superficial cranial musculature, lateral view. Dashed line on maxilla indicates attachment of *ligamentum primordiale*.

consequence of these osteological and myological alterations is a shift of the relative position of the *ligamentum primordiale* and the tendon of A_1. Instead of running in common or parallel as in the plesiomorphous condition, the connective tissue bands in these genera cross at right angles, with the tendon of A_1 passing over the *ligamentum primordiale*.

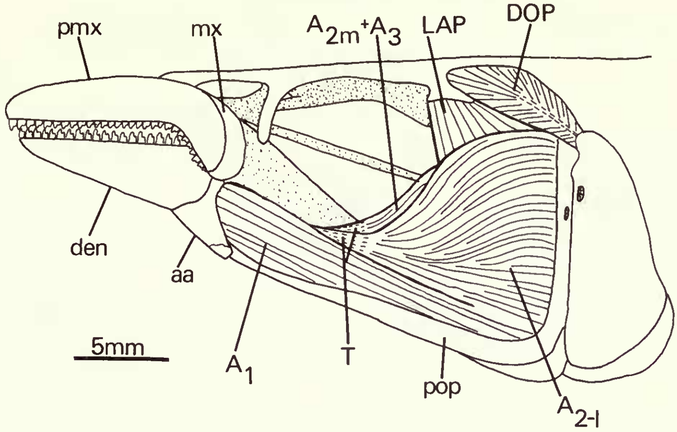

Fig. 43 *Ichthyborus quadrilineatus*, superficial cranial musculature, lateral view.

As discussed earlier the ventral edge of the sphenotic spine undergoes a progressive phylogenetic enlargement within the unit formed by *Distichodus*, *Hemigrammocharax* and *Nannocharax*. Congruent with this alteration of the spine is an expansion in the extent of the origin of the *levator arcus palatini*. This trend is especially pronounced in *Nannocharax* and *Hemigrammocharax* in which the broad ventrally concave sphenotic process serves as an expanded area of origin for the *levator arcus palatini*. Furthermore, in these genera the *dilatator operculi* rather than having the hypothesized plesiomorphous origin from the dilatator fossa has a broad attachment to the lateral surface of the sphenotic. This shift from the generalized characoid condition is carried further in some of the larger *Nannocharax* species examined (*N. fasciatus* and *N. elongatus*).

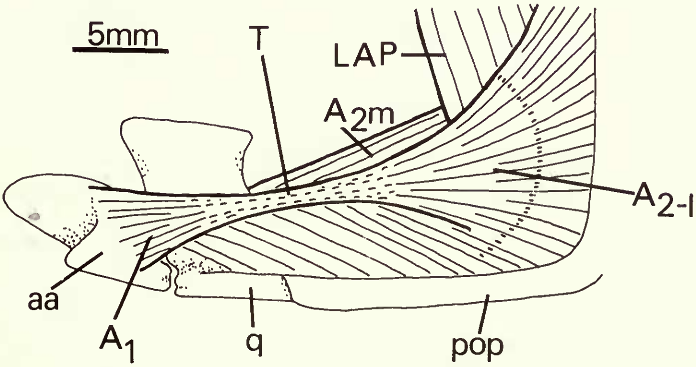

Fig. 44 *Ichthyborus besse*, *adductor mandibulae*, lateral view.

In these species the anterior portion of the *dilatator operculi* arises from the anterior face of the sphenotic and passes medial to the *levator arcus palatini* to insert on the anterodorsal process of the opercle. The broad, shallow depression on the sphenotic and pterotic of *Nannocharax* and *Hemigrammocharax* does not serve as a dilatator fossa, but is instead occupied by the plate-like dermosphenotic present in these genera.

The remaining distichodontid genera, *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*, have the A_1 portion of the *adductor mandibulae* arising from the trough formed by the lateral processes of the quadrate and preopercle. This muscle inserts on the posterolateral and posterior surface of the angulo-articular (Figs 43, 44). Such an insertion differs radically from the tendinous attachment of this muscle section to the maxilla in all other distichodontids. This change and the congruent loss of a definitive *ligamentum primordiale* appears consequent upon the radically altered upper jaw morphology of these genera. These changes result in the elimination of the functional advantage that an attachment of the A_1 to the maxilla provides in less derived forms of distichodontid jaws. These genera, with the exception of *Hemistichodus*, also have a significantly enlarged origin of the *adductor mandibulae* on the lateral and medial surfaces of the hyomandibula and the lateroventral portions of the sphenotic and pterotic. This expanded origin is particularly pronounced in *Eugnatichthys*.

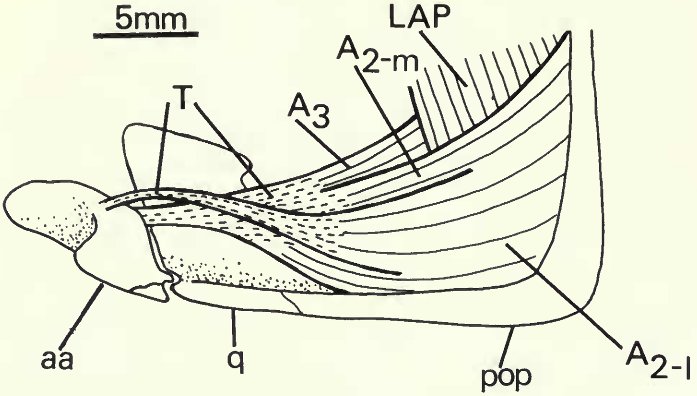

Fig. 45 *Ichthyborus ornatus*, *adductor mandibulae*, lateral view, A_1 portion removed.

Within the above assemblage, both *Ichthyborus* and *Eugnatichthys* present further apomorphic myological characters. The A_1 of *Ichthyborus besse* is distinctive in having its lateral portion autapomorphously altered into a distinct triangular muscle slip which attaches to the lateral portion of A_2 *via* a connective tissue band (Fig. 44). In addition, all *Ichthyborus* species are distinctive among distichodontids in having the lateral portion of the A_2 inserting on the angulo-articular, contrary to the plesiomorphous attachment of this muscle segment on the dentary. This insertion is through an elongate anterior tendon in *Ichthyborus ornatus*, *I. monodi* and *I. quadrilineatus* (Fig. 45) and by way of the aforementioned modified section of the A_1 in *I. besse* (Fig. 44).

Eugnatichthys has the primitively single A_3 portion of the *adductor mandibulae* parasagittally subdivided into two sections. The lateral portion of the A_3 in this genus extends anteriorly to join the medial section of A_2 and inserts in common with that muscle directly on the dentary. This insertion contrasts with the plesiomorphous insertion of the A_3 on the coronomeckelian ossification, an insertion that is retained by the medial portion of the A_3 section of the adductor mandibulae of *Eugnatichthys*.

The *levator arcus palatini* in *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* has an apomorphous expanded origin on the ventral (primitively anterior) surface of the posteroventrally sloping or horizontal sphenotic spine characteristic of these genera. *Phago* and *Belonophago*, in turn, have the muscle origin further expanded onto the ventral face of the frontal in the posterodorsal orbital region; an adaptation unique to these genera among characoids examined. Finally, the *levator arcus palatini* of

Eugnatichthys, *Phago* and *Belonophago* has a distinctly reduced vertical extent relative to that of other distichodontids and consequently does not directly insert onto the hyomandibula. Instead, these genera have the muscle inserting onto that element *via* a broad aponeuroses.

In summary, hypothesized derived states of the *adductor mandibulae*, *levator arcus palatini* and *dilatator operculi* among citharinids and distichodontids are:

1 the insertion of the A_1 portion of the *adductor mandibulae* on the maxilla in *Xenocharax*, *Neolebias*, *Nannaethiops*, *Paradistichodus*, *Distichodus*, *Nannocharax* and *Hemigrammocharax*. This attachment is hypothesized, however, to have been secondarily lost in all other distichodontids.

2 the insertion of the lateral section of the A_2 portion of the *adductor mandibulae* to the A_W *via* a tendon in citharinids.

3 the reduction of the A_3 portion of the *adductor mandibulae* in citharinids.

4 the greatly expanded A_W portion of the *adductor mandibulae* in citharinids.

5 the expanded *dilatator operculi* in citharinids.

6 the reduced lateral portion of the A_2 section of the *adductor mandibulae* in *Paradistichodus*.

7 the elongation of the A_1 portion of the *adductor mandibulae* in *Distichodus*, *Nannocharax* and *Hemigrammocharax*.

8 the relatively dorsal insertion of the lateral portion of A_2 in *Distichodus*, *Nannocharax* and *Hemigrammocharax*.

9 the posterior origin and expanded extent of the A_W portion of the *adductor mandibulae* in *Distichodus*, *Nannocharax* and *Hemigrammocharax*.

10 the expanded origin of the *levator arcus palatini* on the ventrally broadened sphenotic spine in *Nannocharax*, *Hemigrammocharax* and some *Distichodus* species.

11 the shift of the origin of the *dilatator operculi* to the lateral surface of the sphenotic in *Nannocharax* and *Hemigrammocharax*.

12 the insertion of the lateral portion of the A_2 on the angulo-articular in *Ichthyborus*.

13 the expansion of the origin of the A_2 section of the *adductor mandibulae* onto the medial surface of the hyomandibula and ventral surfaces of the pterotic and sphenotic in *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. These genera also have the origin of the *levator arcus palatini* expanded onto the anterior surface of the sphenotic spine.

14 the partial origin of the *levator arcus palatini* from the ventral surface of the frontal in *Phago* and *Belonophago*.

15 the reduction of the vertical extent of the *levator arcus palatini* and its insertion on the hyomandibula through an aponeuroses in *Eugnatichthys*, *Phago* and *Belonophago*.

Swimbladder, intestinal and epibranchial organ forms

Swimbladder

Within the assemblage consisting of the Citharinidae and Distichodontidae, the form of both the anterior and posterior chambers of the swimbladder undergoes several modifications. The generalized swimbladder morphology in characoids consists of two chambers connected by a short narrow tube. The rotund anterior chamber is slightly elongate and is attached by the peritoneal layer surrounding it to the os suspensorium and the triangular connective tissue complex associated with the pars sustentaculum of the Weberian apparatus. The posterior chamber is of slightly greater diameter than the anterior and several times the longitudinal extent.

Although the plesiomorphous relative proportions of the chambers of the swimbladder among characoids is presently unknown, it is noteworthy that in both citharinids and distichodontids the posterior chamber of the swimbladder is distinctly elongate with respect to the anterior (approximately four times the longitudinal length). Despite this uncertainty about the phylogenetic polarity of an elongate posterior swimbladder chamber, the possession of such a structure is, nonetheless, at least congruent with the hypothesis of the monophyly of the unit formed by citharinids and distichodontids among characoids. Is should be emphasized, however, that even if apomorphous for characoids, such an elongate posterior chamber of the swimbladder is also characteristic of the South American characoid family Hemiodontidae and occurs in various forms in some Neotropical characids (e.g. Iguanodectinae, see Vari, 1977).

Within the Distichodontidae, the evenly curved oblong anterior and elongate posterior swimbladder chambers that are plesiomorphous for the family are modified in *Hemigrammocharax* and *Nannocharax*. These genera have anteriorly-directed diverticulae of the anterior swimbladder chamber. These diverticulae extend from the anterior face of the chamber lateral to the ventral process of the os suspensorium and the posterior portion of the triangular connective tissue complex associated with the pars sustentaculum. The extent of these diverticulae range from the slight bulges of *Hemigrammocharax* and generalized *Nannocharax* species to the pronounced anterior diverticulae found in specialized *Nannocharax* species such as *N. niloticus*, *N. gobioides* and *N. intermedius*. The latter *Nannocharax* species also have the posterior swimbladder chamber greatly reduced to a small tubular structure (Fig. 34); an adaptation evidently correlated with their bottom-dwelling habits.

Intestinal form

Two modifications of the morphology and convolution patterns of the intestinal tract distinguish citharinids within the complex formed by the families Citharinidae and Distichodontidae. On the basis of information from ontogenetic and outgroup comparisons, the plesiomorphous form of the intestinal tract among characoids appears to be a moderately looping, smooth-walled system. In both *Citharinus* and *Citharidium*, however, the intestine is elaborated into a highly convoluted system (see Daget, 1962, Fig. 9) characterized by distinctive multiple outpocketings of its terminal loop. Whereas the elongation of the intestine is evidently correlated with the microphagous habits of these genera, the functional significance of the intestinal outpocketings is obscure.

Epibranchial organ form

Epibranchial organs of differing levels of complexity have been described for a variety of Neotropical and African characoids (see Nelson, 1967, p. 73). Within the families under discussion, a slightly developed diverticula in the posterior portion of the gill arches has been reported among distichodontids in *Paradistichodus* (Daget, 1958, p. 1368), *Distichodus* (Daget, 1959, p. 1289), *Xenocharax* (Daget, 1960, p. 41), *Nannocharax* (Daget, 1961, p. 172) and *Neolebias* (Daget, 1965, p. 9). The structure has also been found in *Nannaethiops* and *Hemigrammocharax* during this study. Daget reported that the epibranchial organ was absent in *Ichthyborus besse* (1967, p. 145) and *Hemistichodus* (1968, p. 16). This study has also found such outpocketings to be lacking in the remaining *Ichthyborus* species, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Phago* and *Belonophago*. The lack of epibranchial organs in these genera is considered to be an apomorphous secondary loss on the basis of the presence of such outpocketings in the Citharinidae, which is the sister group to distichodontids, and in all other distichodontids.

Citharinus and *Citharidium*, in contrast, have greatly elaborated epibranchial organs. In these genera the diverticulae are expanded into lobulate muscular structures (Fig. 46) with ramifying internal chambers supported by spicules of bone (see Daget, 1962*a*, Figs 7, 8). Prominent epibranchial organs also occur in the Neotropical characoid families Prochilodontidae and Curimatidae. In neither of those families, however, are these outpocketings as greatly developed as they are in citharinids. Neither do the epibranchial organs of the Neotropical groups have the distinctive lobed forms of those in the Citharinidae. Thus the form of the citharinid epibranchial organs is considered synapomorphous for *Citharinus* and *Citharidium* among characoids.

Olfactory bulbs

Among anotophysans and most characoids the olfactory bulb lies immediately anterior to, and in contact with, the telencephalon and is laterally enclosed by the orbitosphenoid. In this state the olfactory nerve passes anteriorly either through the anteromedial opening in the orbitosphenoid or through foramina in that bone, and extends anterolaterally to the olfactory foramen of the lateral ethmoid. Citharinids and distichodontids, in contrast, have the olfactory bulbs shifted anteriorly to contact or nearly contact the posterior surface of the lateral ethmoid. This shift in olfactory bulb position results in a shortening of the olfactory nerve and an elongation of the olfactory tract. These alterations of the olfactory system are hypothesized apomorphous for these families within characoids. This hypothesis is based both on the widespread distribution of a posterior position of the olfactory bulb among teleosts in general and characoids in particular, and on the ontogenetic anterior movement of the bulb that has been observed in various citharinids and distichodontids.

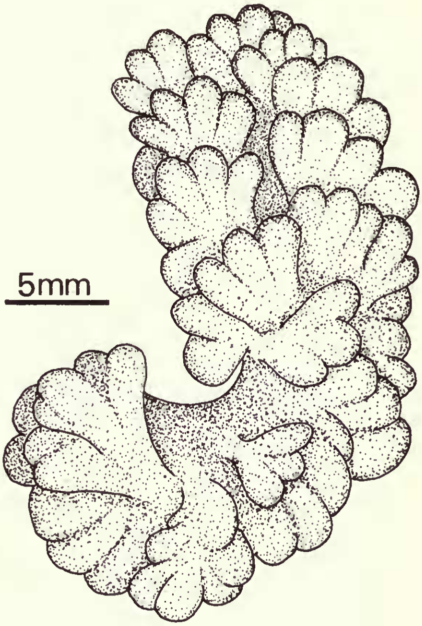

Fig. 46 *Citharidium ansorgei*, epibranchial organ, left lateral view.

Although an anterior position of the olfactory bulb is generalized for cyprinoids and siluroids, among characoids examined during this study such a forward location of the bulb has been found only in citharinids, distichodontids, the genus *Salminus*, some african characids and the family Parodontidae. Adults of *Salminus maxillosus* have the olfactory bulb immediately posterior of the lateral ethmoid, a shift evidently reflected in ontogeny since young *S. hilarii* have the olfactory bulb relatively more posteriorly located. The significance of the forward position of the olfactory bulb for an understanding of the relationships of these enigmatic South American characoids to citharinids and distichodontids is difficult to ascertain. Indeed, it is notable that this genus lacks all other hypothesized derived characters synapomorphous for the Citharinidae and Distichodontidae.

Within the African Characidae the hypothesized plesiomorphous posterior position of the bulb has been found in *Micralestes* (*M. acutidens*, *M. lualabae*, *M. voltae* and *M. occidentalis*), *Phenacogrammus interruptus*, *Rhabdalestes tangensis*, *Virilia pabrensis* and some *Alestes* species (*A. sadleri* and *A. longipinnis*). A slight separation between the bulb and telencephalon is found in *Alestes lateralis* and *A. imberi*, and the bulb has a distinct anterior shift in *Hydrocynus*, *Bryconaethiops* and a variety of *Alestes* species (*A. dentex*, *A. baremose*, *A. liebrechstii*, *A. macrophthalmus*, *A. macrolepidotus*, *A. nurse* and *A. rhodopleura*). This progressive anterior movement in the position of the olfactory bulb within a group that forms a monophyletic unit within the Characidae (see p. 341) was evidently acquired independently of that in citharinids and distichodontids. Finally, within the Parodontidae a slight forward shift of the bulb has been found in *Parodon bimaculatus* and *Apareidon affinis*. The significance of the Parodontidae in the question of the relationships of the families under discussion is reviewed later.

Phylogenetic reconstruction

The preceding descriptions of various osteological and soft anatomical systems have discussed a series of characters providing information relevant to a reconstruction of a hypothesis of generic relationships within the assemblage consisting of the Citharinidae and Distichodontidae. The following discussion deals first with the synapomorphies for the complex formed by citharinids and distichodontids, followed by those derived characters that distinguish subunits of decreasing levels of universality within this assemblage. The resultant phylogeny and its implication for the classification of these families is discussed subsequently.

The most parsimonious hypothesis of relationships based on the derived characters analysed previously is presented in Fig. 47. The apomorphous characters defining the genera and supra-generic assemblages are numbered sequentially, since such a procedure simplifies the visualization of character distribution and generic relationships. The numbering of the characters corresponds to the numbered synapomorphies of the cladogram in Fig. 47. Relationships at the subgeneric level are discussed in detail for only five of the taxa recognized in this study (*Neolebias*, *Ichthyborus*, *Distichodus*, *Nannocharax* and *Hemigrammocharax*) in so far as the conclusions reached in this work are congruent with or at least fail to refute the hypotheses of relationships inherent in the previous definitions of the remaining genera. The characters synapomorphous for subgeneric units in *Neolebias* and *Ichthyborus* are incorporated into the cladograms presented in Fig. 48 and 49.

Families Citharinidae and Distichodontidae

The hypothesized monophyly of the assemblage formed by the Citharinidae and Distichodontidae is supported by the following synapomorphies of these families:

1 the ventral elaborations of the second and third vertebrae and the ventral expansion of the os suspensorium.
2 the bicuspidate tooth form.
3 the fusion of postcleithra 2 and 3.
4 the bifurcate pelvic bone.
5 the fusion of hypurals 1 and 2.
6 the lack of a premaxillary ascending process.
7 the possession of a premaxillary articular fossa.
8 the lack of lateral supraethmoid wings.
9 the lack of a distinct supraethmoid spine.
10 the trifurcate articular complex at the anterior margin of the supraethmoid.
11 the large, ventrally ovate third posttemporal fossa bordered by the epioccipital and exoccipital.
12 the anterior shift of the olfactory lobe.
13 the possession of a suprapreopercle.
14 the lack of an interdigitating symphyseal hinge.

As discussed in the anatomical descriptions, some of the above characters are evidently unique to these families among characoids, whereas others are approximated in characoid outgroups. On the basis of available information, the first four characters would appear to be autapomorphous for the unit formed by the Citharinidae and Distichodontidae among characoids. Characters similar to five to twelve occur in other characoid groups. However, available evidence indicates that their presence in these outgroups is a consequence of convergence rather than the result of immediate common ancestry. Finally, characters 13 and 14, though hypothesized as derived, also occur in characoid groups whose affinities are uncertain at present and thus are possibly sister groups to the unit consisting of citharinids and distichodontids. In addition to the characters listed above, it should also be noted that citharinids and distichodontids have a straight lateral line and an elongate posterior swimbladder chamber, characters whose polarity is, however, presently undetermined.

Within the hypothesized monophyletic assemblage defined by the characters detailed above, two families, the Citharinidae and Distichodontidae, are recognized in this study. Citharinids

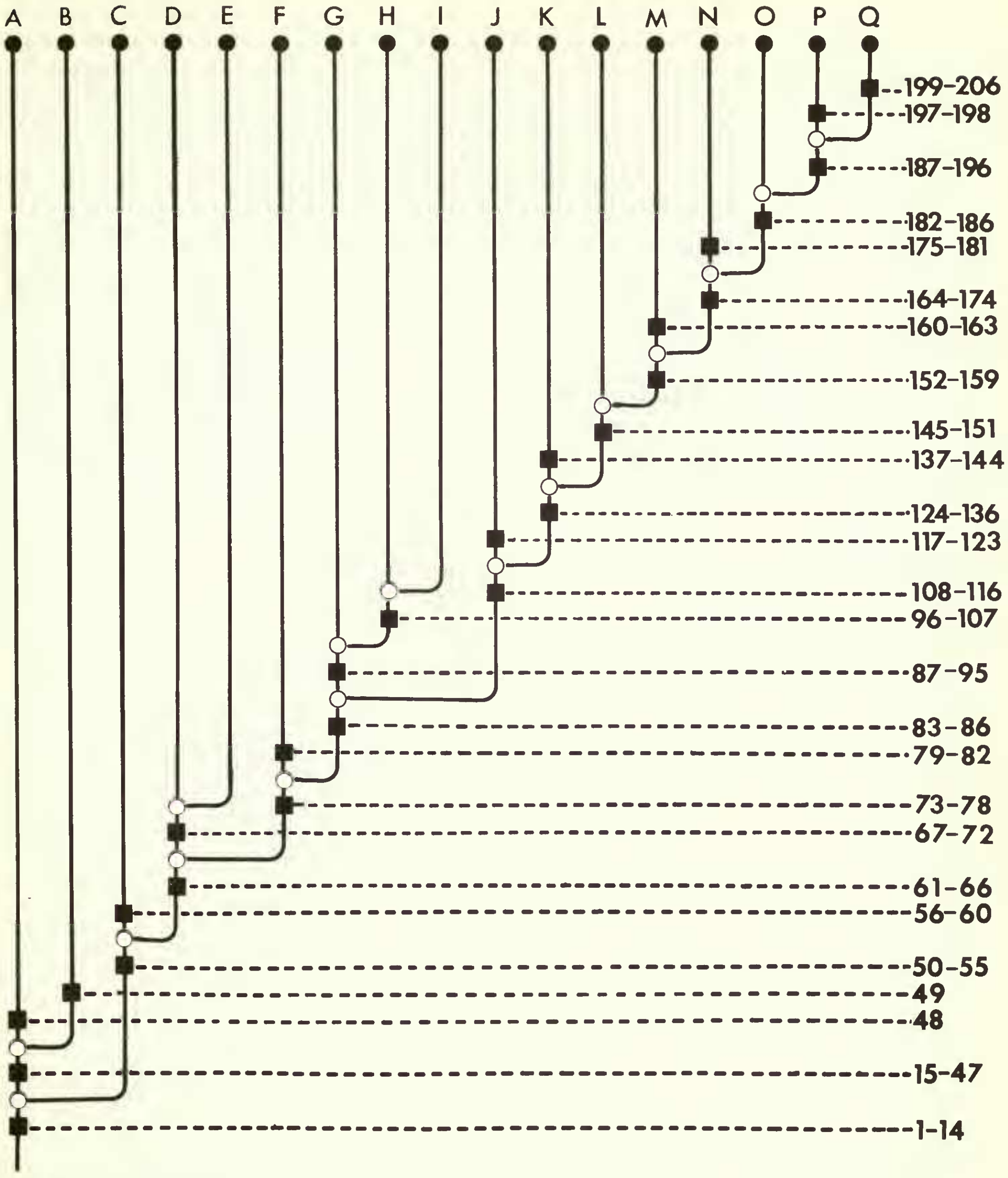

Fig. 47 Cladogram of the most parsimonious hypothesis of relationships in the families Citharinidae and Distichodontidae. Taxa (solid circles): A, *Citharidium;* B, *Citharinus;* C. *Xenocharax;* D, *Nannaethiops;* E, *Neolebias;* F, *Paradistichodus;* G, *Distichodus;* H, *Nannocharax;* I, *Hemigrammocharax;* J, *Hemistichodus;* K, *Ichthyborus;* L, *Microstomatichthyoborus;* M, *Mesoborus;* N, *Eugnatichthys;* O, *Paraphago;* P, *Phago;* and Q, *Belonophago*. Synapomorphies 1–206 correspond to those of the text.

are a highly specialized group characterized by a series of distinctive synapomorphies, but having little intrafamilial variation. Indeed, the differences between citharinid species are primarily meristic and morphometric other than for the single character autapomorphous for each of the contained genera. In contrast, the Distichodontidae, although characterized by few synapomorphies, is very speciose and exhibits a pronounced degree of intrafamilial variation. The significance of these diametrically opposed trends in citharinids and distichodontids is obscure and indeed may only be a function of the differing speciation and extinction rates in these families as viewed at this particular point in time.

Family Citharinidae

As mentioned above, the family Citharinidae is distinguished by a multitude of apomorphous characters. The derived features of citharinids are nearly all related to the pronounced restructuring of the pars sustentaculum and the alterations in their ingestive and digestive systems correlated with their microphagous habits. These characters, in summary, are:

15 the marked expansion of the ventral processes of the second and third vertebrae and os suspensorium.
16 the independent ossification along the anterior and lateral surfaces of the coeliac sheath.
17 the outwards rotation of the replacement tooth trenches, particularly that of the lower jaw.
18 the posterior extension of the premaxilla medially, and the associated development of strong interpremaxillary interdigitations.
19 the ontogenetic reduction in the roof of the premaxillary fossa.
20 the reduction of the maxilla.
21 the loss of maxillary teeth.
22 the loss of the inner dentary tooth row.
23 the enlarged cartilage pad between the palatine and maxilla.
24 the development of a large cartilage pad between the palatine and premaxilla.
25 the ontogenetic reduction of the lateral articular processes of the supraethmoid and their fusion with the enlarged median supraethmoid process.
26 the restructuring of the lower pharyngeal into a fenestrated, dorsally convex, edentulous bone.
27 the fusion of upper pharyngeal tooth plates 4 and 5, and the reduction or loss of the associated dentition.
28 the loss of pharyngobranchial 1.
29 the elongation and anterior shift of pharyngobranchials 2 and 3.
30 the possession of micro-gillrakers.
31 the large, elaborate epibranchial organ.
32 the pronounced flexure in the parasphenoid.
33 the ontogenetic development of a bulbous ventral parasphenoid process.
34 the two broad regions of contact between the lateral ethmoid and orbitosphenoid.
35 the prominent, horizontal bulge at the orbitosphenoid–pterosphenoid joint.
36 the loss of the dorsal posttemporal fossa.
37 the elongate fontanelle extending midway into the supraethmoid.
38 the prominent ridge on the elongate anterodorsal process of the opercle.
39 the extension of the suprapreopercle over the anterodorsal portion of the opercle.
40 the reduced dermosphenotic.
41 the expansion of the dilatator fossa onto the frontal.
42 the attachment of the lateral section of the A_2 portion of the *adductor mandibulae* onto the A_W.
43 the relative reduction of the A_3 portion of the *adductor mandibulae*.
44 the enlargement of the A_W portion of the *adductor mandibulae* into a large muscle extending dorsal of the edge of the angulo-articular.
45 the marked enlargement of the *dilatator operculi*.

46 the elongation of the intestinal tract.
47 the pronounced outpocketings of the terminal portion of the intestine.

Within citharinids, two genera, *Citharinus* and *Citharidium*, are recognized at present. As described previously, the form of the ctenoid scales in *Citharidium* (48) appears to be unique among characoids to this monotypic genus. Traditionally, *Citharinus* has been distinguished from *Citharidium* on the basis of the former taxons having cycloid scales. However, such a scale form is plesiomorphous for characoids and thus cannot serve to define a monophyletic group. The only autapomorphous character for *Citharinus* found during this study is its lack of the parietal portion of the supraoccipital sensory canal (49). Such a loss, which appears to be derived for characoids, was previously noted by Daget (1962*b*, p. 95). Daget has also dealt with the ecology and aspects of the anatomy and taxonomy of both *Citharinus* and *Citharidium* (1962*a* & *b*).

Family Distichodontidae

As defined in this study the family Distichodontidae is both the most speciose and morphologically diverse of the families under consideration. Perhaps as a consequence of these factors, the Distichodontidae was previously subdivided into four subfamilies by Eigenmann (1909) and Regan (1911). More recently two subfamilies (Distichodontinae and Ichthyborinae) or families (Distichodontidae and Ichthyboridae) have been recognized within this assemblage. However, as will be discussed in the Conclusions section, the results of this study have led to the retention of only a single family, the Distichodontidae, for the genera previously partitioned among several subfamilies or families.

Despite this extensive intrafamilial variation, the Distichodontidae is not characterized by a large series of synapomorphous characters. The derived characters supporting the hypothesized monophyletic nature of the family Distichodontidae are:

50 the distinctive ctenoid scales having the ctenii formed by a series of independent ossifications.
51 the posterior process of the lateral ethmoid which extends posteriorly to contact the anteromedial edge of the orbitosphenoid.
52 the deeply bifurcate pelvic bone.
53 the mobility of the premaxilla on the supraethmoid.
54 the anterior shift and reduction or loss of the supraorbital.
55 the attachment of the A_1 portion of the *adductor mandibulae* to the maxilla (this attachment is secondarily lost in some genera, see p. 320).

These apomorphous characters define an assemblage of genera that is, in turn, divisible into two monophyletic subgroups. One unit consists of the genus *Xenocharax*, and the other of *Nannaethiops*, *Neolebias*, *Paradistichodus*, *Distichodus*, *Nannocharax*, *Hemigrammocharax*, *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

In terms of overall body form, myology, osteology and dentition, *Xenocharax* is the least derived member of the monophyletic unit formed by citharinids and distichodontids. This generalized morphology is reflected in the omnivorous diet of this monotypic genus (see Daget, 1960, p. 39). Although characterized by a generalized morphological plan, the genus, nonetheless, possesses a series of apomorphous characters, some of which are unique to *Xenocharax* among characoids examined. These adaptations include:

56 the posterodorsal shift of the longitudinal axis of the vertebrae of the pars sustentaculum.
57 the marked reduction in the angle between the axis of the pars sustentaculum and the axis of the os suspensorium.
58 the subdivision of the suprapreopercle into two bony tubes.
59 the reduction in the branchiostegal number to three.
60 the increase to two inner dentary tooth rows.

Further information on the anatomy, biology and distribution of this genus is provided by Daget (1960).

The subunit of distichodontids formed by *Nannaethiops*, *Neolebias*, *Paradistichodus*, *Distichodus*, *Nannocharax*, *Hemigrammocharax*, *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* has a series of synapomorphies involving alterations to the pterotic and dermosphenotic and their associated sensory canals, together with adaptations of the neurocranium and opercle. The synapomorphous characters shared by these genera are:

61 the posterior expansion of the dermosphenotic over the primitively exposed lateral surface of the pterotic.
62 the shift of the contact of the suprapreopercle to the dermosphenotic.
63 the elaboration of the plesiomorphously Y-shaped dermosphenotic sensory canal system into an H-shaped complex.
64 the decrease in the laterally exposed portion of the pterotic and the reduction of the pterotic sensory canal system to a simple tube.
65 the possession of some form of fenestrated opercle.
66 the reduction of the cranial fontanelle so that it barely extends anterior of the epiphyseal bar.

Two subunits of the assemblage defined by characters 61–66 can in turn be distinguished by their less universal apomorphous characters. The first subunit is formed by the genera *Nannaethiops* and *Neolebias*, while the second consists of *Paradistichodus*, *Distichodus*, *Nannocharax*, *Hemigrammocharax*, *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

The complex formed by the genera *Nannaethiops* and *Neolebias* (the latter in this sense is equivalent to *Neolebias*, *Congocharax* and *Dundocharax* of previous authors) can be defined by the following derived characters:

67 the expansion of the suprapreopercle into a flat plate fitting the posteroventrally concave dermosphenotic.
68 the loss of the suprapreopercular sensory canal segment.
69 the marked secondary reduction or loss of the lateral ethmoid process extending between the lateral ethmoid and orbitosphenoid.
70 the reduction or loss of the portion of the dermosphenotic sensory canal communicating with the suprapreopercular sensory canal.
71 the possession of a ectopterygoid tooth patch.
72 the loss of the sixth hypural.

Among the distichodontid genera with several species, the complex formed by *Nannaethiops* and *Neolebias* is undoubtedly the best understood at the alpha-level. In their revision of these genera, Poll & Gosse (1963) dealt with all of the then known species in addition to describing several new forms. More recently Matthes (1964) described a new species, *Neolebias gracilis*. In the same publication that author removed *N. spilotaenia* to the genus *Congocharax* along with *C. olbrechtsi* which previously had been included in *Hemigrammocharax*. Poll & Lambert (1964), in turn, described a new species, *Congocharax gossei*, and Poll (1967) erected the genus *Dundocharax* for *D. bidentatus* which he described at the same time. Both *Congocharax* and *Dundocharax*, however, share the distinguishing characters of *Neolebias* and as will be discussed are placed into synonymy of that genus.

The cladogram of Fig. 48 shows the hypothesized interrelationships of *Nannaethiops* and *Neolebias* species based on evidence of this study. Characters uniting *Neolebias* and the monotypic genus *Nannaethiops* into a monophyletic unit were discussed above. Apomorphous characters common to subunits of this assemblage are:

(A) the reduction of the lateral line.
(B) the reduction or loss of the posteroventral and posterodorsal segments of the dermosphenotic sensory canal segment.
(C) the loss of one of the infraorbitals at the posterior margin of the orbit.
(D) the shift of the remaining infraorbitals so as to retain a fully ossified orbital rim.
(E) the total loss of the sensory canal systems of the dermosphenotic and pterotic.
(F) the loss of the remaining infraorbital element at the rear of the orbit.

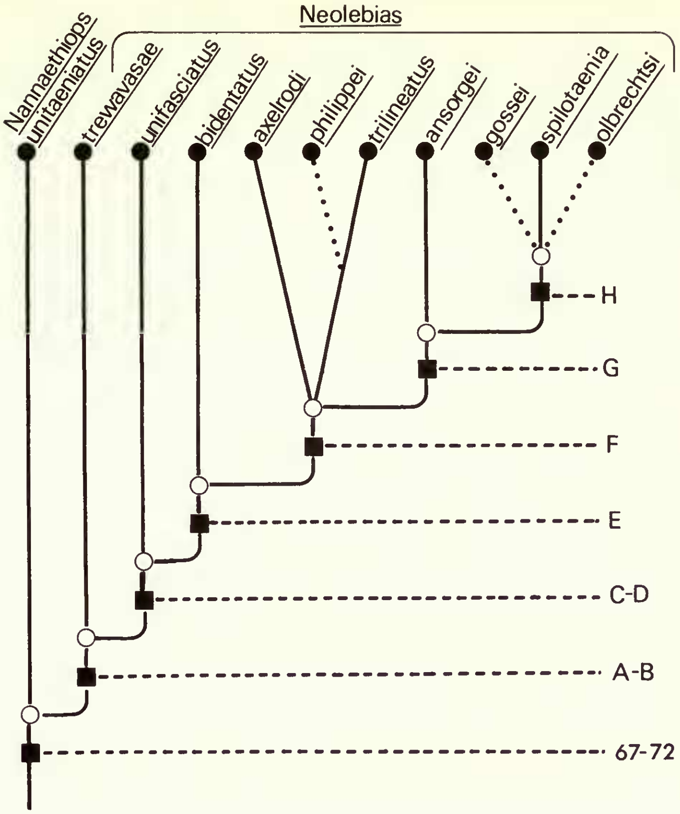

Fig. 48 Cladogram of the most parsimonious hypothesis of relationships in the unit formed by the genera *Nannaethiops* and *Neolebias*. Synapomorphies A–H correspond to those of the text.

(G) the loss of the dermosphenotic.

(H) the distinctive sensory pore system of the head.

Relationships of those species whose hypothesized phylogenetic position is based solely on information from the literature is indicated by dotted lines. *Neolebias phillipei*, as noted by Poll & Gosse (1963), appears to be closely related to *N. trilineatus* with which it shares an increased number of body stripes, a reduced circumpeduncular scale series and a low transverse scale count. *Neolebias olbrechtsi* and *N. gossei* share with *N. spilotaenia* a distinctive cranial sensory pore pattern which is unique to these species among distichodontids (see Poll & Lambert, 1964*b*, p. 407). Whether the former species also have *N. spilotaenia's* distinctive gill arch modifications and loss of infraorbitals 2 and 3 awaits further study. *Neolebias gracilis* of Matthes (1964) cannot be more closely assigned on the basis of literature information. However, it is difficult to visualize how the characters of this species could drastically alter the phylogeny arrived at here. The most parsimonious phylogeny resulting from the described characters necessitates several modifications to the previous taxonomy of species placed in *Neolebias* as a result of this study.

Neolebias bidentatus was originally placed by Poll (1967, p. 129) in the genus *Dundocharax* which was described at the same time. Despite Poll's statement that 'Ce genre est voisin du genre *Hemigrammocharax* . . .', the evidence now available shows it to belong to *Neolebias* as defined in this study. In addition to having the various characters autapomorphous for *Neolebias* among distichodontids, *Dundocharax* also lacks the multitude of apomorphous characters uniting *Hemigrammocharax* to *Nannocharax* and *Distichodus*. *Neolebias spilotaenia*, *N. gossei* and *N. olbrechtsi*, in turn, were placed in *Congocharax* by Matthes (1964) and Poll & Lambert (1964) on the basis of their distinctive cranial sensory pore patterns. Although available evidence supports the hypothesis of the monophyletic nature of the unit formed by these three species, it also indicates that they are assignable to the genus *Neolebias* as defined herein. Although both *Congocharax* and *Dundocharax* from monophyletic subunits of the Distichodontidae (the latter by virtue of its monotypy), reference to the cladogram in Fig. 48 shows that the recognition of both *Dundocharax* (*Neolebias bidentatus*) and *Congocharax* (*N. spilotaenia*, *N. olbrechtsi* and *N. gossei*) as separate genera would result in *Neolebias* (*sensu stricto*) being a non-monophyletic assemblage. This is a consequence of the fact that *Neolebias* is such a sense would not contain all descendants of its hypothesized common ancestor. In light of this inconsistency with a basic taxonomic principle of this study, and in so far as a uniqueness criterion for the determination of generic rank is arbitrary, both *Dundocharax* and *Congocharax* are placed as synonyms of *Neolebias*. *Neolebias* in this broader sense now constitutes a monophyletic subunit of the Distichodontidae.

A difference between the findings of this study and published observations should also be noted. Matthes in his diagnosis of the genus *Congocharax* (1964, p. 76) stated that it has the 'Maxillaire non denté . . .', a statement repeated by Poll & Lambert (1964, p. 336). However, this comment is contrary to the observed presence of three or four maxillary teeth throughout the type series of *Neolebias spilotaenia* (the *Congocharax spilotaenia* of the above workers). Furthermore, it conflicts with Poll & Gosse's statement that this species is characterized by 'Présence de dents a l'angle supérieur de maxillaire.' Whether the reported absence of teeth in *Neolebias gossei* and *N. olbrechtsi* is correct awaits further study. [Since this paper has gone to press, I have had the opportunity to examine specimens of *N. olbrechtsi*. That species has two bicuspidate maxillary teeth and derived characters 1–72 and A–H for *Neolebias*.]

The sister group to the unit formed by *Nannaethiops* and *Neolebias* is the multigeneric assemblage consisting of *Paradistichodus*, *Distichodus*, *Nannocharax*, *Hemigrammocharax*, *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. These genera share a series of synapomorphous jaw and suspensorium modifications including:

73 the lengthening of the horizontal extent of the suspensorium with a resultant forward shift of the articulation between the angulo-articular and quadrate.

74 the pronounced expansion of the premaxillary and dentary replacement tooth trenches.

75 the distinct horizontal shelf on the lateral surface of the quadrate and preopercle.

76 the loss of maxillary teeth.

77 the elongation of the teeth in the outer tooth row of each jaw and their pleurodont attachment to the anterior surface of the replacement tooth trench.

78 the possession of a distinct opercular fenestra.

The subunit of the Distichodontidae defined by these characters is, in turn, divisible into two monophyletic subunits. The first of these consists solely of the genus *Paradistichodus*, whereas the second contains *Distichodus*, *Hemigrammocharax*, *Nannocharax*, *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

The genus *Paradistichodus* contains two species characterized by the following hypothesized apomorphous characters:

79 the reduction in the number of hypurals to five.

80 the elongation of the supraethmoid.

81 the reduction in the number of epurals to one.

82 the reduction of the muscular portion of the lateral section of the A_2 portion of the *adductor mandibulae*.

Daget (1958) has discussed the biology, and aspects of the anatomy of the two nominal *Paradistichodus* species, *P. elegans* from the Chad and Benue systems and *P. dimidiatus* from the Niger and Gambia drainages. However, as discussed by Daget the differences between these nominal species are slight and may be a function of geographic variation.

The assemblage consisting of *Distichodus*, *Nannocharax*, *Hemigrammocharax*, *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* is characterized by the following hypothesized apomorphous characters:

83 the mobile articulation of the angulo-articular with the dentary.

84 the increased mobility of the upper jaw on the supraethmoid.
85 the increased attachment of the mesopterygoid to the neurocranium.
86 the increased envelopment of the palatine by the ectopterygoid and mesopterygoid.

The two subunits definable within the group of genera sharing characters 83 to 86 are the speciose assemblage formed by *Distichodus*, *Nannocharax* and *Hemigrammocharax*, and the multigeneric unit consisting of *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

The hypothesized monophyletic group consisting of *Distichodus*, *Nannocharax* and *Hemigrammocharax* forms a very distinctive unit within distichodontids on the basis of a series of apomorphous characters, some of which are unique to this assemblage within characoids. These characters are:

87 the pronounced restructuring of the overall form of the dentary and the anteroventral reorientation of its longitudinal axis.
88 the reduction or loss of the sensory canal segment in the dentary.
89 the anterior restructuring of the angulo-articular into an anterodorsally or dorsally-directed plate.
90 the marked overlap of the dentary and angulo-articular.
91 the elongation of the outer row of premaxillary and dentary teeth.
92 the reduction or loss of the anteromedial process of the supraethmoid.
93 the dorsal shift of the insertion of the lateral section of the A_2 portion of the *adductor mandibulae*.
94 the origin of the A_W portion of the *adductor mandibulae* from the dorsal edge of the tendon of the A_2 and A_3 sections of the muscle, and the pronounced extension of the A_W posterior of the edge of the angulo-articular.
95 the crossing at right angles of the *ligamentum primordiale* and the tendon of the A_1 portion of the *adductor mandibulae*.

These characters are all either modifications of the jaws, or osteological and myological alterations correlated with the distinctive jaws and jaw action of these genera. Functionally, these alterations have resulted in a system permitting a degree of horizontal dentary motion that is unique among characoids.

Within the hypothesized monophyletic assemblage formed by *Distichodus*, *Nannocharax* and *Hemigrammocharax*, a subunit consisting of *Nannocharax* and *Hemigrammocharax* is definable on the basis of the following synapomorphies:

96 the posteriorly-directed dentary processes flanking the dentary symphysis.
97 the loss of the inner premaxillary tooth row.
98 the loss of the sensory canal segment in the dentary.
99 the loss of the inner dentary tooth row.
100 the reduction or loss of the premaxillary articular fossa.
101 the vertical expansion of the posterior strut of the lateral ethmoid.
102 the horizontal expansion of the hyomandibula.
103 the loss of postcleithrum 1.
104 the development of anterior diverticulae of the anterior swimbladder chamber.
105 the restructuring of the ventral portion of the sphenotic spine into a posteroventrally sloping shelf.
106 the opening of the opercular fenestra to the dorsal margin of the bone.
107 the reduction of the metapterygoid–quadrate fenestra.

Although both the assemblage formed by *Distichodus*, *Nannocharax* and *Hemigrammocharax*, and the unit consisting of *Nannocharax* and *Hemigrammocharax* are defined by a series of apomorphous characters, the monophyly of the genera *Distichodus*, *Hemigrammocharax* and *Nannocharax* is either refuted or brought into question by the results of this study. Previous classifications utilized the larger size, higher dorsal fin-ray count and multiple rows of functional premaxillary and dentary teeth of *Distichodus* as the main characters distinguishing that genus from the unit formed by *Nannocharax* and *Hemigrammocharax*. However, in so far as all citharinids and distichodontids are larger as adults than *Nannocharax* and *Hemigrammocharax* species, the larger size of *Distichodus* species relative to that of these genera appears to be plesiomorphous. Similarly, the high dorsal-fin ray count and inner row of premaxillary and dentary teeth are widespread among distichodontids (the former feature also occurs in citharinids). Thus both of these characters must be considered plesiomorphous for the group formed by *Distichodus*, *Nannocharax* and *Hemigrammocharax*. Consequently none of the characters previously used as distinguishing features of *Distichodus* relative to *Nannocharax* and *Hemigrammocharax* is a valid basis for a hypothesis of the monophyly of *Distichodus*. Furthermore, none of the apomorphous characters found during this study support such a hypothesis. Indeed the results of this investigation indicate that as presently constituted *Distichodus* represents a grade level concept, with some *Distichodus* species more closely related to the unit formed by *Nannocharax* and *Hemigrammocharax* than to their congeners. The characters refuting the hypothesis of the monophyly of *Distichodus* are:

(A) the restructuring of the articular processes of the supraethmoid into pointed prong-like structures in *Distichodus lusosso*, *D. niloticus* and *D. fasciolatus*. This approximates to the hypothesized derived *Nannocharax* and *Hemigrammocharax* forms of these structures, but contrasts with the plesiomorphous flattened condition of the processes in *Distichodus notospilus* and *D. brevipinnis*.

(B) the elongation of the supraethmoid in *Distichodus lusosso*, *D. niloticus* and *D. fasciolatus*. This feature is shared with *Nannocharax* and *Hemigrammocharax* but contrasts with the plesiomorphous square supraethmoid in some *Distichodus* species.

(C) the shift from the transversely elongate articular fossa on the rear of the premaxilla present in *Distichodus notospilus* and *D. brevipinnis* to a dorsally located pit in *D. lusosso*, *D. niloticus* and *D. fasciolatus*. The latter condition approximates to the derived articular fossa form of *Nannocharax* and *Hemigrammocharax*.

(D) the ventral expansion of the sphenotic spine in *Distichodus lusosso* and *D. niloticus*, a modification carried further in *Nannocharax* and *Hemigrammocharax*. This condition contrasts with the plesiomorphous ventrally sharp-edged spine common to some *Distichodus* species.

These characters and associated changes in neurocranial form are congruent with the hypothesis that *D. lusosso*, *D. niloticus* and *D. fasciolatus* are more closely related to the unit formed by *Nannocharax* and *Hemigrammocharax* than to some of their congeners. It is thus concluded that the genus *Distichodus* as presently defined is non-monophyletic. However, the exact distribution of these and other derived characters among the numerous nominal *Distichodus* species awaits further study as does a redefinition of *Distichodus* based on derived characters.

As discussed previously *Nannocharax* and *Hemmigrammocharax* share a multitude of apomorphous characters congruent with the hypothesized monophyly of the unit they form within distichodontids. However, the monophyly of each of these genera is open to question. Previous classificatory schemes differentiated these genera on the basis of the reduced lateral line in *Hemigrammocharax*, in contrast to the retention of the plesiomorphous complete lateral line in *Nannocharax*. However, although it is most parsimonious to assume that a reduced lateral line is derived within distichodontids, as discussed by Roberts (1967, p. 252) there is some doubt as to whether the reduced lateral line of the various *Hemigrammocharax* species results from common ancestry or multiple independent losses. Furthermore, the distribution of derived states of the infraorbital series, fourth upper pharyngeal tooth plate and ossifications of the submaxillary cartilage are incongruent with the hypothesis of the monophyletic nature of both *Nannocharax* and *Hemigrammocharax* as presently defined.

A resolution of the question of the monophyletic nature of the genera *Nannocharax* and *Hemigrammocharax* and of the relationships within the complex formed by *Distichodus*, *Nannocharax* and *Hemigrammocharax* would necessitate a total revision of this speciose assemblage. Such an undertaking is beyond the aim of this study. Thus, until such a study is accomplished, these genera are tentatively retained as presently defined although the hypothesis of the monophyly of *Distichodus* is contraindicated and that of *Nannocharax* and *Hemigrammocharax* cast in doubt. Further information on the ecology, anatomy and taxonomy of some *Distichodus* and *Nannocharax* species can be found in Daget (1959, 1961).

The sister group to the assemblage formed by *Distichodus*, *Nannocharax* and *Hemigrammocharax* consists of the genera *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. These genera form a distinctive subunit of distichodontids sharing the following derived characters:

108 the marked reduction of the maxilla.
109 the loss of the medially-directed anterodorsal maxillary process.
110 the immovable articulation between the maxilla and premaxilla.
111 the prominent posterodorsal dentary process.
112 the elongation of the metapterygoid–quadrate fenestra and an increased contribution of the symplectic to its posterior border.
113 the markedly increased upper jaw mobility.
114 the medial shift of the position of the preopercular sensory canal.
115 the loss of the attachment of the A_1 portion of the *adductor mandibulae* to the maxilla.
116 the strongly developed teeth of the outer tooth row.

The above adaptations are primarily associated with the functionally distinctive jaws characteristic of these genera. As noted earlier, the loss of the attachment of the A_1 portion of the *adductor mandibulae* to the maxilla is considered an apomorphous secondary loss for this assemblage. Among other distichodontids such an attachment is advantageous in contributing to the greater mobility of the upper jaw. However, the restructuring of the jaws in the genera under discussion results in a pronounced motion of the upper jaw without the necessity for an insertion of the A_1 on the maxilla. Indeed, in these genera the retention of such an attachment would be ineffective or of little advantage due to the drastically altered form of the maxilla and its immobile articulation with the premaxilla.

Within the assemblage defined by apomorphies 108–116, two monophyletic subunits are distinguishable on the basis of shared derived characters. These are the genus *Hemistichodus* and the unit formed by *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

The members of the genus *Hemistichodus* are distinguished by a series of jaw and dental modifications, most of which are unique among characoids examined. The apomorphies for the genus are:

117 the greatly reduced maxilla which is totally excluded from the gape.
118 the pronounced development of the posterodorsal dentary ramus.
119 the great reduction and restructuring of the supraethmoid.
120 the modification of the premaxillary articular fossa into a rounded depression on the dorsal surface of the bone.
121 the loss of the inner tooth row on the dentary and premaxilla.
123 the lateral orientation of the replacement tooth trenches.

Hemistichodus consists of three west African and Congo basin species which have a relatively small adult size. Within the genus, *Hemistichodus mesmaekersi* and *H. lootensi* are hypothesized to form a monophyletic group on the basis of their apomorphous medially interrupted lateral line (see Daget, 1968, Fig. 1). These species, in turn, constitute the sister group to the third *Hemistichodus* species, *H. vaillanti*. Daget (1968) has reviewed aspects of the anatomy, biology and taxomony of the members of *Hemistichodus*.

The sister group to *Hemistichodus* within the Distichodontidae is formed by the assemblage consisting of *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. These genera have a series of synapomorphous modifications of the jaws, neurocranium and dermal head bones including:

124 the loss of the posteroventral process of the dentary.
125 the reduction of the infraorbital series to four elements.
126 the interdigitating premaxillary joint or a further derived condition of such a symphysis.
127 the horizontal elongation of the sphenotic and the reorientation of the sphenotic spine into a posteroventrally sloping or horizontal shelf having a reduced lateral extent.
128 the loss of the lateral ridge on the lateral commissure and on portions of the sphenotic and parasphenoid.

129 the reduced contribution of the prootic to the lip of the opening to the posterior myodome.
130 the transverse ridge on the ventral surface of the frontal.
131 the posterior shift of the hyomandibular fossa and lateral commissure.
132 the slender, anteriorly concave hyomandibular.
133 the reduction of the cranial fontanelle to posterior to the epiphyseal bar.
134 the lateral and posterior expansion of the horizontal shelf on the lateral surface of the preopercle.
135 the expansion of the origin of the *adductor mandibulae* onto the medial face of the hyomandibula and lateral surface of the sphenotic and pterotic.
136 the expansion of the origin of the *levator arcus palatini* onto the anterior surface of the sphenotic spine.

These modifications, which are primarily related to the jaws and jaw action, result in a lower jaw motion unique to these genera among characoids (see p. 271). Within this assemblage a dichotomous sister group relationship is hypothesized between *Ichthyborus* (the *Ichthyborus*, *Phagoborus* and *Gavialocharax* of previous authors) and the multigeneric unit consisting of *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

The genus *Ichthyborus* as herein defined is a distinctive assemblage of four species characterized by the following synapomorphous characters:

137 the symphyseal fusion of the dentaries.
138 the enlargement of the anterior tooth cusp.
139 the possession of a median dentary tooth.
140 the form of the angulo-articular-dentary joint.
141 the posterodorsal expansion of infraorbital 4 and the congruent separation of the dermosphenotic from the orbital rim.
142 the marked median shift of the preopercular sensory canal segment in the vertical portion of the bone.
143 the loss of the ligamentous attachment of the palatine to the maxilla.
144 the insertion of the A_1 portion of the *adductor mandibulae* on the angulo-articular.

Together these adaptations result in a distinctive subunit of distichodontids specialized for an ichthyovorous diet, although one subspecies of *Ichthyborus besse* is reported to be a fin eater (see Lek & Lek, 1978). The taxonomic concept of *Ichthyborus* in this work is, however, much broader than that of earlier workers. Figure 49 illustrates the hypothesized relationships of the four species assigned to *Ichthyborus* in this study. The characters synapomorphous for *Ichthyborus* were discussed above. Apomorphous characters common to subunits of this genus are:

(A) the greater relative enlargement of the anterior tooth cusp.
(B) the enlarged canine-like teeth at the front of each jaw.
(C) the loss of the inner dentary tooth row.
(D) the loss of the inner premaxillary tooth row.
(E) the elongation of the jaws.

Previous classifications placed *Ichthyborus monodi* and *I. besse* in the monotypic genera *Gavialocharax* and *Ichthyborus* respectively, whereas *I. ornatus* and *I. quadrilineatus* were assigned to *Phagoborus*. However, in light of the phylogeny arrived at here, such a subdivision is untenable since in such a system *Phagoborus* (the *I. ornatus* and *I. quadrilineatus* of this study) does not form a monophyletic unit. In order to resolve this inconsistency both *Phagoborus* and *Gavialocharax* are synonymized with *Ichthyborus*. This results in *Ichthyborus* (*sensu lato*) forming a monophyletic multispecific subunit of distichodontids. In contrast, the alternative possibility, the erection of a new genus to contain *I. quadrilineatus*, fails to indicate the relationship of its sole species to other members of this complex and further subdivides an already greatly split assemblage.

Finally, a discrepancy between the findings of this study and published information should be noted. Pellegrin (1904) and Boulenger (1909) described *Ichthyborus quadrilineatus* (the *Neoborus quadrilineatus* of those authors) as having a single series of teeth in each jaw. However, in all *I. quadrilineatus* specimens examined an inner row of premaxillary teeth is also present.

The genera *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago* are hypothesized as forming a monophyletic unit on the basis of their common possession of the following derived characters:

145 the enlargement of the posterior tooth cusp.
146 the possession of an immobile interdigitating joint at the rear of the dentary symphysis.
147 the anterior and posterior expansion of the third infraorbital.
148 the form of the angulo-articular-dentary articulation.
149 the loss of the supraorbital.
150 the reduction of the anteromedial supraethmoid process.
151 the possession of a posterodorsal preopercular flange.

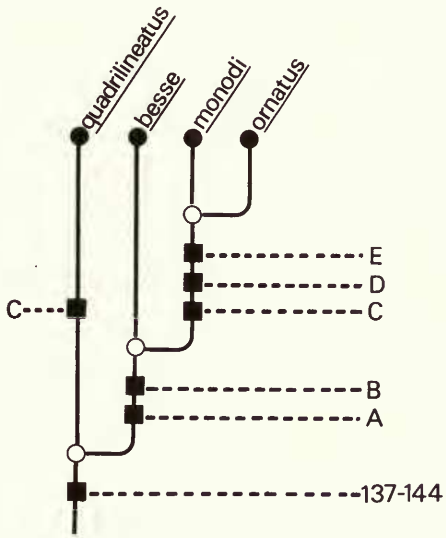

Fig. 49 Cladogram of the most parsimonious hypothesis of relationships in the genus *Ichthyborus*. Synapomorphies A–E correspond to those of the text

Within the subunit of distichodontids defined by apomorphous characters 145–151, a dichotomy is hypothesized between *Microstomatichthyoborus* and the group formed by *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. However, whereas the latter genera share a series of apomorphous characters, no derived feature unique to *Microstomatichthyoborus* in the Distichodontidae has been found in this study. Nonetheless, because of the lack of evidence contraindicating the monophyly of the unit formed by the two nominal *Microstomatichthyoborus* species (*bashforddeani* and *katangae*), the genus is retained for the present.

The genera *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*, in contrast, share the following apomorphous characters:

152 the reorientation of the sphenotic spine into an horizontal shelf.
153 the lateral reduction of the sphenotic spine so as to barely reach laterally to the frontal.
154 the loss of the cartilaginous rod joining the palatine to the maxilla.
155 the pronounced reduction of the laterally exposed portion of the pterotic and a shortening of the pterotic sensory canal.
156 the elongation of the pterosphenoid and orbitosphenoid.
157 the ventral shift of the attachment of the gill arches to the parasphenoid.
158 the pronounced reduction of the cranial fontanelle.
159 the presence of a fossa on the rear of the hyomandibula to receive the dorsal tip of the preopercle.

Characters 152–158 distinguish a generic assemblage which can in turn be divided dichotomously. One subunit consists of the genus *Mesoborus*, whereas the other is formed by the genera *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

Mesoborus is a distinctive genus whose single contained species, *M. crocodilus*, is a voracious predator (Matthes, 1964, p. 65). This life style is reflected in the following autapomorphous modifications:

160 the ontogenetic loss of the anterior tooth cusp resulting in a nearly unicuspidate dentition.
161 the enlarged second to fourth dentary teeth.
162 the development of the anterior premaxillary teeth into canines.
163 the reduction of the second to fourth premaxillary teeth which arise from a distinctly concave region of the premaxilla.

The sister group to *Mesoborus* among distichodontids is formed by the genera *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. This assemblage is characterized by the following apomorphies:

164 the transversely thickened and horizontally shortened angulo-articular.
165 the posteroventral recontouring of the maxilla into a rounded knob.
166 the development of a groove on the lateral surface of the posterodorsal dentary ramus.
167 the marked reduction of the anteromedial supraethmoid process.
168 the expanded, laterally-orientated supraethmoid articular processes.
169 the restructuring of the premaxillary articular fossa into a laterally directed pit.
170 the laterally reduced sphenotic spine which falls short of the edge of the frontal.
171 the reduction of the anterior sphenotic process capping the transverse ridge of the frontal.
172 the pronounced dorsal process of the hyomandibula.
173 the possession of a ventromedial parasphenoid ridge.
174 the reduction of the vertical extent of the *levator arcus palatini* and its attachment to the hyomandibula *via* an aponeurosis.

Most of these characters are either changes in the form of the jaws or alterations in their relationships to each other, the neurocranium and the suspensorium. These adaptations result in a close meshing of the upper and lower jaws during closure of the mouth. This tight fit together with the pronounced gape characteristic of these genera and their enlarged *adductor mandibulae* muscles results in a system well adapted for the fin-nipping habits previously reported for *Phago*, *Belonophago* and *Eugnatichthys* (see Matthes, 1961; Gosse, 1963; Burchard, 1968) and found in *Paraphago* during this study.

This assemblage of genera can, in turn, be dichotomously divided into two monophyletic subunits. These are the genus *Eugnatichthys* and the unit consisting of *Paraphago*, *Phago* and *Belonophago*.

Eugnatichthys is a distinctive genus of distichodontids characterized by the following autapomorphous characters:

175 the massive development of the premaxilla and dentary.
176 the transverse expansion of the maxilla.
177 the transversely expanded angulo-articular.
178 the subdivision of the A_3 portion of the *adductor mandibulae* muscle.
179 the horizontal elongation of the sphenotic, with an associated shift posteriorly of the lateral commissure and hyomandibular fossa.
180 the pronounced development of the median parasphenoid ridge into a knife-like process.
181 the reduction of the dorsal posttemporal fossa.

Eugnatichthys is composed of only two species (*eetveldii* and *macroterolepis*) but is one of the most distinctive genera among distichodontids as a consequence of its relatively massive jaws. These adaptations of the jaws and associated osteological systems, together with the pronounced development of the *adductor mandibulae* muscles, permit these species to bite off relatively thicker fin segments than can any other fin-eaters examined.

The hypothesized sister group to *Eugnatichthys* is formed by the unit consisting of *Paraphago*, *Phago* and *Belonophago*. This assemblage is characterized by the following hypothesized apomorphous characters:

182 the reduction or loss of infraorbital 4.
183 the expansion ventrally of the dermosphenotic.
184 the contact of the posteroventral border of the pterosphenoid with the ascending process of the parasphenoid.
185 the elongation of the jaws.
186 the loss of the anterior sphenotic process plesiomorphously capping the transverse ridge of the frontal.

It should be noted, however, that because *Paraphago* is known only from its syntypes, it was not possible to study the genus myologically, or to analyse those internal osteological characters not amenable to examination by radiographs. It is thus possible that some of the characters listed below as synapomorphies for *Phago* and *Belonophago* are shared with *Paraphago*. Although no characters autapomorphous for *Paraphago* within distichodontids were found during this study, the genus is, nonetheless, monophyletic by virtue of its monotypy.

The remaining distichodontid genera, *Phago* and *Belonophago*, share the following hypothesized synapomorphies:

187 the marked expansion of the supraethmoid articular processes into rounded, laterally-directed structures.
188 the extensive horizontal elongation of the symplectic, metapterygoid and metapterygoid–quadrate fenestra.
189 the loss of infraorbital 4.
190 the pronounced ventral expansion of the dermosphenotic.
191 the pronounced dorsal expansion of infraorbital 3.
192 the heavy bony scales having a prominent bump over the scale focus.
193 the single epural.
194 the very wide contact of the posteroventral margin of the pterosphenoid with the ascending process of the parasphenoid.
195 the ventral expansion of the fused postcleithra 2 and 3.
196 the expansion of the origin of the *levator arcus palatini* onto the ventral surface of the frontal.

Phago and *Belonophago* are, in turn, each characterized by several autapomorphous characters. Derived features of *Phago* are:

197 the thickened, vertically elongate scales.
198 the anteroventrally curved premaxilla that overlaps the anterior end of the dentaries.

Presently four nominal species of *Phago* (*boulengeri*, *intermedius*, *loricatus* and *maculatus*) occur in the literature. However, *P. maculatus* of the Niger drainage is questionably distinct from *P. loricatus* of the same system.

Belonophago is a very distinctive genus having the following autapomorphies:

199 the marked elongation of the jaws.
200 the expansion of the pterosphenoid so as to form the entire anterior surface of the braincase.
201 the median contact between the pterosphenoid and parasphenoid.
202 the extreme elongation of the metapterygoid and symplectic.
203 the loss of the sensory canal system in the dermosphenotic.
204 the loss of the sensory canal system in infraorbital 3.
205 the posteriorly-directed spinous processes on the scales.
206 the secondary loss of the transverse ridge on the ventral surface of the frontal.

The two nominal *Belonophago* species (*tinanti* and *hutsebouti*) are characterized by a markedly elongate, cylindriform shape (see Poll, 1957, Fig. 142). The fin-nipping habits of this genus were reported on by Matthes (1961, p. 78) and confirmed in this study by stomach content analyses.

Convergent characters

The hypothesis of relationships presented above is the most parsimonious derivable from available information on character distribution and polarity in the systems analysed among citharinids and distichodontids. However, as might be expected in such a large diverse assemblage, there occur a number of hypothesized apomorphous characters whose distribution is incongruent with that of the overall most parsimonious hypothesis of relationships. The majority of these incongruities are loss characters. Although loss characters provide useful information for a phylogenetic reconstruction, they can sometimes be misleading in so far as the non-homology of losses can be difficult to ascertain. Apomorphous loss characters which have a distribution incongruent with that of a majority of the derived characters among citharinids and distichodontids are:

(A) the loss of the maxillary teeth in citharinids and all distichodontids other than *Xenocharax*, *Nannaethiops* and *Neolebias*.
(B) the loss of the inner dentary tooth row in citharinids, *Hemistichodus*, some *Ichthyborus* species and the unit formed of *Nannocharax* and *Hemigrammocharax*.
(C) the loss of the inner premaxillary tooth row in *Hemistichodus*, some *Ichthyborus* species and the unit consisting of *Nannocharax* and *Hemigrammocharax*.
(D) the loss of the sixth hypural in *Paradistichodus* and the unit formed by *Neolebias* and *Nannaethiops*.
(E) the loss of one epural in *Paradistichodus* and the group consisting of *Phago* and *Belonophago*
(F) the loss of the cartilaginous connection between the palatine and maxilla in *Ichthyborus* and the assemblage containing *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.
(G) the reduction of the anteromedian supraethmoid process in the group formed by *Distichodus*, *Nannocharax* and *Hemigrammocharax*, and the unit consisting of *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.
(H) the loss of the dermosphenotic sensory canal segment in some *Neolebias* species and the genus *Belonophago*.
(I) the reduction of the lateral line in *Neolebias* and *Hemigrammocharax*.
(J) the reduction of the maxilla in citharinids and the distichodontid genera *Hemistichodus*, *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

Apomorphous gain characters evidently acquired independently several times in the assemblage formed by the Citharinidae and Distichodontidae are:

(A) the elongation of the jaws in some *Ichthyborus* species and the assemblage formed by *Paraphago*, *Phago* and *Belonophago*.
(B) the presence of a second inner dentary tooth row in *Xenocharax* and some *Neolebias trilineatus* specimens.
(C) the elongation of the supraethmoid in *Paradistichodus* and the unit consisting of *Nannocharax*, *Hemigrammocharax* and some *Distichodus* species.
(D) the interpremaxillary interdigitations of citharinids and the group formed by *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*.

In addition to the characters listed above there is also a series of apomorphies which although seemingly convergent within citharinids and distichodontids can, nonetheless, be shown to be non-homologous. Foremost among these is the loss of infraorbitals 4 and 5 in some *Neolebias* species, some *Nannocharax* species and the subunit of distichodontids formed by *Ichthyborus*, *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. As discussed earlier the loss of these bones in each of these groups is achieved by an independent non-homologous method. Similarly, the mode of reduction or loss of the metapterygoid–quadrate fenestra differs between *Neolebias spilotaenia* and the unit formed by *Nannocharax* and *Hemigrammocharax*. In the former the opening is eliminated by an expansion of the symplectic, whereas in the latter genera the fenestra is reduced or lost as a consequence of the approximation of the symplectic and metapterygoid. Similarly, the medially interrupted lateral line is *Hemistichodus* differs from the reduced lateral line of *Neolebias* and *Hemigrammocharax*. In the latter genera, the lateral line is lacking both medially and posteriorly with this reduction limited to the posterior part of the body in some *Hemigrammocharax* species (see *H. angolensis*, Poll, 1967, Fig. 51).

As noted earlier, the canine dentition of the lower jaws of *Mesoborus* and some *Ichthyborus* species differs in which teeth are enlarged. Although both of these taxa have the anterior teeth of the premaxilla enlarged, these canines are non-homologous. In *Mesoborus* the enlarged anterior premaxillary teeth are a consequence of the great expansion of the posterior tooth cusp. In *Ichthyborus*, in contrast, the canines are formed by an enlarged anterior cusp.

Finally, it should be noted that the differences between the reduced maxilla of citharinids and some distichodontids (loss character J) are such as to cast doubt in the homology of these reductions. Similarly, the interpremaxillary interdigitations occurring in citharinids and a subunit of distichodontids (gain character D) are rather different and may have arisen independently.

Thus many of the seemingly convergent characters are, on closer examination, found to be non-homologous. Even in those cases where the homology of the convergencies is not refuted, the overall distribution of apomorphous characters is such that any alterations made to the proposed phylogeny, in order to resolve some or all of these evident convergencies, results in a less parsimonious theory of interrelationships.

Conclusions

The translation of the proposed phylogeny into a classification has necessitated several major changes in the previous generic and suprageneric taxonomy of the genera herein assigned to the families Citharinidae and Distichodontidae. Most previous classifications (Boulenger, 1909; Monod, 1950; Greenwood *et al.*, 1966) recognize three families or subfamilies for this group of genera. Although the taxonomic level applied to any group of organisms is arbitrary, the familial level ranking of Greenwood *et al.*, which is most widely used in the modern literature, is retained.

The family Citharinidae of Greenwood *et al.* (1966) remains unchanged in so far as it was found to represent a monophyletic unit. In contrast, the previous concepts of the Distichodontidae (or subfamily Distichodontinae) included the genera *Xenocharax*, *Nannaethiops*, *Neolebias* (the *Neolebias*, *Congocharax* and *Dundocharax* of previous authors), *Paradistichodus*, *Distichodus*, *Nannocharax* and *Hemigrammocharax* in the family (or subfamily). Reference to the proposed phylogeny shows, however, that such a classification results in the family representing a grade level assemblage. This gradal taxon forms a series of sister groups to a unit composed of *Hemistichodus*, *Ichthyborus* (the *Ichthyborus*, *Phagoborus* and *Gavialocharax* of previous authors), *Microstomatichthyoborus*, *Mesoborus*, *Eugnatichthys*, *Paraphago*, *Phago* and *Belonophago*. This latter assemblage constitutes the family Ichthyboridae or subfamily Ichthyborinae of earlier classifications. In light of the proposed phylogeny we can see that under previous classifications, some distichodontids would be more closely related to ichthyborids than to members of their own family. However, the retention of a gradistic, non-monophyletic taxon is untenable under the systematic procedures adopted as a basis for this study. Consequently, the family Ichthyboridae of Greenwood *et al.* (1966) (the Ichthyborinae of various authors) is sunk into the family Distichodontidae. The family Distichodontidae in this broader sense now forms a monophyletic group within characoids.

As discussed previously, the genera *Congocharax* and *Dundocharax* are placed as synonyms of *Neolebias* in order to resolve the previously non-monophyletic nature of *Neolebias*. The genera *Phagoborus* and *Gavialocharax*, in turn are synonymized into *Ichthyborus* as a consequence of the previous non-monophyly of *Phagoborus*. Finally, although the monophyly of *Distichodus*, *Nannocharax* and *Hemigrammocharax* is refuted or cast into doubt by the results of this study, these taxa are tentatively retained until such time as the subunit they form in the Distichodontidae can be studied in depth.

To summarize, the proposed classification of these families is as follows:

Family Citharinidae
    Genus *Citharinus* Cuvier, 1817
    Genus *Citharidium* Boulenger, 1902

Family Distichodontidae
  Genus *Xenocharax* Günther, 1867
  Genus *Nannaethiops* Günther, 1871
  Genus *Neolebias* Steindachner, 1894
  Genus *Paradistichodus* Pellegrin, 1922
  Genus *Distichodus* Müller and Troschel, 1845
  Genus *Nannocharax* Günther 1867
  Genus *Hemigrammocharax* Pellegrin, 1922
  Genus *Hemistichodus* Pellegrin, 1900
  Genus *Ichthyborus* Günther, 1864
  Genus *Microstomatichthyoborus* Nichols and Griscom, 1917
  Genus *Mesoborus* Pellegrin, 1900
  Genus *Eugnatichthys* Boulenger, 1898
  Genus *Paraphago* Boulenger, 1899
  Genus *Phago* Günther, 1865
  Genus *Belonophago* Giltay, 1929

The question of the relationship of the unit formed by citharinids and distichodontids to other characoids has not been resolved within this study. Various characters, such as the possession of a suprapreopercle, the lack of an interdigitating symphyseal dentary hinge and the anterior shift of the olfactory lobe, occur in groups outside of these families. However, in most cases these outgroups can be shown to be part of larger assemblages whose other members lack the apomorphous character in question. The characoid outgroup that has the greatest number of hypothesized apomorphous characters similar to those of, or occurring within, the unit formed by citharinids and distichodontids, is the Neotropical family Parodontidae. These bottom-dwelling fish, whose sister group is presently undetermined, have an anteriorly trifurcate supraethmoid articulating with the premaxillary articular fossae of the posteroventrally shifted upper jaw. Furthermore, parodontids have a slight anterior shift of the olfactory lobes and a distichodontid type of contact between the lateral ethmoid and orbitosphenoid. Such characters in isolation place parodontids close to the distichodontid genus *Nannocharax*. However, an overall analysis of parodontid anatomy reveals a series of inconsistencies with such an hypothesis. The Parodontidae lack a series of the synpapomorphies defining the unit formed by citharinids and distichodontids including: the modifications of the pars sustentaculum of the Weberian apparatus, the fusion of hypurals 1 and 2, the bicuspidate tooth form, the fusion of postcleithra 2 and 3, the separate suprapreopercle, the ovoid third posttemporal fossa bordered by the epioccipital and exoccipitals and the bifurcate pelvic bone. Furthermore, parodontids lack most of the numerous synapomorphies for distichodontids and for subunits of the Distichodontidae that include *Nannocharax*. Because of the absence of these characters in parodontids and because of other incongruities, it is impossible either to place the Parodontidae as part of a unit formed by the Citharinidae and Distichodontidae within characoids or to consider them as a sister group to that unit. A resolution of this problem posed by the seemingly independent acquisition of various apomorphous characters in parodontids and certain subunits of citharinids and distichodontids awaits a better understanding of characoid interrelationships.

Comparisons with previous classifications

As noted above, the classification arrived at in this study differs from those of Boulenger (1909) and Greenwood *et al.* (1966) which recognized two families or subfamilies within the group forming the family Distichodontidae of this study. Whereas such a division was the most commonly accepted classificatory scheme for the last three-quarters of a century, some workers divided citharinids and distichodontids along different lines. Regan (1911, pp. 21–23) recognized five subfamilies, one of which, his Xenocharacinae, was non-monophyletic according to the phylogeny proposed in this work. Eigenmann (1909, pp. 253–255) also recognized five subfamilies, but with different limits. Although he did not specifically list the genera assigned to each of the taxa, Eigenmann's key shows both his Neolebiinae and Ichthyborinae to be non-monophyletic, even allowing for the fewer species and genera described at that time. Subsequently, Gregory & Conrad (1938, p. 350) expanded the subfamily Citharininae to include *Citharinus*, *Citharidium*, *Nannaethiops*, *Neolebias*, *Xenocharax* and *Hemistichodus*. Their Distichodontinae, in turn, was composed of the genera *Distichodus*, *Nannocharax*, *Ichthyborus*, *Mesoborus*, *Phagoborus*, *Eugnatichthys*, *Paraphago* and *Phago*. However, a comparison of the limits of these taxa with the phylogeny here proposed shows that neither of Gregory & Conrad's subfamilies represents a monophyletic unit. That is, neither contains all the descendants of its hypothesized common ancestor. Monod (1950, p. 58) recognized three subfamilies, Citharininae, Distichodontinae and Ichthyborinae, within the group under discussion. However, his definition of the Distichodontinae (characterized by the 'Articulaire et dentaire articulés par chevauchement latéral . . .' – the *Distichodus* form of lower jaw) excludes *Neolebias*, *Nannaethiops*, *Xenocharax* and *Paradistichodus* from that subfamily. Furthermore, these genera are similarly excluded from the Citharininae and Ichthyborinae under Monod's definition of those subfamilies. Finally, Poll (1973, Fig. 1) lists his Citharininae as consisting of *Citharinus*, *Citharidium*, *Xenocharax*, *Nannaethiops*, *Neolebias*, *Dundocharax*, *Paradistichodus*, *Distichodus*, *Nannocharax* and *Hemigrammocharax* (on p. 114 of his paper he stated that there are eleven citharinid genera. The missing genus of his Fig. 1 appears to be *Congocharax*). The expansion of the family Citharinidae by this group of nominal distichodontid genera, although resolving the non-monophyly of the Distichodontidae (sensu Greenwood *et al.*, 1966), as a consequence of the elimination of the taxon, simultaneously converts the previously monophyletic Citharinidae into a gradal non-monophyletic group.

Comments on the African Characidae

In the course of outgroup comparisons involved in this study of the Citharinidae and Distichodontidae, several characters of relevance to an understanding of the hypothesis of the monophyly of the African Characidae and to relationships within African characids were found. As noted by Roberts (1969, p. 441) the shape of the upper jaw and dentition is distinctive for African characids among characoids. Furthermore, all African characids examined during this study, with the exception of *Lepidarchus*, have a small third posttemporal fossa totally contained within the epioccipital. The possession of this apomorphous character together with the unique jaw and dental modifications described above is consistent with the hypothesis that the African Characidae forms a monophyletic subunit of characoids.

Thus on the basis of available information, African characoids can be assigned to three monophyletic groups: the unit formed by the Citharinidae and Distichodontidae; the assemblage formed by the members of the African Characidae; and the monotypic family Hepsetidae. However, relationships of these groups to each other and to Neotropical characoids are presently undetermined.

Several other characters are of relevance for an understanding of the relationships within the African Characidae and for questions on the validity of the presently recognized generic and suprageneric taxa in this group. In the course of the discussion on the morphology of the anterior orbital region, it was noted that a bony tube surrounding the olfactory tract and bulb was described by Starks (1926, p. 167) for *Alestes liebrechstii* and *A. grandisquamis*. More recently Roberts (1969, p. 441) also noted this orbitosphenoid process in *Alestes baremose*, *A. imberi*, *A. marcolepidotus*, *Bryconaethiops* and *Hydrocynus*, and it has also been found in *Alestes dentex* and *A. macrophthalmus* during this study. This bony tube, which is lacking in all other African characids examined, is hypothesized as being apomorphous for these taxa among characoids on the basis of ontogenetic and outgroup comparisons. Those species with an orbitosphenoid tube also have the premaxillae joined by interpremaxillary interdigitations. As discussed earlier, both the broadened contact of the premaxillae anterior to the supraethmoid spine, and the associated symphyseal interdigitations are considered apomorphous and thus indicative of the monophyletic nature of the assemblage formed by the taxa possessing them. Congruent with these apomorphic modifications of the premaxillae and orbitosphenoid is the forward shift of the olfactory bulb in *Hydrocynus*, *Bryconaethiops* and various *Alestes* species (*imberi*, *dentex*, *liebrechstii*, *macrophthalmus*, *macrolepidotus*, *nurse*, *rhodopleura* and *lateralis;* the condition of the orbitosphenoid and premaxillae is unknown for the last three species). Such a derived anterior shift of the olfactory bulb is lacking among the other *Alestes* species and African characid genera examined. On the basis of these characters (the orbitosphenoid tube, the anterior shift of the olfactory bulb and the interdigitation of the premaxillae) it appears that the above *Alestes* species and the genera *Bryconaethiops* and *Hydrocynus* form a monophyletic subunit of the African Characidae.

Further studies are required to determine the exact distribution of the above derived osteology and neurological characters within African characids. Nonetheless, the available evidence contraindicates the inherent hypotheses of the monophyly of the genus *Alestes* and the subfamily Alestiinae as now defined. The genus *Alestes*, in its present sense, does not form a monophyletic unit in so far as the distribution of apomorphous characters indicates that some of its members are more closely related to species of the genera *Bryconaethiops* and *Hydrocynus* than to the remaining *Alestes* species. A redefinition of *Alestes* as a monophyletic unit must, however, await a detailed anatomical study of African characids and a phylogenetic analysis based on information from derived characters, both those discussed previously and others.

Roberts (1969, p. 442) divided the African Characidae into two subfamilies. These were the Hydrocyninae limited to the genus *Hydrocynus* and the Alestiinae for all other African characids. However, although the Hydrocyninae of such a classificatory scheme represents a monophyletic unit, the Alestiinae of that system is an unnatural grouping. As detailed above, the genera *Hydrocynus* and *Bryconaethiops* share a series of derived characters and form a monophyletic assemblage with some *Alestes* species. Consequently, a subdivision of African characids into two subfamilies along the lines proposed by Roberts results in some members of the subfamily Alestiinae (*Bryconaethiops* and various *Alestes* species) being more closely related to members of another subfamily (Hydrocyninae) than they are to the remaining taxa within their own subfamily. Thus the Alestiinae of Roberts must be considered a gradal non-monophyletic assemblage. Although the exact distribution of the derived characters discussed above is undetermined, the evidence is sufficient to indicate that the Hydrocyninae of Roberts (1969) should be sunk into the Alestiinae in order to resolve the present non-monophyly of the latter subfamily. The Alestiinae in this broader sense forms an evidently monophyletic assemblage within the Characoidea.

Acknowledgements

A number of individuals and institutions have been instrumental to the completion of this study.

I thank Dr Donn E. Rosen for directing my interests towards questions of characoid interrelationships. Dr P. Humphry Greenwood and Mr Gordon J. Howes contributed significantly to this study by their informative comments on characoid morphology and interrelationships, together with helpful criticisms of earlier drafts of the manuscript. Mr Howes and Mrs Margaret Clarke were most helpful in locating specimens, preparing radiographs and other assistance during this study.

The majority of the research associated with this project, together with the synthesis of the results, was undertaken in the Department of Zoology, British Museum (Natural History). Research at that institution was supported by a NATO Postdoctoral Fellowship to the author. Supplemental studies were undertaken at the American Museum of Natural History and the final draft of the paper was prepared at the Smithsonian Institution, Washington D.C. under a Smithsonian Postdoctoral Fellowship.

Drs D. F. Thys van den Audenaerde (Musee royal de l'Afrique centrale), C. L. Smith (American Museum of Natural History) and S. H. Weitzman (National Museum of Natural History) kindly lent me specimens under their care.

References

Alexander, R. McN. 1962. The structure of the Weberian apparatus in the Cyprini. *Proc. zool. Soc. Lond.* **139** : 451–473.

—— 1964*a*. The structure of the Weberian apparatus in the Siluri. *Proc. zool. Soc. Lond.* **142** : 419–440.

—— 1964*b*. The evolution of the Weberian apparatus in the Cobitidae. *Proc. zool. Soc. Lond.* **143** : 177–190.

—— 1966. Physical aspects of swimbladder function. *Biol. Rev.* **41** : 141–176.

Boulenger, G. A. 1898. Poissons nouveaux du Congo. Deuxième partie. *Annls Mus. r. Congo Belge* (*Zool.*) **1** : 22–38.

—— 1899. Poissons nouveaux du Congo. Quartième partie. *Annls Mus. r. Congo Belge* (*Zool.*) **1** : 59–96.

—— 1902. Description of a new characinid fish (*Citharidium ansorgei*, n. g. et sp.) discovered by Dr. W. J. Ansorge in Southern Nigeria. *Ann. Mag. nat. Hist.* ser. 9, **7** : 144–145.

—— 1909. *Catalogue of the fresh-water fish of Africa in the British Museum* (*Natural History*). London.

Burchard, J. E. 1968. Observations on *Phago loricatus*, an ectoparisitic fish from the Niger delta region of West Africa. *J. Zool., Lond.* **155** : 1–4.

Cuvier, G. 1817. *La règne animal*, Vol. 2: Poissons. Paris.

Daget, J. 1958. Le genre *Paradistichodus* (Poissons, Characiformes). *Bull. Inst. fr. Afr. Noire* **20** : 1360–1378.

—— 1959. Note sur les *Distichodus* (Poissons, Charciformes) de l'Ouest africain. *Bull. Inst. fr. Afr. Noire* **21** : 1275–1303.

—— 1960. Le genre *Xenocharax* (Poissons,Characiformes). *Revue Zool. Bot. Afr.* **61** : 35–48.

—— 1961. Note sur les *Nannocharax* (Poissons, Characiformes) de l'Ouest africain. *Bull. Inst. fr. Afr. Noire* **23** : 165–181.

—— 1962*a*. Le genre *Citharidium* (Poissons, Characiformes). *Bull. Inst. fr. Afr. Noire* **24** : 505–522.

—— 1962*b*. Le genre *Citharinus* (Poissons, Characiformes). *Revue Zool. Bot. Afr.* **66** , 81–106.

—— 1965. Le genre *Nannaethiops* et *Neolebias* (Poissons, Characiformes). *Revue Zool. Bot. Afr.* **72** : 1–24.

—— 1967. Le genre *Ichthyborus* (Poissons, Characiformes). *Cah. Off. Rech. Sci. Tech. Outre-mer*, sér. Hydrobiol. **1** : 139–154.

—— 1968. Le genre *Hemistichodus* (Poissons, Characiformes). *Cah. Off. Rech. Sci. Tech. Outre-mer*, sér. Hydrobiol. **2** : 11–20.

David, L. & Poll, M. 1937. Contribution à la faune ichthyologique du Congo Belge. *Annls Mus. r. Congo Belge* (*Zool.*) **3** : 189–294.

Eastman, C. R. 1917. Dentition of *Hydrocyon* and its supposed fossil allies. *Bull. Am. Mus. nat. Hist.* **37** : 757–760.

Eigenmann, C. H. 1909. The freshwater fishes of Patagonia, and an examination of the Archiplata–Archhelenis theory. *Rep. Princeton Univ. Exped. Patagonia* **3** (Zool.) : 225–372.

Giltay, L. 1929. Un characide nouveaux de Congo Belge (*Belonophago hutsebouti*, n. g., n. sp.) de la sous-famille des Ichthyborinae. *Revue Zool. Bot. Afr.* **18** : 271–276.

Gosse, J. P. 1956. Dispositions spéciales de l'appareil branchial des *Tilapia* et *Citharinus*. *Annls Soc. r. zool. Belge* **86** : 305–308.

—— 1963. Le milieu aquatique et l'écologie des poissons dans la région de Yangambi. *Annls Mus. r. Afr. cent.* (*Zool.*) **116** : 115–271.

Gregory, W. K. 1933. Fish skulls; a study of the evolution of natural mechanisms. *Trans. Am. phil. Soc.* (N.S.) **23** : 76–481.

—— **& Conrad, G. M.** 1936. The structure and development of the complex symphysial hinge-joint in the mandible of *Hydrocyon lineatus* Bleeker, a characin fish. *Proc. zool. Soc. Lond.* 975–984.

—— —— 1938. The phylogeny of the characin fishes. *Zoologica* **23** : 319–360.

Greenwood, P. H., Rosen, D. E., Weitzman, S. H. & Myers, G. S. 1966. Phyletic studies of teleostean fishes with a provisional classification of living forms. *Bull. Am. Mus. nat. Hist.* **131** : 339–455.

Günther, A. 1864. *Catalogue of the fishes in the British Museum.* Vol. 5. London.

—— 1865. Description of a new characinoid genus of fish from West Africa. *Ann. Mag. nat. Hist.* ser. 3, **15** : 209–210.

—— 1867. New fishes from the Gabon and Gold coast. *Ann. Mag. nat. Hist.* ser. 3, **20** : 110–117.

—— 1871. Report of several collections of fishes recently obtained for the British Museum. *Proc. zool. Soc. Lond.* 652–667.

Hennig, W. 1966. *Phylogenetic systematics.* Urbana.

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

Lek, S. & Lek, S. 1978. Régime alimentaire d'*Ichthyborus besse besse* (Joannis, 1835) (Pisces, Citharinidae) du bassin du lac Tchad. *Cybium.* sér. 3, **3** : 59–75.

Matthes, H. 1961. Feeding habits of some central African freshwater fishes. *Nature*, Lond. **192** : 78–80.

—— 1964. Les poissons du lac Tumba et de la région d'Ikela. *Annls Mus. r. Afr. cent.* (*Zool.*) **126** : 1–204.

Monod, T. 1950. Notes d'ichthyologie ouest-africaine. *Bull. Inst. fr. Afr. Noire* **12** : 1–71.

Müller, J. & Troschel, F. H. 1845. *Horae Ichthyologicae*. Berlin.

Nelson, E. M. 1949. The swimbladder and Weberian apparatus of *Rhaphiodon vulpinis* Agassiz, with notes on some additional morphological features. *J. Morph.* **84** : 395–523.

Nelson, G. J. 1967. Epibranchial organs in lower teleostean fishes. *J. Zool., Lond.* **153** : 71–89.

—— 1973*a*. The higher-level phylogeny of vertebrates. *Syst. Zool.* **22** : 87–91.

—— 1973*b*. Negative gains and positive losses; a reply to J. G. Lundberg. *Syst. Zool.* **22** : 330.

—— 1973*c*. Relationships of clupeiomorphs, with remarks on the structure of the lower jaw in fishes. *Zool. J. Linn. Soc.* **53** (Suppl. 1) : 333–349.

Nichols, J. T. & Griscom, L. 1917. Freshwater fishes of the Congo basin obtained by the American Museum Congo expedition 1909–1915. *Bull. Am. Mus. nat. Hist.* **37** : 653–756.

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

—— 1977. Cartilage bones, dermal bones and membrane bones, or exoskeleton versus endoskeleton. *Linn. Soc. Sympos. Ser.* **4** : 71–121.

Pellegrin, J. 1900. Poissons nouveaux ou rares du Congo française. *Bull. Mus. natn. Hist. nat. Paris* **6** : 177–182, 348–354.

—— 1904. Characinides nouveaux de la Casamance. *Bull. Mus. natn. Hist. nat.* Paris **10** : 218–221.

—— 1922. Poissons de l'Oubanghi-Chari recueillis par M. Baudon. Description d'un genre, de cinq espèces, et d'un variété. *Bull. Soc. zool. Fr.* **47** : 64–76.

Poll, M. 1957. Les genre des poissons d'eau douce de l'Afrique. *Annls Mus. r. Congo Belge.* (*Zool.*) **54** : 1–191.

—— 1967. Contribution à la faune ichthyologique de l'Angola. *Publ. cult. Co. Diam. Angola* **75** : 1–381.

—— 1973. Nombre et distribution géographique des poissons d'eau douce africains. *Bull. Mus. natn. Hist. nat.* Paris **150** : 113–138.

—— **& Gosse, J. P.** 1963. Revision des genre *Nannaethiops* Günther 1871 et *Neolebias* Steindachner 1844 et descriptions de trois espèces nouvelles (Pisces, Citharinidae). *Annls Mus. r. Afr. cent.* (*Zool.*) **116** : 1–36.

—— **& Lambert, J.** 1964*a*. *Congocharax gossei* sp. n. du Gabon (Ogooué) (Pisces, Citharinidae). *Revue Zool. Bot. Afr.* **70** : 336–340.

—— —— 1964*b*. Au sujet de *Barbus miolepis* Blgr. et des espèces voisines au synonymes (Pisces, Cyprinidae). *Revue Zool. Bot. afr.* **70** : 405–411.

Regan, C. T. 1911. The classification of the teleostean fishes of the order Ostariophysii. 1. Cyprinoidea. *Ann. Mag. nat. Hist.* ser. 8, **8** : 13–32.

Roberts, T. R. 1966. Description and osteology of *Lepidarchus adonis*, a remarkable new characoid fish from West Africa. *Stanford ichthyol. Bull.* **8** : 209–227.

—— 1967*a*. Tooth function and replacement in characoid fishes. *Stanford ichthyol. Bull.* **8** : 231–247.

—— 1967*b*. *Virilia*, a new genus of sexually dimorphic characoid fishes from west Africa, with remarks on characoids having an incomplete lateral line. *Stanford ichthyol. Bull.* **8** : 251–259.

—— 1969. Osteology and relationships of the Prochilodontidae, a South American family of characoid fishes. *Bull. Mus. comp. Zool. Harv.* **145** : 213–235.

—— 1974. Osteology and classification of the Neotropical characoid fishes of the families Hemiodontidae (including Anodontinae) and Parodontinae. *Bull. Mus. comp. Zool. Harv.* **145** : 213–235.

Rosen, D. E. 1973. Interrelationships of higher euteleostean fishes. *Zool. J. Linn. Soc.* **53** (Suppl. 1) : 397–513.

—— **& Greenwood, P. H.** 1970. Origin of the Weberian apparatus and the relationships of the ostariophysan and gonorhynchiform fishes. *Am. Mus. Novit.* 2428. 25 pp.

Starks, E. C. 1926. Bones of the ethmoid region of the fish skull. *Stanford. Univ. Publ. Biol. Sci.* **4** : 137–338.

Steindachner, F. 1894. Die Fische Liberia's. *Notes Leyden Mus.* **16** : 1–94.

Vari, R. P. 1977. Notes on the characoid subfamily Iguanodectinae, with a description of a new species. *Am. Mus. Novit.* 2612. 6 pp.

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

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

Manuscript submitted for publication 20 July 1978

530